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FISHERY ECOSYSTEM PLAN OF THE SOUTH ATLANTIC REGION
VOLUME II: SOUTH ATLANTIC HABITATS AND SPECIES

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ABBREVIATIONS AND ACRONYMS

ABC	Allowable Biological Catch
ALS	Accumulative Landings System
ACCSP	Atlantic Coastal Cooperative Statistics Program
B	A measure of fish biomass either in weight or other appropriate unit
BMSY	The biomass of fish expected to exist under equilibrium conditions when fishing at FMSY
BOY	The biomass of fish expected to exist under equilibrium conditions when fishing at FOY
BCURR	The current biomass of fish
C	Catch expressed as average landings over some appropriate period
DSEIS	Draft Supplemental Environmental Impact Statement
EFH	Essential Fish Habitat
EFH-HAPC	Essential Fish Habitat - Habitat Area of Particular Concern
EIS	Environmental Impact Statement
ESA	Endangered Species Act of 1973
F	A measure of the instantaneous rate of fishing mortality
FCURR	The current instantaneous rate of fishing mortality
FMSY	The rate of fishing mortality expected to achieve MSY under equilibrium conditions and a corresponding biomass of BMSY
FOY	The rate of fishing mortality expected to achieve OY under equilibrium conditions and a corresponding biomass of BOY
FEIS	Final Environmental Impact Statement
FMU	Fishery Management Unit
MARMAP	Marine Resources Monitoring Assessment and Prediction Program
MFMT	Maximum Fishing Mortality Threshold
MMPA	Marine Mammal Protection Act of 1972
MRFSS	Marine Recreation Fisheries Statistics Survey
MSFCMA	Magnuson-Stevens Fishery Conservation and Management Act
MSST	Minimum Stock Size Threshold
MSY	Maximum Sustainable Yield
NEPA	National Environmental Policy Act of 1969
OY	Optimum Yield
RIR	Regulatory Impact Review
SEDAR	Southeast Data, Assessment and Review
SFA	Sustainable Fisheries Act
SIA	Social Impact Assessment
SPR	Spawning Potential Ratio
SSR	Spawning (biomass) per Recruit
TMIN	The length of time in which a stock could be rebuilt in the absence of fishing mortality on that stock
TAC	Total Allowable Catch

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Description and Distribution

Freshwater ecosystems are increasingly recognized as vitally linked to the ecological function and health of estuarine and marine ecosystems, essential fish habitats, and food webs supporting valuable fisheries. While freshwater environments account for less than 2.5 percent of the earth's total volume of water they are indispensable to the health, function, and fishery production of the world's marine ecosystems (Rosenberg et al. 2000, World Commission on Dams 2000). In simple terms, freshwater systems including wetlands and deepwater habitats form a vital boundary between land and the sea. Inland watersheds and their freshwater systems are vitally linked with estuarine and marine waters through an inter-connected web of ecological functions and processes (Lambou and Hearn 1983, Odum et al. 1983).

The South Atlantic Shelf Ecosystem is contiguous with ten large Piedmont river basins (those with watershed boundaries extending from the ocean through the Coastal Plain to the Piedmont physiographic province), and many smaller coastal rivers, bays, and sounds located wholly within the Coastal Plain. The major Piedmont river basins are associated with some of the most productive estuarine and coastal marine systems of the continental shelf including the Albemarle-Pamlico Sound (fed by the Roanoke, Chowan, Pamlico, and Neuse River basins), the Cape Fear estuary (fed by the Cape Fear Basin), the Bulls Bay-Santee Delta-Winyah Bay estuarine system (fed by the Yadkin-Pee Dee, Waccamaw, and Santee Basin), the Savannah estuary, the Altamaha, and the St. Johns – St. Mary's Basin and estuarine system. The influences of these large river basins and their substantial freshwater inflows extend well beyond their estuarine deltas, many kilometers onto the nearshore continental shelf during seasonal high flow periods. The watersheds described contain a broad diversity of freshwater wetland and deepwater habitat classifications.

Freshwater ecosystems of the South Atlantic watersheds above the normal limits of saline waters may be conceptualized into two major categories: deepwater habitats and wetlands. In each category are many sub-classifications depending upon presence and characteristics of vegetation, substrate composition, and water flow or tidal characteristics (Cowardin et al. 1979). Major freshwater systems include riverine flowing water and lacustrine deepwater habitats, tidal and non-tidal palustrine emergent marsh, extensive tidal and non-tidal forested floodplain wetlands, and submersed rooted vascular aquatic bed habitats. The systems described are continuously connected and functionally inseparable from coastal estuarine and marine habitats for federally managed species.

A detailed discussion of freshwater wetland and deepwater habitats, their diverse flora and fauna, and ecological interactions is beyond the scope of this document. With respect to their importance to marine and estuarine fisheries, intact freshwater systems collectively provide many vital ecological functions as described previously.

Ecological Role and Function

Among the more important functions and processes are continuous export of habitat-building substrates including clay, gravel and sand from inland areas; export of essential mineral nutrients, dissolved and particulate organic carbon and living biomass from watersheds to estuarine and coastal marine systems. The abundance, distribution, and movements of migratory fauna (migratory diadromous and potamodromous fishes, estuarine fishes and crustaceans) reflect significant transports of nutrients, carbon, and biomass to and from marine ecosystems and inland freshwater systems (Garman 1992, Polis et al. 1997, Gross et al. 1998).

In addition to the ecological biomass and nutrient transfers between marine and inland waters illustrated by diadromous species, seasonal freshwater inflows to estuaries and nearshore marine environments have influenced the synchrony of reproductive cycles and peak periods of growth and migration of many important fish, shellfish, and marine mammal species. Among the more well-known Atlantic coast species whose life cycles are in part dependent upon estuaries and the many inputs such as organic carbon and nutrients from inland waters are penaeid shrimp, blue crabs, oysters, menhaden, mullet, gag grouper, cobia, king and Spanish mackerel, red drum and seatrouts, bluefish, flounder, bottlenosed dolphin, and many others (Odum et al. 1983).

Riverine habitats form the flowing freshwater connection linking watersheds and their extensive wetland habitats with estuarine and marine systems. The natural flow regime is the key driving physical variable for the riverine system (Anderson et al, 2006). The timing, duration, and frequency of naturally occurring river flows are critical for maintenance and survival of plant and animal communities downstream that have evolved in synchrony for millennia. Seasonal flow pulses act as biological triggers for fish and invertebrate migration; and flood events create and maintain riverine, estuarine, and coastal marine habitats by scouring and transport of sediments. The riverine food web is based predominantly on respiration rather than primary production directly from photosynthesis occurring within the river itself. The primary production supporting riverine fauna is allocthonous, or originating elsewhere in the form of dissolved and particulate organic carbon from decaying terrestrial vegetation or adjacent palustrine wetlands. Except in very large rivers phytoplankton is absent, and the attached diatoms and filamentous algae, aquatic mosses and rooted vascular plants contribute only a small fraction of the total primary and secondary productivity supporting riverine fauna. Decaying vegetation from land is exported by surface runoff directly to flowing waters, or may be stored in palustrine wetlands before export through surface or subsurface flow. River-borne dissolved and particulate organic carbon and nutrients are exported in large quantities to estuarine and coastal marine waters, providing direct support for food webs and marsh building processes (Lambou and Hearn 1983, Russell-Hunter 1970, Turner 1977, Odum 1984.

Migratory fauna play strong roles in nutrient and biomass cycling and connectivity among marine and estuarine, riverine, palustrine, and terrestrial habitats. Diadromous fishes including American shad and river herring make long ocean migrations from the North Atlantic to ascend South Atlantic Rivers to spawn each year. Conversely, juveniles complete early development and growth in inland waters then migrate to sea in large numbers, representing a major export of biomass and nutrients to estuarine and marine food webs. Spawning and outmigration of diadromous species represent major ecological pathways for exchange of nutrients and biomass, interconnecting watersheds, estuarine, and marine ecosystems (Freeman et al. 2003). A review of historic accounts and records from the 19th century reveals that huge spawning runs (likely in the millions in each major river basin) of alosines ascended to the Piedmont to spawn in mainstem rivers and tributaries (Baird 1887, Limburg et al. 2003). Shad spawning migrations are naturally timed to coincide with periods of increased riverine zooplankton populations, which provide vital food for larval and post larval shad. Late winter and spring zooplankton populations follow the increase in allocthonous energy-rich organic detritus and dissolved complex organic carbon compounds exported from adjacent freshwater wetlands (Lambou and Hearn 1983, Crecco et al. 1981). Conversely, imports of marine derived biomass, nutrients and carbon by migratory diadromous fishes provide important trophic support for riverine and adjacent wetland and terrestrial food webs (Garman 1992). Anadromous shad and other alosines subsidize upper trophic levels in riverine, estuarine, and coastal marine waters including predatory fishes and marine mammals (Garman and Macko 1998, MacAvoy et al. 2000, Odum 1983). Nutrient and energy subsidies afforded by anadromous shad and river herring are comparable to the salmon of the Pacific Northwest, where the nutrient and energy subsidies have been well documented in recent years (Ben-David et al. 1998, and Gresh et al. 2000). Large runs of salmon have been shown to provide important inputs of marine derived prey and nutrients to coastal and inland waters. Similarly, Garman (1992) estimated that the James River, Virginia, received significant annual inputs of nutrient-rich biomass from anadromous shad and herring of approximately 155 kg/ha before blockage of spawning runs by dams in the 1870s. Although not estimated by Garman, the outmigration of juvenile alosines to estuarine and oceanic waters is likely to be at least comparable in trophic significance. Anadromous shad and herring provide important energy and biomass subsidy for higher trophic levels containing recreationally and commercially important predatory fish species in both inland and coastal marine waters. Garman and Macko (1998) reported that predatory fishes taken in tidal waters after alosine spawning runs had greater than 35% and up to 84% (MacAvoy et al. 2000) of their biomass carbon derived from marine sources, based on stable isotope analyses. The ecological contribution of anadromous alosines and the catadromous American eel to both inland and marine ecosystems and fisheries is likely to be substantial, although greatly reduced from historical levels due to documented declines in populations. Baird, in his landmark report of the Commissioner of Fish and Fisheries in 1887 hypothesized the connections among inland river basins, migratory diadromous fishes and support for commercially valuable marine fish and mammalian species populations.

Species composition and community structure

Freshwater ecosystems of the South Atlantic watersheds above the normal limits of saline waters may be conceptualized into two major categories: deepwater habitats and wetlands. In each category are many sub-classifications depending upon presence or absence of vegetation, substrate composition, and water flow or tidal characteristics.

Deepwater Habitats: The Riverine and Lacustrine Ecosystems

Freshwaters in in this category may be further subdivided into lentic, or lacustrine habitats; and lotic or flowing riverine habitats. Lacustrine habitats of South Atlantic river basins may be both natural and man-made, with man made impoundments by far the more prominent features of the landscape compared with natural lakes. The following discussion on deepwater habitats will focus primarily on the riverine environment. Riverine habitats extend from the inland limit of estuarine waters to the southern Appalachian highlands, gradually dividing into a myriad of successively smaller streams highly integrated with the terrestrial landscape, both ecologically and geologically. Coastal Plain sections are predominantly low-gradient, slower flowing meandering rivers with broad, level floodplains and many backwaters, sloughs, and oxbows. Approaching the Piedmont, the floodplain narrows as the gradient increases at the fall-line, which marks the inland limit of ocean submersion during past interglacial periods. Through the fall-line zone the stream gradient increases gradually with rapids sections containing bedrock, boulder and cobble-gravel substrates becoming more common. Piedmont sections characteristically contain reaches of rocky substrates and rapids interspersed with lower-gradient slow flowing run and pool habitat. The variety of flow and substrate characteristics in fall-line and Piedmont river sections provides habitat niches for diverse assemblages of aquatic species including invertebrates, resident and diadromous fishes.

Fall zone and Piedmont rapids sections are important spawning habitat for many migratory anadromous fish including American shad and other alosines, striped bass, shortnose and Atlantic sturgeon. Construction of dams during the past century has resulted in blockage of anadromous fish spawning migrations at or below the fall line, with consequent reductions in production capability for anadromous fish including alosine species important as prey for many federally managed estuarine and marine fish species. The trophic effects of apparent large reductions in anadromous prey species on managed fisheries during the preceding century is potentially significant, although further study is needed to establish the magnitude of those effects.

Rivers and streams (fauna)

Most diadromous fishes of interest to the SAFMC inhabit the Coastal Plain for some portion of their life cycle. Anadromous species, such as sturgeons, alosids, and striped bass, historically made upstream migrations up to above the fall line to spawn (Menhinick, 1991; Jenkins and Burkhead, 1993). It is unclear as to if these species feed during their spawning migration. However, American shad (*Alosa sapidissima*) consume a variety of invertebrates during each life stage and may consume small fishes as adults. American eels prey on American shad eggs, larvae, and juveniles in freshwater, and striped bass (*Morone saxatilis*) consume juvenile American shad (ASMFC, 1999).

Striped bass feed on mobile planktonic invertebrates in the larval stage, larger invertebrates and small fishes in the juvenile stage, and on schooling clupeid fishes as adults. They serve as prey for other piscivorous fishes and non-fish predators (ASMFC, 2003). Young-of-year shortnose sturgeon (*Acipenser brevirostrum*) have been found to feed on insect larvae and amphipods, whereas a major prey item for adults is freshwater mussels (NMFS, 1998). Atlantic sturgeon (*Acipenser oxyrhynchus*) similarly feed on mussels, worms, shrimp, and small bottom-dwelling fishes (ASFMC, 1998).

The catadromous American eel (*Anguilla rostrata*) adults migrate to the ocean to spawn, but during the resident (yellow eel) stage they occupy a diversity of habitats within river systems, including headwater streams (Helfman et al., 1984). This phase of the American eel is able to reach the extreme upper portions of the river it inhabits. Eel are opportunistic feeders, feeding on phytoplankton, insects, snails, worms, crustaceans, and a multitude of fish species (ASMFC, 2000). Of all the diadromous fish species, only American eel gets significantly above the fall line.

In the upper Coastal Plain, the most common resident fishes in a Georgia river were largemouth bass (*Micropterus salmoides*), spotted sucker (*Minytrema melanops*), and bowfin (*Amia calva*), followed by chain pickerel (*Esox niger*), black crappie (*Pomoxis nigromaculatus*), spotted sunfishes (primarily *Lepomis* spp.), warmouth, yellow bullhead (*Ictalurus natalis*), American eel, lake chubsucker (*Erimyzon sucetta*), flat bullhead, channel catfish (*Ictalurus punctatus*), and madtom catfish (*Noturus* sp.) (Wharton, 1978). The most numerous resident fishes in lower Coastal Plain river in Georgia were the the silvery chub (*Hybognathus nuchalis*), shiner species (*Notropis* spp.), the channel catfish, flat bullhead (*I. platycephalus*), pirate perch (*Aphredoderus sayanus*), largemouth bass, warmouth (*Lepomis gulosus*), bluegill (*Lepomis macrochirus*), redbreast (*Lepomis auritus*), and two crappies (*Pomoxis* spp.)

Rivers and streams (flora)

The only vascular plants found in Coastal Plain rivers and streams are aquatic bed species growing along the shallow perimeter of channels near of the estuarine end of the riverine system. The tidal fresh- and freshwater aquatic bed communities are diverse, with numerous plant species that vary in dominance depending upon the influence of salinity, turbidity, and other environmental factors. The aquatic bed communities of southeastern United States blackwater streams, medium rivers, and low-salinity backbays and lagoons are described to varying degrees in Hackney et al. (1992).

In tidal freshwater, aquatic beds generally grow in a zone extending approximately from mean low water to depths of several meters depending upon water clarity (Odum et al., 1984). This zone often lies adjacent to emergent low marsh and can encompass the entire channel of small, shallow tidal fresh creeks. Studies indicated that while aquatic beds occurred from 10 to 160 cm in depth, maximum density occurred at 60 cm (Davis and Brinson, 1976; Ferguson and Wood, 1994). Most aquatic bed species establish roots in soft benthic muds, and produce herbaceous outgrowths perennially. Stand density and extent are extremely variable, and many species are subject to drastic fluctuations in their populations from year to year, or in some cases within a given season (Southwick and Pine, 1975; Bayley et al., 1978).

The presence of aquatic beds appears to diminish in southeastern rivers with distance traveled inland and upstream. They have been rarely reported in Piedmont streams (Mulholland and Lenat, 1992); are considered locally abundant in some larger blackwater streams and rivers but rare in small blackwater streams (Smock and Gilinsky, 1992); may be abundant in some medium-sized rivers (Garman and Nielson, 1992); and can be extensive in some low-salinity (the term “low-salinity as employed herein is synonomous with the term “oligohaline”) backbays and lagoons (Moore, 1992). Larger Piedmont rivers may support a greater variety of plant forms than the smaller streams because of the presence of different substrate types, greater stability of fine-grain sediments and greater light availability.

Water-weeds (*Elodea* spp.), pondweeds (*Potamogeton* spp.) and water-milfoils (*Myriophyllum* spp.) are some of the prevalent species in littoral zones of the Atlantic Coast (Odum et al., 1984 and literature therein). In Virginia, some freshwater aquatic beds are composed of various naiads (*Najas* spp.) and wild celery (*Vallisneria americana*). Macroscopic algae found growing amid these vascular plants include species of the genera *Nitella*, *Spirogyra* and *Chara*. In North Carolina, species present in the oligohaline and freshwater portions of Albemarle and Currituck Sounds were recorded by Ferguson and Wood (1994). Species present, in order of frequency of occurrence were: widgeon grass (*Ruppia maritima*), wild celery, Eurasian water-milfoil (*Myriophyllum spicatum*), bushy pondweed (*Najas quadalupensis*), sago pondweed (*Potamogeton pectinatus*) and redhead grass (*Potamogeton perfoloiatus*). The presence of these species and others was also documented by Davis and Brinson (1976) for the Pamlico River estuary. Investigations in the upper portion of the Pamlico River estuary and a tributary, Durham Creek, documented the presence of wild celery, naiad (*Najas* spp.), pondweeds, widgeon grass, and also macroalgal muskgrasses (*Chara* spp. and *Nitella* spp.). Wild celery and pond weed were the dominant species present.

Species present in Florida (St. Johns River) include water milfoil and wild celery (Garman and Nielson, 1992) and water weed (*Elodea* spp.) and *Hydrilla* (freshwater portions of Indian River Lagoon, Gilmore, 1977). Estuarine tributaries of Pamlico Sound, specifically Jacks and Jacobs Creeks of the South Creek system, were surveyed over 17 months for distribution and biomass of submerged macrophytes by Davis, Bradshaw, and Harlan (1985). The rooted macrophytes present were *Ruppia maritima* and *Zannichellia palustris*. *Ruppia* was present primarily during the warm season, while *Zannichellia* was present primarily during the cool season; both species were present in June. Davis et al. (1985) concluded that the contributions of aquatic macrophytes to community structure in these creeks should be highly variable since their biomasses are highly variable.

Freshwater Marshes

In lower regions of the Coastal Plain, there is an increasing importance of floodplain wetlands (Junk et al. 1989), including freshwater marshes, riverine swamp forest, bottomland hardwood forests, off-channel sloughs and other floodplain features. Tidal and non-tidal freshwater marshes have much greater plant diversity than that found in salt marshes occurring in the more saline portions of estuaries (Johnson et al., 1974, Odum et al. 1984). Typical communities include various species of sedges, millets, rushes, giant cane (*Arundinaria gigantea*), arrowhead (*Sagittaria* spp.), pickerelweed (*Pontederia cordata*), arrow arum (*Peltandra virginica*), and smartweed (*Polygonum* spp.)(Street et al., 2005). Marshes of the Mid-Atlantic and Georgia Bight regions can contain as many as 50 to 60 species at a single location, and are comprised of a number of co-dominant taxa (Odum 1978, Sandifer et al. 1980). Among the more conspicuous species which occur in both regions are arrow-arum, pickerelweed, wild rice (*Zizania aquatica*), and cattails (*Typha* spp.). In South Carolina and Georgia, marshes are often nearly a monospecific stand of giant cutgrass or a mixed community dominated by one or more species described in the Odum et al. (1984) description of community types listed below, plus sawgrass (*Cladium jamaicense*), alligatorweed (*Alternanthera philoxeroides*), plumegrass (*Saccharum* sp.), giant cordgrass (*Spartina cynosuroides*) or soft-stem bulrush (*Scirpus validus*).

Freshwater marshes may extend for some distance up the rivers before being replaced by cypress (*Taxodium distichum*)-gum (*Nyssa* sp.) or hardwood swamps. Shallow freshwater marshes contain a variety of species including cattails, several bulrushes (*Scirpus* spp.), smartweeds, aneilema (*Aneilema* sp.), arrowhead, arrow arum, and others. The deeper freshwater marshes are more extensive; in the mid-1970s they occupied approximately 25,000 acres along the Georgia coast. In many areas this marsh type is comprised almost exclusively of giant cutgrass (*Zizaniopsis miliacea*), with stands of sawgrass occurring intermittently. Around the deeper margins of the marsh, stands of cattail are common and wild rice occurs in sporadic stands. In the deeper creeks and potholes, submersed and floating–leaved plants are dominant (Johnson et al., 1974).

Most tidal fresh marsh flora consists of: 1) broad-leaved emergent perennial macrophytes such as spatterdock (*Nuphar luteum*), arrow-arum, pickerelweed and arrowheads; 2) herbaceous annuals such as smartweeds, tear-thumbs (*Polygonum sagittatum* and *P. arifolium*), burmarigolds (*Bidens* spp.), jewelweed (*Impatiens* sp.), giant ragweed (*Ambrosia trifida*), water-hemp (*Anaranthus cannabinus*), and water-dock (*Rumex verticillatus*); 3) annual and perennial sedges, rushes and grasses such as bulrushes (*Scirpus* spp.), spike-rushes (*Eleocharis* spp.), umbrella-sedges (*Cyperus* spp.), rice cutgrass (*Leersia oryzoides*), wild rice, and giant cutgrass; 4) grasslike plants or shrub-form herbs such as sweetflag (*Acorus calamus*), cattail, rose mallow (*Hibiscus moscheutos*) and water parsnip (*Sium suave*); and 5) a handful of hydrophytic shrubs, including button bush (*Cephalanthus occidentalis*), wax myrtle (*Myrica cerifera*), and swamp rose (*Rosa palustris*).

The nine community types of riverine and palustrine wetlands are:
1) Spatterdock Community: Spatterdock can occur in pure stands, especially in late spring, in areas of marsh adjacent to open water. These areas may be below the level of mean low water, so that the stands are submerged during high tide. They may occur on submerged point bars on the meanders of tidal creeks. Later in the growing season, some of the spatterdock may be overtopped by other species which commonly inhabit the low intertidal zone, including arrow-arum, pickerelweed and wild rice.

2) Arrow-arum/Pickerelweed Community: Arrow-arum is an extremely cosmopolitan species which grows throughout the intertidal zone of many marshes. This species forms its purest stands in the low intertidal portions of the marsh in spring or early summer (Odum et al. 1984). Pickerelweed is equally as likely to dominate or co-dominate this lower marsh zone, although its distribution is usually more clumped than arrow-arum. Both species tolerate long periods of inundation. Other species which may be associated with this community type include burmarigolds and wild rice, and less frequently, arrowhead, sweetflag and smartweeds.

3) Wild Rice Community: Wild rice is conspicuous and distributed widely throughout the Atlantic Coastal Plain. It can completely dominate a marsh, producing plants which exceed 4 m (13 ft) in height in August and September. It may not be noticeable until mid-summer when it begins to overtop the canopy of the shorter plants, which usually consist of arrow-arum, pickerelweed, spatterdock, arrowhead, smartweed and burmarigolds.

4) Cattail Community: Cattails are among the most ubiquitous of wetland plants and are principal components of many tidal freshwater marshes (Odum et al. 1984). Cattails are mostly confined to the upper intertidal zone of the marsh. They are usually found with one or more associates, including arrow-arum, rose mallow, smartweeds, jewelweed and arrowhead. They will also form dense, monospecific stands, especially in disturbed areas where they may co-occur with common reed (*Phragmites communis*).

5) Giant Cutgrass Community: Giant cutgrass, also called southern wild rice, is an aggressive perennial species confined predominantly to wetlands south of MD and VA. It dominates many of the tidal freshwater marshes, excluding other species. If it occurs in a mixed stand, other species present include sawgrass, cattails, wild rice, alligatorweed, water parsnip and arrow-arum.

6) Mixed Aquatic Community: The mixed aquatic community consists of an extremely variable association of freshwater marsh vegetation. It generally occurs in the upper intertidal zone of the marsh and is composed of a number of co-dominant species which form a mosaic over the marsh surface. Species present include arrow-arum, rose-mallow, smartweeds, water-hemp, burmarigolds, sweetflag, cattails, rice cutgrass, loosestrife (*Lythrum* spp.), arrowhead and jewelweed.

7) Big Cordgrass Community: Big cordgrass (*Spartina cynosuroides*) is often seen growing in nearly pure stands in narrow bands along tidal creeks and sloughs, or on levee portions of low-salinity marshes. Arrow-arum and pickerelweed are associated with big cordgrass in these locales, but when stands extend further up onto the marsh, this species will intermix with cattails, common reed, rice cutgrass and wild rice.

8) Bald Cypress/Black Gum (Riverine Swamp) Community: The bald cypress/black gum (*Nyssa sylvatica*) community generally is ecotonal between the marsh itself and wooded swamp or upland forest. Situated in the most landward portions of the tidal freshwater marsh at approximately the level of mean high water, this community consists of a mixture of herbs, shrubs and trees. Additional overstory species present include tupelo gum, red maple and ash, and shrubs such as wax myrtle and buttonbush. The understory may contain typical marsh plants, although they may be reduced in number and quantity due to shading by the canopy.

9) Bottomland Hardwood Community: Bottomland hardwood forests contain mostly oaks (*Quercus* sp.) [overcup (*Q. lyrata*), water (*Q. nigra*), laurel, (*Q.laurifolia*) swamp (*Q. palustris*), chestnut (*Q. prinus*)], sweet gum (*Liquidambar styraciflua*), green ash, cottonwoods (*Populus* sp.), willows (*Salix* sp.), river birch (*Betula nigra*), and occasionally pines (*Pinus* spp.) (Street et al., 2005).

Biota of freshwater marshes

In freshwater marshes, the microbenthos is primarily composed of amoebae and the slightly larger macrobenthos is composed of amphipods, oligochaete worms, freshwater snails, and insect larvae (such as midge, mosquito, and crane fly larvae). Midge larvae, for example, serve as food for fishes, frogs, and diving birds. When the pupae emerge as adults, they are additionally exploited by surface-feeding birds and fishes. Copepods and cladocerans are abundant in tidal creeks. The Asiatic clam (*Corbicula fluminea*) has spread throughout the coastal marshes of the southern states.

Fishes that use tidal freshwater marshes can be classified into four groups: freshwater, estuarine, diadromous, and estuarine-marine. The freshwater fishes are species that spawn and complete their lives within freshwater areas. The three main families of these freshwater fishes are cyprinids (minnows, shiners, carp), centrarchids (sunfishes, crappies, bass), and ictalurids (catfish). Juveniles of all of these species are most abundant in the shallows, often using submerged vegetation for protection from predatory fishes. Predatory species include the sunfishes, largemouth bass (*M. salmoides*), black crappie (*Pomoxis nigromaculatus*), gars (Lepisosteus spp.), pickerels (*Esox* spp.), and bowfin (*Amia calva*).

The estuarine fishes complete their entire life cycle in the estuary and extend their range into the freshwater marshes. Abundant estuarine fishes include the bay anchovy (*Anchoa mitchilli*), tidewater silverside (*Menidia beryllina*), and schools of killifishes (*Fundulus* sp.) that utilize the shallow marsh areas. Juvenile hogchokers (*Trinectes maculatus*) and naked gobies (*Gobiosoma bosci*) use tidal freshwater areas as nursery grounds.

The diadromous fishes include both anadromous and catadromous species. The adult life stage of the anadromous and semi-anadromous species moves through the freshwater marshes during their upstream spawning migration. The tidal freshwater areas are major nursery grounds for juveniles for many of these species, such as striped bass (*Morone saxatilis*). The young of the majority of the Atlantic Coast clupeids such as the *Alosa* spp. and *Dorosoma* spp. are found in peak abundance in tidal fresh waters, where they feed on small invertebrates and serve as important forage fish for striped bass, white perch (*Morone americana*), and catfish (*Ictalurus* sp.). Juvenile Atlantic (*Acipenser oxyrhynchus*) and shortnose sturgeon (*Acipenser brevirostrum*) may spend several years in freshwater before moving into more saline waters. Catadromous American eel (*Anguilla rostrata*) are habitat generalists that inhabit coastal freshwater areas, marsh creeks, and the marsh itself.

The estuarine-marine fishes include marine spawners having juveniles that move into the freshwater marshes. These fishes that move into the tidal freshwater marshes include menhaden (*Brevoortia tyrannus*), spot (*Leiostomus xanthurus*), croaker (*Micropogonias undulatus*), silver perch (*Bairdiella chrysoura*), spotted seatrout (*Cynoscion nebulosus*), black drum (*Pogonium cromis*), summer flounder (*Paralichthys dentatus*), snook (*Centropomus undecimalis*), and tarpon (*Megalops atlanticus*) (Mitsch and Gosselink, 1993).

Coastal freshwater marshes may support the largest and most diverse populations of birds. Wading birds such as the great blue heron (*Ardia herodias*), green heron (*Butorides striatus*), and bitterns (*Ixobrychus exilis* and *Botaurus lentiginosus*) feed on fishes and benthic invertebrates (Mitsch and Gosselink, 1993). The king rail (*Rallus elegans*) occurs in freshwater marshes, is known to nest in giant cutgrass and bulrush, and feeds on freshwater insects, fishes, crustaceans, and amphibians that are abundant in mats of alligator-weed (Johnson et al., 1974). Gulls (*Larus* spp.), terns (*Sterna* spp.), and kingfishers (*Megaceryle alcyon*) are common. Piscivorous birds of prey using freshwater marshes include eagles (*Haliaeetus leucocephalus*) and ospreys (*Pandion haliaetus*) (Mitsch and Gosselink, 1993).

The American alligator (*Alligator mississippiensis*) is known to move between freshwater and brackish marshes, but its preferred habitat is the tidal freshwater marsh (Johnson et al., 1974; Mitsch and Gosselink, 1993). Piscivorous mammals that are most closely associated with coastal freshwater marshes include muskrat (*Ondatra zibethicus*), otter (*Lutra canadensis*), mink (*Mustela vison*), raccoon (*Procyon lotor*), and marsh rice rat (*Oryzomys palustris*) (Mitsch and Gosselink, 1993).

Biota of Riverine Swamp Forests

The production of wood in deepwater swamps results in an abundance of substrate for invertebrates to colonize. High abundance and diversity of invertebrates have been found in permanently flooded swamps. These organisms are very dependent, directly or indirectly, on the abundant detritus in these systems. Such species include crayfish, clams, oligochaete worms, snails, freshwater shrimp, midges, amphipods, and various immature insects.

Fishes represent both temporary and permanent residents of riverine swamp forests in the Southeast. The sloughs and backswamps are valuable to fishes for spawning and feeding during the flooding season. When flooding ceases, the deepwater swamps often serve as a reservoir for fishes, although fluctuating water levels and sometimes low dissolved oxygen levels can be less than optimal for aquatic life. Some species, such as bowfin, gar, and certain top minnows (*Fundulus* spp. and *Gambusia affinis*) are better adapted to periodic anoxia because of their ability to utilize atmospheric oxygen. Often several species of minnows dominate the riverine swamp forests, while most larger fishes are temporary residents of these wetlands (Mitsch and Gosselink, 1993). The most characteristic fauna of this habitat are top minnows, killifishes (*Heterandria formosa*, *Lucania parva*), swamp darter (*Etheostoma fusiforme*), pirate perch (*Aphredoderus sayanus*), lake chubsucker (*Erimyzon sucetta*), yellow bullhead (*Ictalurus natalis*), flier (*Centrarchus macropterus*), warmouth (*Lepomis gulosus*), and top predators represented by bowfin and pickerels (*Esox* spp.) (Wharton et al., 1982). Estuarine-dependent species that are found on river floodplains include hickory shad (*Alosa mediocris*), blueback herring (*Alosa aestivalis*), and alewife (*Alosa psuedoharengus*) (Street et al., 2005). Yellow-crowned night heron (*Nycticorax violacea*), green heron, great blue heron, great egret (*Casmerodius albus*), and white ibis (*Eudocimus albus*) occur in this habitat (Wharton et al., 1982). These riverine swamp forests also serve as suitable habitat for the American alligator, as well as several species of snakes (*Agkistrodon piscivorus*; *Natrix* sp.) that feed primarily on frogs, small fishes, salamanders, and crayfish (Mitsch and Gosselink, 1993). Mink, raccoon, rice rat, and otter are also associated with this habitat (Wharton et al., 1982).

Biota of Bottomland Hardwood Forests

The most important local environmental condition is the hydroperiod, which determines the “moisture” or “anaerobic” gradient. This varies in time and space across the floodplain and is a determining factor in the species of vegetation that are present. Upslope from the deep swamps the soils are semipermanently inundated or saturated and support species such as black willow (*Salix nigra*), silver maple (*Acer saccharinum*), cottonwood, overcup oak, water hickory (*Carya aquatica*), green ash, red maple, and river birch. Fish use of bottomland hardwoods is restricted to periods of inundation. Other inundation fauna include oligochaetes, copepods, isopods, ostracods, nematodes, midge fly larvae, amphipods, water mites, and collembola (minute wingless arthropods). Some crayfish species use bottomland hardwoods throughout the entire year (Wharton et al., 1982).

Riverine and Freshwater Wetlands as Essential Fish Habitat

At the upstream borders of estuarine systems lies a vast network of freshwater rivers and streams that drain a mosaic landscape. Managed species spending part of their life cycle in this region include river herrings, American shad, sturgeon, striped bass, hickory shad, American eel, and Atlantic menhaden. The particular portion of their life cycle spent in freshwater areas varies by species. One species (*Atlantic menhaden*) is only a peripheral user of the lowermost freshwater areas, while the majority is anadromous species (herrings, shads, sturgeons, and striped bass) that use riverine channels and/or their wetland borders as spawning and nursery habitat. American eel is a catadromous species that spends nearly its entire adult life in either freshwater (females) or estuarine areas (males); only leaving to visit its spawning grounds in the Sargasso Sea.

Of all the species comprising the commercial harvest, anadromous species are likely the most stressed. Both river herring and sturgeon have experienced major declines in harvest and have not recovered along the Atlantic coast (ASMFC 1998; Street et al. 2005). Striped bass have also experienced a period of very low abundance followed by restoration efforts that have brought the species back to viability in the Albemarle Sound. Achieving a viable population level for river herring and sturgeon will depend on the spawning stock entering and leaving the system, as well as the conditions encountered within the system. Those conditions include variable temperature, chemical composition, and flow conditions determined by geology, elevation gradient, size and morphology of the channel formations, tidal influence, climatic patterns, land cover characteristics, and inhabiting biological communities (including fishing activities).

While some managed species rely directly upon conditions within freshwater systems, the majority of commercial species inhabit the downstream estuarine system. Therefore, the water and materials transported to estuarine systems from upstream freshwater sources is a vital component of the larger ecosystem. This is where freshwater habitat types can be distinguished based on their role in ecosystem production. There are riparian swamp forests, off-channel sloughs, marshlands, submerged aquatic beds, channels, and unvegetated stream margins. The proportion of each habitat comprising freshwater systems varies by region of the southeast. In some regions, tidal freshwater marshlands cover relatively more area than riparian swamp forests (SAFMC 1998). In these systems, there can be less woody structures for attachment by river herring eggs, but there is more primary production available for downstream consumers in the form of labile organic matter (Van Dyke 1978; Turner 1978).

The recurrent flooding in riparian swamp forests and off-channel sloughs during late winter and spring is of direct importance to river herring. The vegetation made available by rising flood waters provides an ideal attachment site for herring eggs (Wharton et al. 1982). The timing and duration of flooding are also important in the successful spawning of river herring and other anadromous species. During prolonged periods of elevated flow and floodplain inundation, the dissolved oxygen levels in backwater areas can plummet, creating a drain of hypoxic water from the swamps (Junk et al. 1989). Seasonal flooding can also contribute a great deal to production in downstream areas, in the form of dissolved and particulate organic matter (i.e. detritus). As a general rule, watersheds with greater riparian wetland coverage export more organic carbon to downstream estuaries than watersheds with less riparian wetlands (Mitsch and Gosselink 1993). Other indirect benefits of riparian wetlands to downstream fisheries were described in the ecological role and function section above.

Channels transport the majority of water in riverine systems and provide a basic corridor function for diadromous fish species. The channel also contains spawning habitat for striped bass, American shad, and sturgeon during late winter to early spring (Street et al. 2005). In freshwater systems regulated by hydropower facilities, suitable flow patterns can be disrupted. In North Carolina, the Roanoke River Water Flow Committee was established in 1988 specifically to address the issue of flows on the lower Roanoke River. As a result, operation of the dam on Roanoke River was changed to meet the flow requirements of striped bass during their spawning period from April to June (DMF striped bass FMP 2004). Other management actions demonstrating actual returns, in terms of American shad and river herring populations, have included the bypassing of major obstructions and the stocking of fry (SRAFRC 2005).

In summary, the production of diadromous fishery species from freshwater riverine systems appears closely linked to riparian wetland area, unobstructed reach of stream network, and flow regulations.

3.1.2 Submersed Rooted Vascular (aquatic bed-oligohaline, tidal fresh and freshwater)

Description and Distribution

Throughout this section, the term "aquatic bed" is used to describe areas of submersed rooted aquatic vascular vegetation which occur in oligohaline (0.5 to 5 ppt salinity), tidal fresh or freshwater portions of estuaries and their tributary rivers. This term is employed in the Cowardin et al. (1979) classification of wetland and deepwater habitats of the United States, accompanied by the modifier "rooted vascular," to define areas of such vegetation. Such aquatic beds may occur in the estuarine (for beds in oligohaline areas), riverine (tidal fresh or freshwater portions of rivers) or palustrine (oxbow lakes, backswamps) systems as defined in Cowardin et al. (1979). "Aquatic bed" is also the term employed in the land cover classification system developed for use in the national Coastal Change Analysis Program (Clamus et al. 1993) to describe such habitat.

In tidal freshwater, aquatic beds generally grow in a zone extending approximately from mean low water to depths of several meters depending upon water clarity (Odum et al., 1984). This zone often lies adjacent to emergent low marsh and can encompass the entire channel of small, shallow tidal fresh creeks. Most aquatic bed species establish roots in soft benthic muds, and produce herbaceous outgrowths perennially. Stand density and extent are extremely variable, and many species are subject to drastic fluctuations in their populations from year to year, or in some cases within a given season (Southwick and Pine, 1975; Bayley et al., 1978).

The presence of aquatic beds appears to diminish in southeastern rivers with distance traveled inland and upstream. They have been rarely reported in Piedmont streams (Mulholland and Lenat, 1992); are considered locally abundant in some larger blackwater streams and rivers but rare in small blackwater streams (Smock and Gilinsky, 1992); may be abundant in some medium-sized rivers (Garman and Nielson, 1992); and can be extensive in some low-salinity (the term "low-salinity as employed herein is synonomous with the term "oligohaline") backbays and lagoons (Moore, 1992). Macrophytes may be more abundant in larger rivers of the Piedmont, especially along river margins where sediments are more stable (J.J. Haines, personal communication as cited in Mulholland and Lenat, 1992). Larger Piedmont rivers may support a greater variety of plant forms than the smaller streams because of the presence of different substrate types, greater stability of fine-grain sediments and greater light availability.

Limited information is available on the distribution and extent of aquatic beds in Estuarine Drainage Areas (EDAs) of the South Atlantic. Much of the general distribution information in this section is derived from several of the chapters in Hackney et al. (1992), and from Odum et al. (1984). Distribution in EDAs of the South Atlantic region is discussed from the headwaters to the estuaries. Additional information is available from review of National Wetland Inventory (NWI) maps, although much of the aquatic bed habitat may have been overlooked as a consequence of the small size of individual meadows or beds, presence of tree canopy over the stream which precluded detection, or turbid waters present at the time aerial photographs were taken. On those maps which do include aquatic bed, it is mapped as one of the following: Estuarine, intertidal or subtidal aquatic bed in low-salinity backbays and lagoons; riverine, intertidal or subtidal aquatic bed in the tidal fresh portions of rivers; and lacustrine, limnetic aquatic bed in the case of Lake Mattamuskeet (Cowardin et al., 1979). The Statea of North Carolina is presently conducting aerial photography of SAV for mapping.

North Carolina

Ferguson (Ferguson and Wood 1994; and unpublished data) identified species (Table 3.1-1) and mapped the distribution and extent of aquatic beds in Currituck, Albemarle, Croatan, Roanoke and Pamlico Sounds in NC. With the exception of Currituck Sound and certain Albemarle Sound sub-estuaries, the shallow portions of the Neuse and Pamlico Rivers and Croatan and Roanoke Sounds are largely devoid of aquatic bed habitat due to physiological stress from variable salinity, chronic turbidity and highly colored water from coastal swamp drainage. Salinities greater than 5 ppt can be too high for low salinity species. Historical meadows of aquatic bed habitat in these low salinity waters are largely missing or reduced in aerial extent, based on anecdotal accounts, having been heavily impacted by development of coastal lands and eutrophication. Total acreage for the low salinity aquatic bed habitat mapped is approximately 11,000 acres, of which 55% is in Currituck Sound. Forty percent is in sub-estuaries associated with Albemarle Sound (R. Ferguson, National Ocean Service, Beaufort, NC, unpublished data).

Table 3.1-1. Low salinity tolerant and low salinity requiring plant species of North Carolina estuaries (Source: Ferguson and Wood, 1994).

Taxonomic Name	Common Name	Salinity Range ------‰-------
Rupia maritima	widgeon grass	0 - 36
Vallisneria americana	wild celery	0 - 10
Myriophyllum spicatum	eurasian water milfoil	0 -10
Najas guadalupensis	bushy pondweed	0 - 10

Potamogeton perfoliatus	redhead grass	0 - 20
Potamogeton pectinatus	sago pondweed	0 - 9
Zannichellia palustris	horned pondweed	0 - 20
Alternantheria philoxeroides	alligatorweed	0 - ?
Nuphar luteum	spatterdock	0 - ?
Ultricularia sp.	bladderwort	0 - ?

(1990) For photographs and general ecological information on theses species. Species of SRV thrive in fresh and oceanic water which has been classified according to salinity by Cowardin et al. (1979). Two species, eel grass (*Zostera marina*) and shoal grass (*Halodule wrightii*) are true seagrasses, requiring salinities >5.0 ‰ to survive. One species, widgeon grass (*Ruppia maritima*), is euryhaline. The remaining ten species are most frequent at salinities < 5.0 ‰ (ibid; Batuik et al., 1992).

South Carolina

Species of aquatic bed vegetation recorded in South Carolina blackwater streams include *Sparganium americanum*, which is tolerant of low-light conditions. It is found in fully canopied, second-order Cedar Creek in the Congaree Swamp National Monument, SC. Wild celery and pondweed (*Potamogeton epihydrus*) were common in Upper Three Runs Creek, a tributary of the Savannah River located at the Savannah River Plant site in South Carolina (Morse et al., 1980).

Georgia

Nelson and Scott (1962) reported that river weed (*Podostemum ceratophyllum*) dominated the benthic flora of a rock outcrop reach of the Middle Oconee River, GA.

Free-flowing sections of the Savannah River hosted *Potamogeton*, *Callitriche*, and *Najas*, as well as *Podostemum*. Aquatic moss, *Fontinalis*, and large growths of the macroalga, *Nitella*, have also been observed in some areas of the Savannah River.

Large beds of macrophytes often occur in the backwaters of large, uncanopied rivers such as the Ogeechee River, GA, and Chowan River, NC (Dennis, 1973; Twilley et al., 1985; Wallace and O'Hop, 1985).

Florida

Aquatic macrophytes, both aquatic beds and emergent, are abundant and diverse throughout the floodplain of the St. Johns River (Garman and Nielson 1992). Species which dominated the freshwater portions of the river included pondweeds (*Pontederia* spp.), water milfoil (*Myriophyllum*) and wild celery (*Vallisneria*) (Cox et al. 1976).

Freshwater aquatic bed also occurs in the fresh portions of the Indian River Lagoon (Gilmore 1977). Species present included water weed, hydrilla (*Hydrilla verticillata*), water hyacinth (*Eichornia crassipes*), water lettuce (*Pistia stratiotes*) or pickerel weed (*Pontederia lanceolata*).

Ecological Role and Function

Although macrophytes have rarely been reported in Piedmont stream tributaries of EDAs (Mulholland and Lenat 1992), because vascular plants usually do not occur in the shaded portions of Piedmont streams, species such as wild celery may grow in areas exposed to direct sunlight. Some researchers believe that the lack of vascular plants in Piedmont streams is the result of unstable sediments, moderate to high stream gradients, and the large variations in streamflow typical of most Piedmont streams (M.G. Kelly, personal communication as cited in Mulholland and Lenat 1992). An exception to this is the river weed (*Podostemum ceratophyllum*). This species grows attached to rock surfaces and is therefore not dependent on stable sediments. Productivity of river weed was greatest during moderate and stable streamflow, when the stream bed was completely flooded but the water velocities were not great.

In blackwater streams, light intensity is an important limiting factor to aquatic bed growth. Incident light is affected by both canopy development over small streams during the growing season, and by light attenuation in larger rivers (Smock and Gilinsky 1992). Discharge pattern is also probably important. Highly developed macrophyte beds in Upper Three Runs Creek, South Carolina, were attributed to that stream's more constant discharge versus others with more fluctuating discharges (W.R. English, personal communication as cited in Smock and Gilinsky 1992). Many aspects of the dynamics of aquatic beds in the upper Pamlico River estuary are reviewed in Davis and Brinson (1976). They and other authors (Harwood 1976; Reed 1976a,b; Zamuda 1976a,b; Vicars1976a-c) documented the density, depth and distance from shore; seasonal dynamics; growth dynamics; biomass; areal and temporal distribution; macrophyte decay dynamics; and total macrophyte production and nutrient accumulation.

Submerged aquatic beds (especially the floating-leaf variety) present during warmer months serve as nursery habitat for young diadromous fish (herring, shad, striped bass, and American eel) looking for both microinvertebrate food and refuge within the vegetation (Paller 1987; Cooper et al. 1994). Numerous studies have also documented higher abundances of macro- and microinvertebrates food sources in freshwater aquatic beds than in adjacent unvegetated areas (literature review in SAFMC 1998). The use of freshwater marshlands as nursery habitat for young diadromous fish has not been well documented. However, Yosso and Smith (1997) found that larvae and juvenile fish accounted for 79% of the total number of fish collected in a tidal freshwater marsh of Virginia. Another study found that freshwater shrimp densities were significantly higher in tidal marsh creeks with aquatic beds than creeks without aquatic beds (Rozas and Odum, 1987a), suggesting the importance of a low-tide refuge for small aquatic organisms (including young diadromous fish). Freshwater aquatic beds and marshlands thus seem very important as nursery and foraging habitat for diadromous species. The net community production in tidal freshwater marshes has been estimated to surpass that of saltmarshes (Odum 1978). The autumn dieback and decomposition of freshwater marsh plants and aquatic beds vegetation undoubtedly provides organic material for productivity in downstream estuaries of the southeast.

Species composition and community structure

The tidal fresh- and freshwater aquatic bed communities are diverse, with numerous plant species that vary in dominance depending upon the influence of salinity, turbidity and other environmental factors. It is likely that such communities occur to some extent in the tidal fresh and freshwater portions of most rivers in the South Atlantic, as far inland as the Piedmont reaches of main stem rivers and larger tributaries. The aquatic bed communities of a portion (GA, NC, SC) of the states under jurisdiction of the South Atlantic Fishery Management Council are described in Odum et al. (1984). The aquatic bed communities of southeastern United States Piedmont streams, blackwater streams, medium rivers and low-salinity backbays and lagoons are described to varying degrees in Hackney et al. (1992).

Water-weeds (*Elodea* spp.), pondweeds (*Potamogeton* spp.) and water-milfoils (*Myriophyllum* spp.) are some of the prevalent species in tidal freshwater wetlands of the Atlantic Coast (Odum et al. 1984 and literature therein).

In North Carolina, species present in the oligohaline and freshwater portions of Albemarle and Currituck Sounds were recorded by Ferguson and Wood (1994). Species present, in order of frequency of occurrence were: widgeon grass (*Ruppia maritima*), wild celery, Eurasian water-milfoil (*Myriophyllum spicatum*), bushy pondweed (*Najas quadalupensis*), sago pondweed (*Potamogeton pectinatus*) and redhead grass (*Potamogeton perfoloiatus*). The presence of these species and others was also documented by Davis and Brinson (1976) for the Pamlico River estuary. Investigations in the upper portion of the Pamlico River estuary and a tributary, Durham Creek, documented the presence of wild celery, naiad (*Najas* spp.), pondweeds (*Potamogeton foliosus* and *P. perfoliatus*), widgeon grass, and also macroalgal muskgrasses (*Chara* spp. and *Nitella* spp.). Studies indicated that while aquatic beds occurred from 10 to 160 cm in depth, maximum density occurred at 60 cm. Wild celery and pond weed were the dominant species present.

Estuarine tributaries of Pamlico Sound, specifically Jacks and Jacobs Creeks of the South Creek system, were surveyed over 17 months for distribution and biomass of submerged macrophytes by Davis et al. (1985). The rooted macrophytes present were *Ruppia maritima* and *Zannichellia palustris*. *Ruppia* was present primarily during the warm season, while *Zannichellia* was present primarily during the cool season; both species were present in June. Davis et al. (1985) concluded that the contributions of aquatic macrophytes to community structure in these creeks should be highly variable since their biomasses are highly variable.

Species present in Florida (St. Johns River) include water milfoil and wild celery (Garman and Nielson 1992), water weed (*Elodea* spp.) and *Hydrilla* (freshwater portions of Indian River Lagoon, Gilmore 1977).

Submersed Rooted Vascular as Essential Fish Habitat

The review of the literature conducted for this document suggests that relatively few studies have been performed in the South Atlantic region to specifically investigate use of this habitat by managed species or their prey (with the notable exception of the work done in the Northeast Cape Fear River, NC by Dr. Courtney Hackney and students at the University of North Carolina-Wilmington, and in estuarine tributaries of the Pamlico River by faculty and students at East Carolina University).

In other regions, such as the Chesapeake Bay and northern Gulf of Mexico, use of tidal freshwater aquatic beds by managed species and their prey is better documented. It seems likely, therefore, that tidal fresh aquatic beds serve directly as EFH in the South Atlantic region because they are used as nursery habitat. Freshwater aquatic beds also provide functions which support species and other EFH in the South Atlantic region through two primary avenues: 1) provision of functional attributes which maintain downstream EFH value in the estuarine portions of South Atlantic EDAs, such as binding substrates, facilitating sediment deposition, conducting nutrient uptake, and generating detritus in a manner similar to seagrasses; and 2) providing shelter and forage for species which serve as important prey for managed species, such as Atlantic menhaden (*Brevoortia tyrannus*), mullet (*Mugil* spp.), alosids (*Alosa* spp.), grass shrimp (*Palaemonetes* spp.) and others. Davis and Brinson (1980, 1983) reported that submerged rooted plants are often temporary features of the littoral zone, disappearing and perhaps reappearing with changing environments. They concluded that information on the seasonal and yearly variations in standing biomass of various aquatic macrophytes was needed to assess the potential contribution of these plants to ecosystem structure and function (Davis et al. 1985).

Submersed rooted vascular vegetation in tidal fresh- or freshwater portions of estuaries and their tributaries performs the same functions as those described for seagrasses (see Section 3.2.3). Specifically, aquatic bed meadows possess the same four attributes: 1) primary productivity; 2) structural complexity; 3) modification of energy regimes and sediment stabilization; and 4) nutrient cycling. Primary production forms complex, three dimensional physical structures which consist of a canopy of leaves and stems and roots and rhizomes buried in the sediments or attached to rocky substrate (in Piedmont stream tributaries). The physical structure provides substrate for attachment of macroalgae and macroinvertebrates, shelter from predators, frictional surface area for modification of water flow and current turbulence, sediment and organic matter deposition, and the physical binding of sediments. Aquatic bed organic matter, like that of seagrasses, cycles and stores nutrients, providing direct and indirect nutritional benefits to macroinvertebrate herbivores and detritivores.

Two of the potential benefits derived from aquatic beds were tested in field experiments conducted by Rozas and Odum (1988). They conducted studies to determine whether relative predation pressure is less in aquatic beds than in unvegetated areas, and whether fish food availability is greater in aquatic bed than in nearby unvegetated areas. They found that aquatic beds in tidal freshwater marsh creeks not only afford protection from predators, but also provide a rich foraging habitat. By foraging in aquatic bed habitat, fish consume larger prey and may have higher growth rates, lower mortality, and higher fecundity (Rozas and Odum 1988).

While the information on the use of aquatic beds in tidal fresh- and freshwaters appears scant, additional information should be generated in the future due to the development of new techniques (Rozas and Minello 1997). Enclosure devices, including throw traps and drop samplers, generally produce less variability in sampling and their catch efficiency does not appear to vary substantially with the type of habitat. These devices should be employed in aquatic beds to collect additional data to document the role which brackish, tidal fresh and freshwater submersed rooted macrophytes play in sustaining managed species and to clarify their EFH role.

Tidal fresh- and freshwater aquatic beds serve as an important substratum and refuge for macroinvertebrates which serve as prey for fish. In the Middle Oconee River, GA, river weed hosted *Simulium* pupae and *Calopsectra* (*Tarytarsus*) larvae (Nelson and Scott 1962). Nelson and Scott concluded that much of the river weed was not used directly as a food source by invertebrates, but entered the detrital food chain after being dislodged from rock surfaces during high flow or drying out when exposed to air during low flow. Approximately one-half of the total plant detritus on the bottom of this reach of the Middle Oconee was river weed.

The macroinvertebrates upon which some fish species feed exhibit seasonality in Piedmont streams which corresponds to the presence of species of importance to managed species. In Piedmont streams, studies of seasonal fluctuations in macroinverbebrate abundance show peaks in spring and autumn in both density (Stoneburner and Smock 1979; Reisen and Prins 1972) and taxa richness (Lenat 1988). These peaks correspond with the periods when spring-spawning alosids (shads and herrings) and their fall out-migrating juveniles are most likely present. Pre-spawning hickory shad, *Alosa mediocris*, gathering in Albemarle Sound in late winter, commonly eat fish prey, primarily of the Family Clupeidae; hickory shad migrating upstream in the Roanoke River to spawn consume fish and insects (Batsavage and Rulifson 1998). In some cases, macroinvertebrates may serve not only as a direct source, but also an indirect source of sustenance as well. In blackwater rivers which contain beds of water lily (*Nuphar luteum*), much of the production enter the food chain through grazing by water lily beetles (*Pyrrhalta nymphaea*) (Wallace and O'Hop 1985). At least one investigator believes that the annual cycle of water lily abundance in many Coastal Plain rivers may be the major factor influencing seasonal variation in macroinvertebrate abundance (D.R. Lenat, personal communication as cited in Smock and Gilinsky 1992). Since alosids, herrings in particular, spawn in such beds, spawning adults and emerging larvae may benefit from the availability of prey in the form of macroinvertebrates themselves, or in the form of zooplankton or other species which make use of the detritus produced by invertebrate grazing.

Macroinvertebrate abundance is higher in macrophyte beds and on their fronds or leaves than in sandy substrates (Smock et al., 1985; W.R. English, personal communication as cited in Smock and Gilinsky, 1992). This abundance is attributed to the fact that aquatic beds stabilize sediment and are an important substrate, and upon their death, become food for invertebrates, a role similar to that played by seagrasses (see Section 3.2.3). Thorp et al. (1997) determined that macroinvertebrate density in Potomac River aquatic beds was two orders of magnitude higher and substantially more diverse than at open water sites. They interpreted their results to support the hypothesis that water-column macroinvertebrates are greatly enhanced in the presence of aquatic bed habitat. Rozas and Reed (1994) found that nekton habitat segregation with depth was largely influenced by submersed aquatic vegetation and salinity as well as water depth. Paller (1987) determined that larval fish assemblages in macrophyte beds were 160 times higher in standing stock than those in adjacent open channels, and that larvae concentrated in the interior of aquatic beds rather than at the ecotone between the aquatic beds and open channels.

Macrophyte beds can also be a source of increased zooplankton prey. Cooper et al. (1994) documented the extent of water lily (*Nuphar lutea*) beds in the lower Roanoke River and their use by larval fishes. They found that the formation of water lily beds is dependent upon water temperature and level of the river but generally begins in early April, with die-back at the end of August or early September. Coverage in the estuary can be substantial; the Roanoke River delta contained about 314,000 m^2 of surface area, representing anywhere from 3% to 40% of river surface area. Cooper et al. (1994) determined that these beds offered important refuge for young fish while allowing them to have access to adjacent open-water zooplankton. *Daphnia*, *Bosmina*, and copepods were found more frequently in adjacent open-water samples, while other cladocerans were more common in water lily beds. Cladocerans and rotifers were the primary prey taxa of larval fishes in water lily beds and cladocera and copepods were the primary taxa in open water. Fish taxa utilizing this habitat included, in order of abundance, sunfishes (centrarchids), shads and herrings (clupeids), minnows (cyprinids), white perch, darters, juvenile menhaden, carp (*Cyprinus carpio*), American eel juveniles (*Anguilla rostrata*), pirate perch (*Aphredoderus sayanus*), Atlantic needlefish (*Strongylura marinus*), brown bullhead (*Ictalurus natalis*) juveniles, striped bass (*Morone saxatilis*), suckers (*Moxostoma* spp.), inland silverside (*Menidia beryllina*), and yellow perch (*Perca flavescens*).

Overall, macroinvertebrate abundance in blackwater streams is much higher than historically believed (Smock and Gilinsky 1992). Species richness is comparable to other types of southeastern streams previously viewed as more diverse. Blackwater streams and other Coastal Plain streams and their associated aquatic beds are important spawning and nursery areas for many fish species, including anadromous species which serve as prey for at least one managed species (bluefish) and likely for others. Use of blackwater streams by anadromous species as spawning sites and as nursery areas is widespread and documented by field observations (Davis and Cheek 1966; Baker 1968; Pate 1972; Gasaway 1973; Frankensteen 1976; Smock and Gilinsky 1992). Highest numbers of fish are present generally from April through June, although fish may arrive earlier in the south and later in the north. Arrival of adults corresponds with the highest flows, thus the greatest area of inundated floodplain (see Section 3.1.1). Both anadromous and resident species move onto the floodplains to spawn, and those species which have adhesive eggs undoubtedly use aquatic bed vegetation as a substrate.

The life history aspects of anadromous alewife and blueback herring in freshwater along the Atlantic Coast was reviewed by Loesch (1987). The two species occur together (i.e., are sympatric) from New Brunswick and Nova Scotia to upper South Carolina. Alewives alone occur north of Nova Scotia and bluebacks alone south to Florida. Both species are important prey species for managed species, and both use aquatic bed habitats for spawning in different parts of the range. Where the two species occur together, alewife preferentially uses habitats likely to contain aquatic beds, while blueback use swifter main channel areas. In the South Atlantic, bluebacks use aquatic bed habitats in oxbow lakes and other backwaters. Both species travel far upstream when access permits, increasing the likelihood that they would use riverine aquatic bed habitats. Loesch (1987) does not address microhabitat requirements for spawning, and does not provide any information about whether juveniles use aquatic beds during their nursery residence in freshwaters.

Studies conducted by Rozas and Hackney (1983,1984), and Rozas and Odum (1987a, b), have documented the importance of oligohaline and freshwater creeks and associated aquatic beds as nurseries for species of significance as prey to managed species. Oligohaline wetland habitats were found to be likely of equal importance as higher salinity marshes for two important estuarine species, spot (*Leiostomus xanthurus*) and Atlantic menhaden (*Brevoortia tyrannus*). Additional species significant as prey were also dominant in oligohaline tidal creeks and associated aquatic beds, including grass shrimp (*Palaemonetes pugio*) and bay anchovy (*Anchoa mitchilli*). Recruitment of small juvenile fishes was found to correspond with the period of greatest aquatic bed areal cover. Average densities of fauna were significantly greater in aquatic beds than over nearby unvegetated creek bottoms in the fall. The aquatic beds of tidal freshwater marsh creeks were considered most important as habitat for forage fishes. In experiments where the aquatic bed vegetation was removed from tidal fresh creeks, the number of grass shrimp on adjacent marshes decreased, but the average density of fishes was not reduced. The authors concluded that the proximity of aquatic beds and the depth of adjacent creeks are the most important factors that influence the abundance of nekton on tidal freshwater marshes (Rozas and Odum 1987a).

Anadromous species are also important seasonal components of main stem rivers which originate in the mountains or Piedmont. These include rivers such as the Roanoke, Tar-Pamlico, Neuse and Cape Fear in NC; Pee Dee, Santee, and Cooper in SC; Savannah, Ogeechee and Ocmulgee in GA, and St. Johns in FL. Other rivers not included in this list primarily drain the Coastal Plain and are blackwater rivers. Since their presence seasonally overlaps with the presence of aquatic beds in these systems, it is likely that adults may use these areas for spawning and perhaps feeding. The eggs, larvae and juveniles which are present in these systems from spring through the fall are much more likely to use aquatic bed habitat for cover and foraging.

The river with the highest potential for EFH designation due to both indirect and direct use by Council-managed species may be the St. Johns in FL (Tagatz, 1967; Cox and Moody, 1981; Hocutt et al., 1986; Swift et al., 1986; Garman and Nielson, 1992). Tagatz (1967) reported 115 euryhaline species (species which tolerate a wide range of salinity), including clupeids (shads and herrings) and sciaenids (such as red drum, weakfish, spot, croaker and others). These species occurred at great distances upstream from the river mouth, presumably because of the extended tidal influence due to the St. Johns low gradient, and also to the presence of refugia in the form of salt springs which occur in the river.

Many of the macroinvertebrates which occur in the oligohaline (low salinity) portions of the backbays and lagoons of the South Atlantic region may use the aquatic beds which occur there, especially the crustaceans. These species in some cases constitute important species managed by the Council (e.g. the penaeid shrimps) or are important prey for other managed species (e.g., blue crabs which are prey for red drum, grass shrimp which are prey for many other species). Because many of the shrimps and crabs have well-developed osmoregulatory capabilities (the ability to adjust to changing salinity), the low and often variable salinities that occur in areas such as Currituck Sound, Albemarle Sound, Pamlico Sound, Core and Bogue Sounds, and SC and GA sounds and backbays, do not pose the stress which they do for other organisms (Moore, 1992). On the South Atlantic coast, the penaeid shrimp species which appears most likely to use aquatic beds in tidal fresh and freshwater areas is the white shrimp (*Litopenaeus setiferus*), although it does not apparently penetrate fresh waters as far on the South Atlantic Coast as it does in the Gulf of Mexico (Odum et al. 1984). Although brown shrimp (*Farfantepenaeus aztecus*) do occasionally occur in the fresher areas of lagoons such as Albemarle Sound (R. Eager, R.W. Laney, J.W. Kornegay and S.W. Winslow, unpublished data) they are not abundant in such areas.

Perhaps the most abundant macrocrustaceans which may use aquatic beds in tidal fresh and freshwater areas of southeastern EDAs are the grass shrimp, species of the genus *Palaemonetes*. There are four species which occur along the South Atlantic Coast: *P. paludosus*, restricted to freshwaters of rivers and which is abundant in tidal fresh areas; *P. pugio* which occurs in low-salinity areas; *P. intermedius*, also present in low-salinity areas; and *P. vulgaris*, which generally remains in areas of greater than 10 ppt salinity, but which presumably could move into areas occupied by aquatic beds during dry periods when salinities are higher and freshwater flows diminished. Williams (1984) notes that the three estuarine species all occur preferentially in beds of submersed aquatic vegetation, hence the name "grass" shrimp. Freshwater shrimp of the genus *Macrobrachium*, and freshwater crayfish (*Procambarus* spp.) also occur in tidal fresh- and freshwater portions of South Atlantic rivers (Rozas and Hackney 1984); however, their importance in the diet of Council-managed species or their prey is unknown.

Another significant crustacean which occurs in tidal fresh- and freshwater aquatic bed is the blue crab (*Callinectes sapidus*). Fully grown blue crabs, especially males, occur not uncommonly far upstream in coastal rivers and at least one large coastal lake, Lake Mattamuskeet in North Carolina (Moore 1992; Rulifson and Wall 1998). Whether the lake was historically isolated or was connected to the nearby estuary is somewhat in doubt, but it was unquestionably altered in the mid-1800s by the construction of a drainage canal dug by slaves (Lake Landing Canal), and then later in the early part of this century by additional canals which facilitated access by estuarine species (Forrest 1998). During one week (April 23 - May 2, 1997), over 1,300 blue crabs with an average carapace width of 1.5 inches migrated into the lake, documenting its value as a nursery for this species (Rulifson and Wall 1998). Juvenile blue crabs characteristically occur at the lowest salinities in estuarine ecosystems (Tagatz 1968).

Other euryhaline species which currently use Lake Mattamuskeet and its extensive aquatic bed habitats include Atlantic needlefish (*Strongylura marina*), striped mullet (*Mugil cephalus*) and tidewater silverside (*Menidia menidia*). The anadromous alewife and white perch (*Morone americana*) also use the lake for spawning (Rulifson and Wall 1998).

3.2 Estuarine/inshore systems

3.2.1 Estuarine Emergent (salt marsh and brackish marsh)

Description and Distribution

One of the dominant features of the Coastal Plain of the southeastern U.S. is its extensive saltmarshes. Saltmarshes are transitional areas between land and water, occurring along the intertidal estuarine shorelines where salinity ranges from near ocean strength to near fresh in upriver marshes.

The saltmarsh is a type of wetland. Wetlands are classified on the basis of their hydrology, vegetation and substrate. The most widely used classification system, that proposed by Cowardin et al. (1979), classifies wetlands into five ecological systems, one of which is the "Estuarine System." The Estuarine System is further divided into the "Subtidal" and "Intertidal" subsystems. "Emergent Wetland" is one of eight classes of wetlands within the Estuarine Intertidal Subsystem. Estuarine emergent wetlands are characterized by the presence of erect, rooted, herbaceous hydrophytes dominated by salt-tolerant perennial plants. In the southeastern U.S., saltmarsh cordgrass (*Spartina alterniflora*), saltmeadow cordgrass (*S. patens*), big cordgrass (*S. cynosuroides*), needlerush (*Juncus roemerianus*), and narrow-leaved cattail (*Typha angustifolia*) are major components of the estuarine emergent plant community.

In this section, the term "saltmarsh" encompasses "brackish marsh," as well. Although there is no clear distinction between the commonly used terms "saltmarsh" and "brackish marsh," the latter typically refers to estuarine emergent wetlands with salinities near the lower end of the mixohaline range, which includes oligohaline (0.5-5.0 ppt), mesohaline (5.0-18.0 ppt), and polyhaline (18.0-30.0 ppt) salinity regimes. By contrast, "saltmarshes" can also occur in salinity regimes that are fully marine or "euhaline" (30.0-40.0 ppt), as well as in hyperhaline (>40 ppt) environments. Characteristic plant species vary along a continuum from high salinity "saltmarshes," which are typically dominated by *S. alterniflora* in the southeast, to lower salinity "brackish marshes," where species such as *S. cynosuroides* and *J. romerianus* achieve greater dominance. Because tidal brackish marshes are transitional areas between saltmarshes and tidal freshwater marshes, brackish marshes include species from both habitats, and, therefore, have relatively high plant diversity.

Saltmarshes occur in each of the states in the South Atlantic Region. The total area of saltmarshes in this region is approximately 894,200 acres (Field et al. 1991). It is estimated that saltmarshes in the South Atlantic account for 21% of the nation's total salt marshes (Field et al. 1992). Unlike the Gulf Coast states, particularly Louisiana, which have lost thousands of acres of estuarine emergent marsh due to a variety of causes including erosion, saltwater intrusion, subsidence sea-level rise, sediment deprivation and physical alteration, the acreage of estuarine emergent marsh throughout the remainder of the southeastern U.S. has remained relatively stable from the mid-1970s to mid-1980s (Hefner et al. 1994).

In the southeastern U.S., South Carolina has the greatest saltmarsh acreage (365,900 acres), followed by North Carolina (212,800 acres) and Georgia (213,200 acres). Florida (east coast) has the least saltmarsh acreage (106,000 acres). The Albemarle-Pamlico Sound (NC) and the St. Andrews-Simons Sounds are the estuarine drainage areas (EDA) with the greatest marsh habitat.

Table 3.2-1 presents baseline estimates of coastal wetland acreage by estuarine drainage area in the South Atlantic region compiled through a cooperative effort of NOAA and USFWS (NOAA, 1991a). Figure 3.2-1 shows the estuarine drainage areas in the South Atlantic Region for which the estimates have been compiled.

Table 3.2-1. Coastal wetlands by estuarine drainage area in the South Atlantic (Source: NOAA 1991a).

	(Acres X 100)				
Estuarine Drainage Area[a]	Salt Marsh[b]	Fresh Marsh[b]	Forested and Scrub[b]	Tidal Flats[b]	Total[b]
1 Albemarle/Pamlico Sounds (8)	1,576 (14)	365 (3)	9,062 (80)	311 (3)	11,314
2 Bogue Sound (65)	211 (22)	11 (1)	616 (64)	118 (12)	956
3 New River (46)	41 (16)	5 (2)	203 (81)	45 (1)	252
4 Cape Fear River (13)	90 (6)	97 (6)	1,291 (86)	20(1)	1,498
5 Winyah Bay (30)	124 (2)	308 (5)	5,472 (93)	6 (0)	5,910
6 North and South Santee Rivers (88)	129 (7)	174 (9)	1,613 (84)	1 (0)	1,916
7 Charleston Harbor (10)	268 (14)	169 (9)	1,540 (78)	8 (0)	1,985
8 St. Helena Sound (100)	916 (21)	321 (7)	3,036 (71)	25 (1)	4,299
10 Savannah Sound (100)	322 (11)	141 (5)	2,428 (84)	9 (0)	2,900
11 Ossabaw Sound (82)	245 (10)	40 (2)	2,282 (89)	4 (0)	2,571
12 St. Catherine's/ Sapelo Sounds (29)	352 (40)	46 (5)	461 (53)	13 (2)	872
13 Altamaha River (35)	79 (7)	81 (7)	976 (86)	2 (0)	1,138

14 St. Andrews/ Simmons Sounds (66)	1,134 (20)	157 (3)	4,420 (77)	59 (1)	5,771
15 St. Marys R./Cumberland Sound	N/A	N/A	N/A	N/A	N/A
16 St. Johns River (96)	168 (2)	2,646 (25)	7,665 (73)	2 (0)	10,481
17 Indian River (95)	24 (2)	591 (57)	368 (36)	45 (4)	1,028
18 Biscayne Bay (79)	104 (3)	1,556 (41)	2,059 (55)	49 (1)	3,769
South Atlantic Total	6,666 (11)	6,743 (11)	44,615 (76)	747 (1)	58,770

a. Values in parentheses represent the percent of county grid sampled by NOAA. Areas with less than 100 percent coverage may not be completely mapped by the U. S. Fish and Wildlife Service.

b. Values in parentheses represent the percent of total Estuarine Drainage Area wetlands grid sampled by NOAA.

Saltmarshes occur in the intertidal zone in coastal and estuarine waters. The coastal physiography of the northern and southern part of the South Atlantic Bight (e.g. North Carolina and Florida) is dominated by shallow water lagoons behind sand coastal barrier shoreline. In the central portion (e.g. South Carolina and Georgia) there are depositional marsh-filled lagoons. In both these systems, marshes may occur in vast expanses, in narrow fringing bands, or as small "pocket marshes" interspersed among higher elevation areas. Although marshes may develop in sandy sediments, especially in high-energy areas, marsh development typically leads to sediments with fine particle-size (mud) and high organic matter content. In most physical settings, marshes can accrete sediments, and thus maintain their elevation in relation to the rising sea level that is occurring over most of the South Atlantic Coast. Salt marshes persist longest in low-energy protected areas where the rate of sediment accretion is greater than or equal to the rate of subsidence (Mitsch and Gosselink 1986).

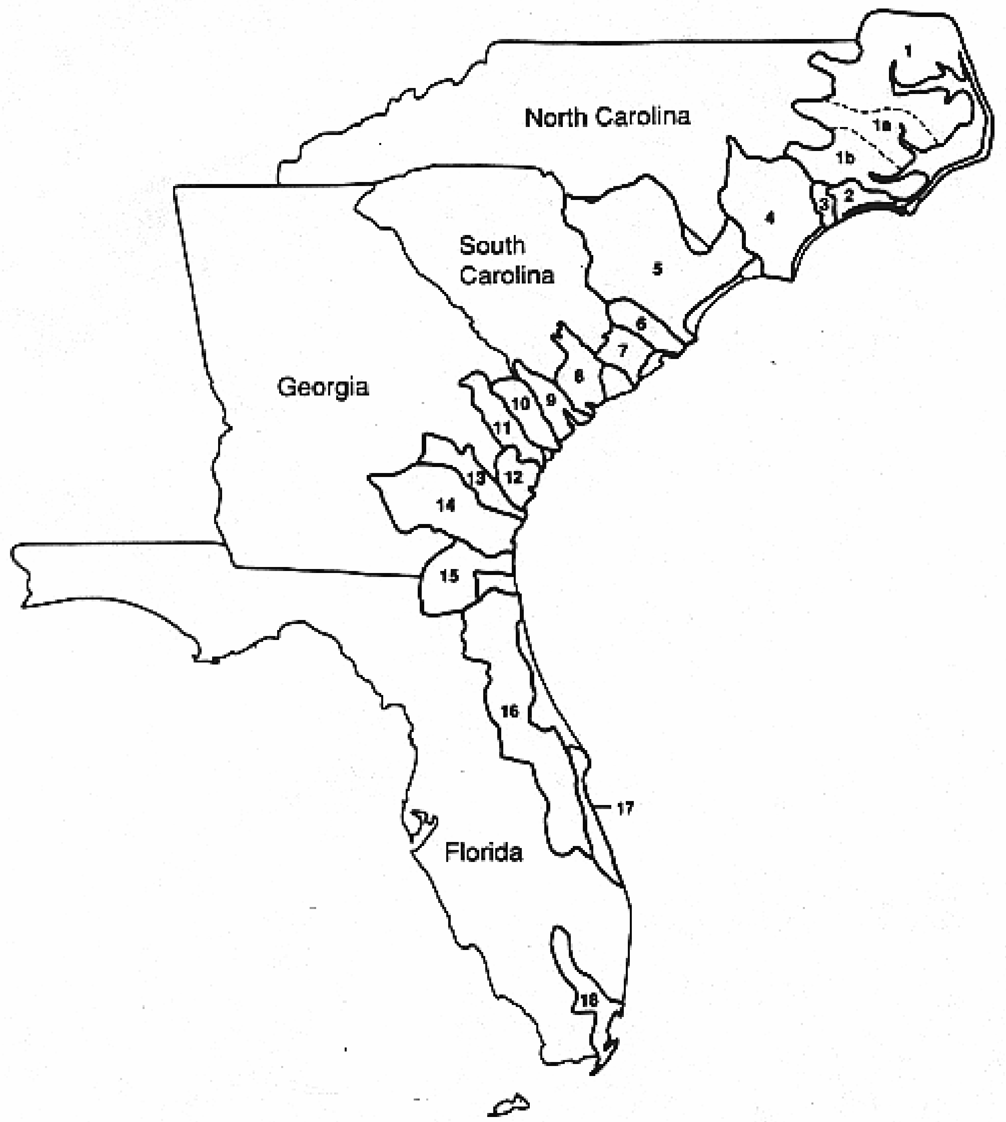


Figure 3.2-1. Estuarine drainage areas in the South Atlantic Region (Source: NOAA 1991a).

Ecological Role and Function

Structure and function of a saltmarsh are influenced by tide, salinity, nutrients and temperature. The saltmarsh can be a stressful environment to plants and animals, with rapid changes occurring in these abiotic variables (Gosselink 1980; Gosselink et al. 1974). Although species diversity may be lower than in other systems, the saltmarsh is one of the most biologically productive ecosystems in the world (Teal 1962; Teal and Teal 1969). The high primary productivity that occurs in the marsh, and the transfer of detritus throughout the estuary from the marsh, provides the base of the food chain supporting many marine organisms.

Few aquatic species feed directly on living plant tissue in salt/brackish marsh (i.e., periwinkle), and their productivity is very low compared to that of detritivores and consumers of microalgae (Wiegert and Freeman 1990; Steel 1991; SAFMC 1998a). However, biotic interactions with primary consumers can result in degradation or loss of wetlands. Recent study results from the southeastern United States suggest that blue crab predation on plant-eating snails may prevent the snail from overgrazing the marsh grass (Silliman and Bertness 2002).

Detrital and bacterial production from salt/brackish marsh exhibits some of the highest recorded values per unit area of any ecosystem in the world (Wiegert and Evans 1967). Slow-moving or sessile species residing in salt/brackish marsh and contributing to secondary production include fiddler crabs, mud snails, amphipods, oysters, clams, and ribbed mussels (Wiegert and Freeman 1990). Based on data from Georgia marshes, biomass of these resident species exceeded 15 g carbon/m2, and consisted of 80-200 fiddler crabs, 400-700 periwinkle snails or mud snails, and 7-8 mussels (Wiegert and Freeman 1990). The resident estuarine fishes (i.e., killifish, grass shrimp, sheepshead minnow) are an important link between estuarine production and transient predatory fish populations (Wiegert and Freeman 1990; Kneib 1997). Salt-brackish marsh edge also provides important feeding areas for blue crabs, red drum, flounder, seatrout and other large predators searching the edge of complex structure near deeper water, as illustrated by greater predation on grass shrimp with increasing depth in shallow-estuarine water (Clark et al. 2003).

It has been estimated that 45% of salt marsh production is exported to the estuarine system in the form of detritus, dissolved organic matter, and transient nekton (i.e., grass shrimp and killifish; Teal 1962). The biomass of secondary production going in and out with the tide (fish, shrimp) is less well known than resident species biomass (Kneib and Wagner 1994). The exported production of brown and white shrimp is probably the best known and most significant to coastal fisheries (Turner 1977; Wiegert and Freeman 1990). The estimated yield of shrimp from North Carolina was 107 lb per acre of intertidal vegetated bottom (Turner 1977), where intertidal vegetation included "salt marsh macrophytes, *Spartina* spp. [and] *Juncus* spp." However, recent research suggests that wetlands vary greatly in their role as exporters or importers of organic matter (Wiegert and Freeman 1990). This variation could be the result of variable erosion or deposition rates among seasons or wetland areas.

Primary production in salt/brackish marshes is converted into fish production through several pathways. Using sulfur, carbon, and nitrogen isotopes to trace organic matter flow in the salt marsh estuaries of Sapelo Island, Georgia, Peterson and Howarth (1987) found two major sources of organic matter used in fish production: *Spartina* (detritus) and algae. The relative importance of each source is determined by the feeding mode, size, location, and trophic position of the marsh and estuarine consumers (Peterson and Howarth 1987). For example, benthic microalgae probably support herbivorous snails, whereas detritus supports sheepshead minnows, mummichogs, and their prey. Attached algae can be found on the marsh grass itself, the intertidal mudflats, and the shallow subtidal bottom near the marsh. Pinckney and Zingmark (1993) compared production rates of benthic microalgae in various bottom types in an estuarine system (North Inlet, South Carolina). Short *Spartina* marsh accounted for the greatest amount of microalgal productivity (44.6%) in the system, followed by intertidal mudflats (22%), tall *Spartina* marsh (18%), and shallow subtidal bottom (<1 m mean low water) (13%). Sand flats accounted for only 3% of the total annual microalgal production (Pinckney and Zingmark 1993).

Many saltmarshes are drained by an intricate network of tidal creeks. These creeks and the adjacent marsh function as nursery areas for larval and juvenile finfish, crustaceans, and mollusks, and as a critical fisheries habitat to adult species. Greater than 95% of the commercial species in the United States are estuarine dependent species (Feierabend and Zelazny 1987 as cited in Mitsch and Gosselink 1993). Most of the juveniles of fishery species found in salt/brackish marsh nurseries were spawned offshore during winter. The larvae were transported through inlets and into estuarine waters where they settled in the upper (low salinity) or lowermost (high salinity) reaches of estuarine creek systems (Ross 2003). The peak of juvenile settlement generally occurs in spring through early summer, although the peak is correlated more with water temperature (Ross and Epperly 1985). Settlement in upper reaches is particularly beneficial to spot and croaker, where growth and survivorship are enhanced compared to lower reaches (Ross 2003). If movement to general regions of the estuary is largely passive (Pietrafesa et al. 1986; Pietrafesa and Janowitz 1988), the viability of spot and croaker stocks could be reduced by hydrodynamic conditions resulting in more settlement to lower regions of the estuary (Ross 2003). This settlement pattern could also occur in other estuarine-dependent species.

The marsh not only provides food, structure, and refuge from predators to fishery organisms, but also regulates the amount of freshwater, nutrient and sediment inputs into the estuary. In addition to its function as an essential fisheries habitat, the marsh plays a vital role in the health and water quality of the estuary. The position of saltmarshes along the margins of estuaries and their dense stands of persistent plants make them valuable for stabilizing the shoreline and for storing floodwaters during coastal storms.

Species composition and community structure

Flora

There are more than one hundred species of vascular flora and algae that compose the various intertidal macrophytic communities that are common to the estuaries of the South Atlantic Bight (SAB) (Beccasio et al. 1980). Most of those communities are tidally influenced marshes and, to a lesser degree, tidally influenced shrub and forest communities. South of the St. John River estuary in northern Florida the wetland communities of the lagoonal estuaries of the lower Florida peninsula gradually change from a marsh dominated landscape to a shrub community dominated by mangroves.

The macrophytes identified in this section are all influenced in their growth characteristics by salinity in the water. Salinities in south Atlantic estuaries generally range from 30.0 ppt or above (essentially sea strength) at the mouths of coastal inlets to less than 0.5 ppt at the upper reaches of the estuaries under the influence of freshwater outflow from coastal plain streams and rivers (Odum et al. 1984).

The tolerance of salinity in the water column and in the soils that serve as substrate directly influence the composition of the plant community. Salinity in combination with the periodicity of inundation due to tidal action and downstream discharge, soil chemistry, soil type, shading and erosion all result in a predictable model of the zonation of individual species and, at times, discrete plant communities.

Because salt marshes in the southeastern U.S. are influenced by the twice daily rise and fall of tides, they are subject to rapid changes in salinity, temperature and water depth. Salinity, frequency and extent of flooding of the marsh determine the types of plants and animals found there. The low marsh zone floods twice daily, while the high marsh floods only during storms and unusually high tides. One plant, smooth cordgrass (*Spartina alterniflora*), dominates the regularly flooded lowmarsh. Smooth cordgrass is the most abundant plant in southeastern marshes and is responsible for much of the marsh's productivity. *S. alterniflora* is able to tolerate salinities from sea strength to freshwater, as well as the saturated soils that are characteristic of twice-daily tidal inundation. *S. alterniflora*, a true grass, commonly occurs in vast stands growing on the fine grained soils that have been deposited in the low energy coastal lagoons and drowned river valleys behind the barrier islands that fringe the oceanic shoreline. Within the vertical zonation of the tidal amplitude *S. alterniflora* occurs from an elevation that generally equates to mean tide level up to mean high water. *S. alterniflora* exhibits three growth forms, tall, medium and short. The tall form dominates the immediate shorelines of the tidal stream banks at an elevation from mean tide level up to slightly below the mean high tide level and to a horizontal depth shoreward of about two meters. The stem height commonly attains one to one and a half meters. The medium form is found from the stream side levee horizontally into the interior of the marsh. Stem density is less dense that the tall form and stem height averages up to about one meter. The short form grows in the interior portion of the marsh where sediments are finer and less well-drained. Stem density can be higher than the medium growth form and stem height averages about 0.2 to 0.3 meters or shorter. This growth pattern is attributed to a combination of periodicity of tidal inundation, soil salinity, soil saturation, nutrient availability and other less predictable factors. The zonation and stem density, however, play a key role in the use of *Spartina* marshes by consumer organisms.

The second most common marsh plant that occurs in the region is *Juncus roemerianus*. *J. roemerianus*, like *Spartina alterniflora*, is found in all of the estuaries of the SAB. Less salt tolerant and not as well adapted to longer periods of inundation as *S. alterniflora*, *J. roemerianus* is found in the higher elevations of tidal coastal marshes. In salinity regimes higher that 15 ppt *J. roemerianus* is found in dense monospecific stands often in a zone between the *Spartina* and high ground. Stem height averages one meter but may approach two meters.

Diversity of the vascular plant community increases at higher tide elevations and at lower salinities. In the outer portions of the estuary, *Spartina patens* or saltmeadow cordgrass, occurs between mean high water and spring high water. Other plants characteristic of the high marsh are *Salicornia virginica* and *Distichlis spicata*. In more brackish portions of the estuary, *S. alterniflora* is replaced by *Spartina cynosuroides* and *Scrirpus olneyii*.
Several species of macroalgae may become abundant within salt marsh tidal creeks and on the marsh surface, particularly in early spring. These include *Ulva*, *Codium*, *Gracilaria* and *Enteromorpha*. These macroalgal communities, although ephemeral, can provide both refuge and food resources to marsh consumer organisms. Additionally, a diverse community of benthic and epiphytic microalgae inhabits the marsh surface and the stems of marsh plants. This community is composed of diatoms, cyanobacteria, and photosynthetic bacteria, and may represent a significant portion of marsh primary production. The primary production of this algal community also plays an important role in supporting fisheries production in salt marsh habitats.

Fauna

Estuarine intertidal marshes provide habitat for Council-managed species, other fish, shellfish, and invertebrates, as well as endangered and threatened species, furbearers and other mammals, waterfowl, wading birds, shorebirds and other birds, and reptiles and amphibians. Beyond the estuaries, exported marsh nutrients, detritus, and prey species contained in the food web ultimately add to the ecosystems supporting additional managed species such as coastal migratory pelagics (i.e. mackerels) and species in the snapper grouper complex.

In contrast to freshwater marshes, salt marshes have low species diversity of the higher vertebrates, but high species diversity of invertebrates. The invertebrate community in salt marshes is composed of various macrofaunal and mesofaunal species. The macrofaunal community is dominated by various species of crabs (e.g., fiddler and blue crabs), gastropod molluscs (such as *Littorina irrorata*), polychaetes and amphipods. These are the primary foragers of marsh vegetation, detritus and mesofauna. The mesofaunal community consists of protozoa, nematodes, copepods, annelids and rotifers. These organisms primarily feed on the microbial population, which chiefly consists of various species of bacteria and fungi. *Spartina alterniflora* supports a large number of epiphytic fungi, which not only contribute carbon and nutrients, but also participate in decomposition of standing biomass.

The number of macroinvertebrate species in southeastern salt marshes is limited due to the often extreme changes in salinity, temperature, drainage and exposure that can occur. Although species diversity may be limited, densities for some taxa can be quite high. Zonation affects number of species as well with numbers generally increasing from the marsh surface to the subtidal areas. Among the more conspicuous and numerous inhabitants of salt marshes are the decapod crustaceans and mollusks.

Salt marshes provide habitat for several decapod species along the southeastern coast. Rapid fluctuations in water quality variables such as salinity, temperature, and dissolved oxygen restrict the number of decapods that occur in the salt marsh. The protection afforded by marsh grass stem structure and the abundant food supply of salt marshes make them important nursery habitats for larval and juvenile stages of decapod species such as blue crab, white shrimp, and grass shrimp. Subadult stages move into intertidal marshes along the creek edge on incoming tides and penetrate the interior marshes during flood tide (Kneib and Wagner 1994). Resident species such as fiddler crabs (*Uca* spp.) burrow preferentially in sediments with intermediate densities of *Spartina* root mats (Bertness and Miller 1984). Fiddler crabs and grass shrimp are important prey of piscine, avian, and mammalian marsh inhabitants.

Table 3.2-2 reviews examples of fishes and crustaceans common to southeastern U.S. marshes. These organisms utilize the marsh structure (including the stems of emergent vascular plants, attached macroalgae, substrate materials such as shells and sediments, attached living oysters and mussels, residual tidal pools, and accumulated woody flotsam). Some feed directly on the vegetation, especially decapods and gastropods. Some species, are not found within the marsh, but derive substantial food resources from marsh plants as detritus. The protection afforded by the stem structure and intertidal water levels provides spawning habitat for some fish species, such as killifish, atherinids and gobiids, but most fishes associated with the marsh are recruited as larvae or early juveniles (Boesch and Turner 1984). Taxa spawning in or near the marsh are considered residents, but the most of the fish species (but not necessarily most of the biomass) are seasonally transient (Weinstein 1979). Transients spawn elsewhere, either upstream in freshwater (e.g., striped bass), or downstream in the coastal waters (e.g., flounders) (Schreiber and Gill 1995), and occupy the marsh habitat primarily as juveniles in the warmer months. Some of these species do not penetrate into the marsh, but are strongly linked to it in the adjacent fringing water.

Table 3.2-2. List of select macrofaunal species observed in collections from some marsh habitats located in the southeastern United States (Source: NMFS, 1998).

Species	Common Name	Resident Status	Macrophyte Genera	Fisheries Value
FISH				
Anchoa spp.	anchovy	M	Sp, Sc, Ty	P
Anguilla rostrata	American eel	M	Sp, Ju	C/P
Archosargus probatocephalus	sheepshead	M	Sp	R/C/P
Bairdiella chrysoura	silver perch	M	Sp, Sc, Ty, Ju	R/P
Brevootia tyrannus	Atlantic menhaden	M	Sp, Sc, Ty	R/C/P
Cynoscion nebulosus	spotted seatrout	M	Sp, Ju	R/C/P
Cyprinodon variegatus	sheepshead minnow	R	Sp, Ju	P
Dorosoma cepedianum	gizzard shad	F	Sc, Ty	C/P
Eucinostomus sp.	mojarra	M	Sp, Sc, Ty, Ju	P
Fundulus spp.	killifish	R	Sp, Sc, Ty, Ju	R/P
Gambusia affinus	mosquito fish	R	Sc, Ty, Ju	P
Gobiidae	gobies	R	Sp, Sc, Ty, Ju	P
Ictalurus catus	white catfish	F	Sc, Ty	R/C/P
Lagodon rhomboides	pinfish	M	Sp, Sc, Ty, Ju	R/P
Leiostomus xanthurus	spot	M	Sp, Sc, Ty, Ju	R/C/P
Lepomis gibbosus	pumpkinseed	F	Sc, Ty	R/P
Lutjanus griseus	gray snapper	M	Sp	R/C/P
Lutjanus synagris	lane snapper	M	Sp	R/C/P
Lucainia parva	rainwater killifish	R	Sp, Ju	P
Menidia spp.	silversides	R	Sp, Sc, Ty, Ju	P
Micropogonias undulatus	Atlantic croaker	M	Sc, Ty	R/C/P
Micropterus salmoides	largemouth bass	F	Sc, Ty	R/C/P
Morone saxatilis	striped bass	F	Sp, Sc,Ty	R/C/P
Mugil spp.	mullet	M	Sp, Sc, Ty, Ju	R/P
Orthopristis chrysoptera	pigfish	M	Sp	R/P
Paralichthys spp.	flounder	M	Sp, Sc, Ty, Ju	R/C/P
Pogonias cromis	black drum	M	Sp	R/C/P
Pomatomus saltatrix	bluefish	M	Sp, Sc, Ty	R/C/P
Pomoxis nigromaculatus	black crappie	F	Sc, Ty	R/C/P
Sciaenops ocellatus	red drum	M	Sp	R/C/P
Sphyraena barracuda	great barracuda	M	Sp	R/P
Symphurus plagiusa	black cheek tonguefish	M	Sp	P
Urophycis spp.	hake	M	Sp	R/C/P
DECAPODS				
Callinectes sapidus	blue crab	M	Sp, Sc, Ty, Ju	R/C/P
Menippe mercenaria	stone crab	R	Sp	R/C/P
Palaemonetes spp.	grass shrimp	R	Sp, Sc, Ty, Ju	P
Penaeus spp.	penaeid shrimp	M	Sp, Sc, Ty, Ju	R/C/P
Uca spp.	fiddler crabs	R	Sp, Ju	R/C/P

Letter codes for the Resident Status heading are R = resident, M = transient (marine spawner), F = transient (freshwater spawner); for the Macrophyte Genera heading are Sp = *Spartina* spp., Sc = *Scirpus* sp., Ty = *Typha* spp., Ju = *Juncus* spp.; and for the Fisheries Value heading are R = recreational, C = commercial, P = prey species.

Marshes as Essential Fish Habitat

It is estimated that over 95% of the finfish and shellfish species harvested commercially in the United States are wetland-dependent (Feierabend and Zelanzy 1987). Coastal wetlands are implicated when you consider the huge majority of commercial fishing occurs in estuarine and marine systems. Within the coastal wetlands category, there are a relative small number of anadromous species that are dependent on riverine forested wetlands for spawning and nursery habitat rather than estuarine marsh. But they only account for a small fraction of species in the commercial catch. The vast majority of finfish and shellfish could thus be considered dependent on estuarine wetlands.

The detritus and attached microalgae made available to secondary consumers by the presence of marsh grass forms the contribution of estuarine marsh production to commercial fisheries production. However, the environment creating individual salt marshes can differ such that more or less production is exported and available for consumption. Species associated with adjacent mud flats and channels benefit more from the presence of marsh plants as more production is exported. There are also species that use marsh grass more directly as refuge and/or foraging areas. Of all the SAFMC managed species, red drum and shrimp are considered most dependent on salt marsh habitat (SAFMC 1998).

Turner (1977) demonstrated the association between shrimp and intertidal habitat (defined as salt marsh or mangroves) at a regional scale. The study compared the commercial harvest of shrimp in various locations with areal estimates of salt/brackish marsh coverage. The results indicated a strong correlation between shrimp yield and area of estuarine vegetation, with little correlation between yield and estuarine area, average depth, and volume. The relationship between shrimp harvest (y) and area of estuarine marsh (e) was quantified in the following equation (where x is degrees latitude):

$$Y = 159e-0.070(x)$$

However, it should be noted that annual shrimp abundance is highly dependent on weather conditions, in addition to fishing mortality and habitat changes (DMF shrimp management plan – draft 2005).

The relationship between red drum production and estuarine marsh areas has not been quantified to the same level as that of shrimp. Juvenile red drum are found year-round over a wide array of salinity and habitats, although they seem to prefer sheltered, nearshore areas of coastal rivers and submerged aquatic vegetation (SAV) growing near marsh grass behind barrier islands (Ross and Stevens 1992). However, there is substantial evidence for the association of red drum with salt marsh habitat from diet studies. A summary of study results in DMF (2000) found the diet of juvenile red drum was comprised of predominantly mud crabs and fiddler crabs, the latter being closely associated with marsh habitat (Weigert and Freeman 1990).

3.2.2 Estuarine Shrub/Scrub (Mangroves)

Description and Distribution

Mangroves represent a major coastal wetland habitat in the southeastern United States, occupying in excess of 200,000 hectares along the coastlines of all Gulf coast states, Puerto Rico, and the U. S. Virgin Islands; small areas of introduced species are also present in southern California and in Hawaii. In the southeastern U.S., collectively three species comprise true "mangrove" forest: the red (*Rhizophora mangle* L), black (*Avicennia germinans* L. Stearn), and white (*Laguncularia racemosa* L. Gaertn.f.) (Figure 3.2-2); the buttonwood (*Conocarpus erectus* L.), although frequently referred to as a mangrove, does not meet the definition proposed by Tomlinson (1986). The growth of mangroves appears limited by inter-specific competition to coastal and estuarine systems and more inland areas subject to saline intrusions. The largest areas of mangrove forests are found along the coastal areas of Florida south of Latitude 28^{o} 00 N. About 90% of this is located in the four southernmost counties of the Florida peninsula: Miami-Dade, Monroe, Collier, and Lee Counties (Gilmore and Snedaker 1993; Figure 3.2-3).

The three mangrove species of the southeastern U.S. exhibit unique productivity maxima that vary with local soil salinity and flooding regimes. Consequently the composition, and even growth forms of mangrove forests are a function of the interplay between static topography and dynamic hydrology. In recognition of this interplay, several classification systems for mangrove forests have been proposed. While the first such systems were based on differences in mean water depth (Provost 1973, Tabb et al. 1974), that of Lugo and Snedaker (1974) was based on physiogamy. The classification scheme originally proposed by Lugo and Snedaker (1974) has undergone several revisions (i.e., Snedaker 1989, Gilmore and Snedaker 1993) and is the most widely cited mangrove classification system today. A brief description of these types follows.

Mangrove fringe forests occur along sheltered coastlines with exposure to open water of lagoons and bays and are almost exclusively dominated by red mangrove. The tree canopy foliage forms a vertical wall. The characteristics of this mangrove habitat type are related to the patterns of tidal inundation through which detrital materials and propagules are exported from the system during ebb tides. These fringe forests commonly have a shoreline berm or an interior wrack line (i.e., build up of detritus).

Overwash mangrove islands are ecologically similar to fringe forests because of their high frequency of tidal inundation, but here the entire area is completely covered by tidal waters on almost every tidal cycle. Because of the overwash phenomenon there is an infrequent build up of a detrital berm or development of a shoreline berm.

Riverine mangrove forests occur in riverine areas that have estuarine water exchange. This is the most productive of the forest types (Table 3.2-3). The high productivity is attributed to reduced salinity and the fact that freshwater runoff from land mixes with minerals in seawater to provide complete mineral nutrients required for growth. This high production contributes organic detrital material to the adjoining low-salinity system.

Table 3.2-3. Characteristics of mangrove forest types of southern Florida (Source: Gilmore and Snedaker, 1993).

	Mangrove Types				
Characteristics	Fringe Forest	Overwash Forest	Riverine Forest	Basin Forest	Dwarf Forest
Forest height (m)	7.65	6.37	12.64	12.14	<1.0
Mean stand diameter (cm)	8.31	11.12	19.37	10.53	1.75
Complexity Index[b]					
Trees	26.44	13.17	38.77	18.41	1.5
Saplings	1.54	2.17	22.76	4.09	--
Litter production (mg/ha/yr.)	9.00	9.00	12.98	6.61	1.86

[a] Data are averages.

[b] Complexity Index utilizes tree height, density, and number of species as independent variables and the sum of present contribution of individual species (Pool et al. 1977).

Basin mangrove forests exist in inland topographic depressions not flushed by all high tides. This habitat type may experience seasonal periods of hypersaline soil water, which can limit mangrove growth and induce mortality. Black mangroves normally dominate, but invasion by Australian pine (*Casuarina equisetifolia*) and Brazilian pepper (*Schinus terebinthifolius*) is very common.

Dwarf mangrove forests occur in areas where nutrients, freshwater inflow and tidal activity limit tree growth. Although all of the species can exist in a dwarf form, in southeast Florida large areas of the southeastern Everglades are dominated by dwarf red mangrove forest, and this area has increased in recent years (Ross et al. 2000).

Black Mangrove

White Mangrove

Red Mangrove

Figure 3.2-2. Illustrations of red mangroves, black mangroves, and white mangroves with propagules, flowers, and leaves (Source: Odum et al. 1982).

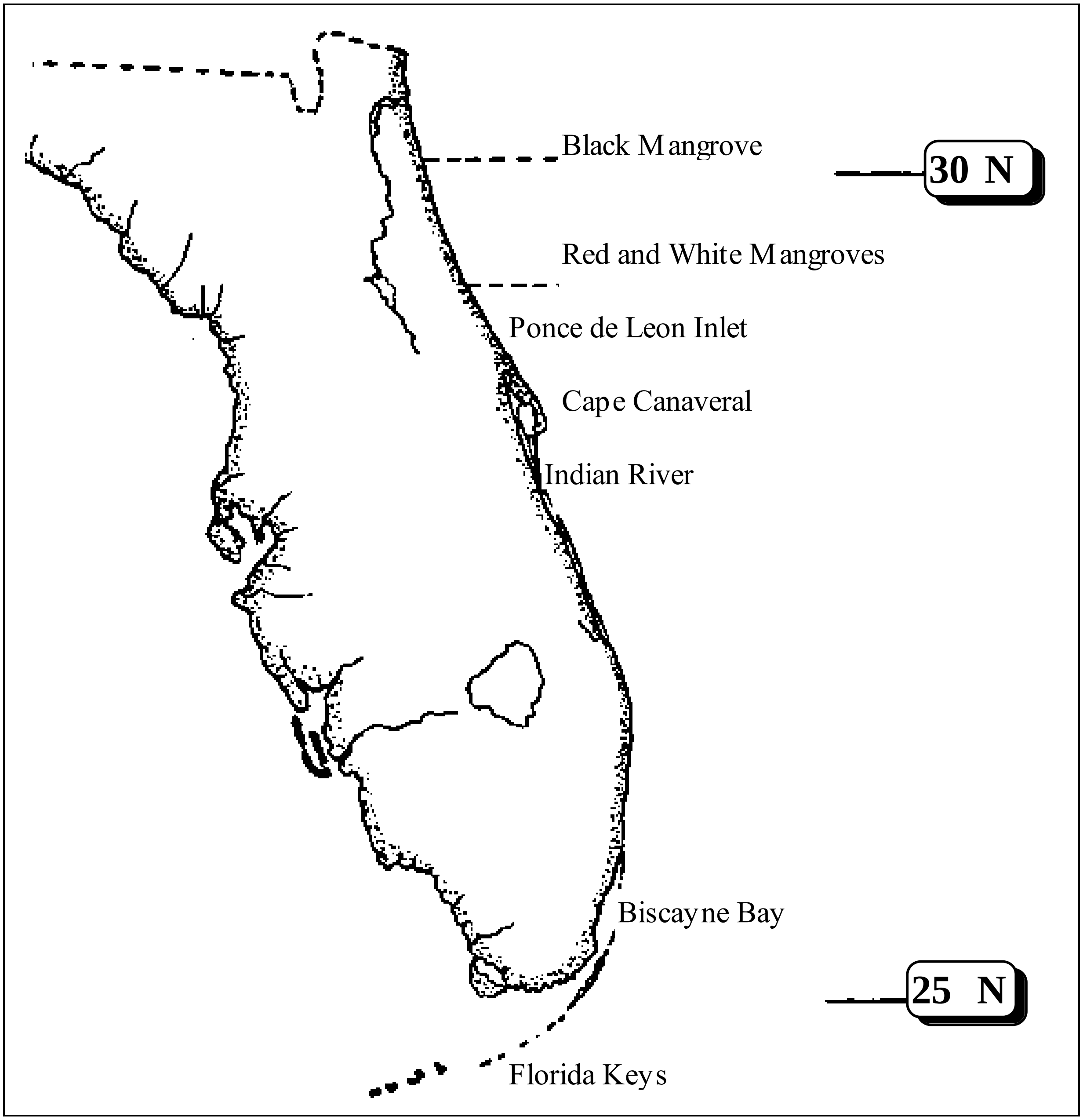


Figure 3.2-3. Approximate northern limits for the red mangrove, black mangrove, and white mangrove in Florida (in Odum et al. 1982 based on Savage 1972).

Ecological Role and Function

Odum et al. (1982) provided a detailed account of the ecology of mangroves in South Florida. More recent publications provide updated summaries of ecology, fishery value, and research information from the limited literature that exists on mangrove habitat (Baran & Hambrey 1998, Alongi 2002, Manson et al. 2005a, Manson et al. 2005b, Faunce & Serafy 2006). Cintron-Molero (1992) provided a succinct summary of the functional values of mangrove ecosystems. Mangrove ecosystems provide many goods and services beneficial to humans. In Asia and South America, mangroves have been managed for lumber, firewood and charcoal. Mangrove habitats, particularly riverine, overwash, and fringe forests, provide shelter for juvenile and adult fish and invertebrates. In addition, they contribute dissolved and particulate organic detritus to adjacent waters in support of estuarine food webs. Because they are occupied by high proportions of juveniles belonging to fishery species, and these individuals eventually leave mangroves to join the exploited adult phase inhabiting adjacent estuaries or coral reefs, mangroves possibly enhance secondary production in fishes. Mangroves also support the secondary production of birds. For example, the foraging and reproductive success of wading birds such as Roseate Spoonbills (*Ajaia ajaia*) greatly depends on the availability, quantity, and quality of mangrove forests and their associated fauna (Lorenz 2001). In addition to their direct biological value, mangroves help shape the geomorphology of the coastline, retard land loss through erosion, and contribute to the heterogeneity of landforms that provide shelter, foraging grounds and nursery areas for terrestrial organisms. The structure of the mangrove forest buffers interior coastal areas from gale winds and storm surge, protecting human settlements (UNEP 2006).

Species composition and community structure

Gilmore and Snedaker (1993) divided mangrove faunal communities into seven spatial guilds that are defined by microhabitat associations. These are dynamic groupings with species often moving from one guild to another during ontogeny or with changes in environmental conditions (Table 3.2-4). The aquatic components of the community, both fish and invertebrates, are contained in fish and invertebrate use, spatial guilds I, III, IV and V are most relevant, but Guilds II, VI and VII cannot be discounted because they contain the arboreal and terrestrial components of the community, many of which are predators or scavengers on the fish and invertebrate fauna. Various life stages of fish and invertebrates are found in mangrove habitat, with occurrence determined by accessibility and body depth relative to water depth. Fishery species, both fish and invertebrates, are primarily represented in Table 3.2-4 as transients commonly using the fringe, riverine, and overwash island mangrove forests (Guild I). Adults of the same species are, in most cases, found in adjacent seagrass meadows, in reef structures, or elsewhere offshore. In Florida, spiny lobsters (*Panulirus argus*) and pink shrimp (*Farfantepenaeus duorarum*) are the most important commercial and recreational invertebrates commonly found among the prop-roots of red mangroves. Fish species listed as mangrove transients in Table 5 that are important in Florida recreational or commercial fisheries include common snook (*Centropomus undecimalis*), sheepshead (*Archosargus probatocephalus*), black drum (*Pogonias cromis*), red drum (*Sciaenops ocellatus*), gray snapper (*Lutjanus griseus*), and dog snapper (*Lutjanus jocu*). Tarpon (*Megalops atlanticus*), also listed in Table 3.2-4, is found in mangrove creek habitat. Many small species make up the rest of the fish and invertebrate communities found in mangrove areas of the southeastern U.S. and listed in Table 3.2-4. This list also includes the goliath grouper, *Epinephelus itajara*; presently under "no-take" protected status. Other protected species found in one or more type of mangrove habitat include the West Indian manatee (*Trichechus manatus*), American crocodile (*Crocodyllus acutus*) American alligator (*Alligator mississippiensis*), juvenile bull sharks (*Carcharhinus leucas*), lemon sharks (*Negaprion brevirostris*), and Atlantic stingray (*Dasyatis sabina*).

Table 3.2-4. (inert Snedaker and Gilmore table here)

Mangroves as Essential Fish Habitat

For economically important fishery species in the U.S., flooded mangrove habitats provide feeding opportunities and increased refuge from predation relative to open habitat. A quantitative understanding of the use of mangroves by fish and invertebrates is still being developed, hampered by difficulties in quantitative sampling in mangroves, where red mangrove prop roots and black mangrove pneumatophores pose formidable obstacles to most quantitative sampling approaches (Faunce and Serafy 2006).

In a review of the pertinent literature, Faunce and Serafy (2006) found that roughly one in five purported "mangrove-fish" surveys failed to sample this habitat per se. This has undoubtedly produced unrepresentative data in specific cases and has probably led to unfounded conclusions about the nature and extent of fish utilization of mangroves in general. It may, for example, have led to inclusion of a few species on the Gilmore and Snedaker (1993) (Table 3.2-4) list that do not belong there. Despite these drawbacks, generalizations can be made regarding the importance of U.S. mangrove habitat to fisheries.

Evidence linking mangrove habitat to fisheries production mainly has been based on a simple correlative approach relating fisheries to mangroves (Manson et al. 2005, and references therein). Fishery production is appreciably higher in coastal areas off estuarine mangrove forests than off non-mangrove coasts (Marshall 1994). Similarly, greater densities of several species have been recorded adjacent to bays containing mangroves than those without them (Nagelkerken et al. 2001, Dorenbosch et al. 2004, Mumby et al. 2004). Heald and Odum (1968) may have been the first to propose the role of fringe and overwash mangrove forests as nurseries for a variety of economically valuable species in the U.S. This paradigm has been largely based on repeated observations that mangroves contain greater densities of juvenile fishes compared to adjacent habitats. However, the mangrove fringe typically occupies a smaller area than those habitats to which it is often compared (e.g. seagrass beds or mud flats), and the differences may not reflect overall abundance. Furthermore, few studies have been made comparing faunal density in mangrove habitat to that in adjacent habitat, and some of these have used different sampling methods in the two habitats, making the comparison somewhat questionable. On the other hand, the same gear may differ in efficiency when applied to different habitats, so this also is an issue.

Nurseries are habitats whose inhabitants exhibit greater growth, survival, density, and successful export to adult populations relative to surrounding habitats (Beck et al. 2001, Adams et al. 2006). By this definition, despite decades of work, there is little empirical evidence that mangroves are nursery habitats for fishery species. Manson et al. (2005) noted a deficiency in survival and growth information worldwide. Studies of growth of individual species in U.S. mangroves may be limited to the work of Robertson and Duke (1990) and Faunce (2005). A meta-analysis of comparative data on density in mangrove and alternate habitat by Sheridan and Hays (2003) suggested that faunal density was significantly higher in alternate habitats than in mangrove habitat, but survival was significantly higher in mangrove habitat. They considered these results preliminary because of the small number of data sets covered.

Food availability may be enhanced within mangrove habitat. Experimental manipulations have found that structure with attached epibionts attracted significantly more fish than bare stakes (Laegdsgaard and Johnson 2001), suggesting that structure may increase the availability of potential food items. Greater densities of a planktonic crab larvae actively selected by predatory fishes have been found in Queensland mangroves (Robertson et al. 1988). The work of Odum and Heald (1975) provided convincing evidence that nutrient export from estuarine mangroves supports a "detrital food web" that propagates to forage items for juveniles of exploited species. Species such as common snook (*Centropomus undecimalis*), goliath grouper (*Epinephelus itajara*), sheepshead (*Archosargus probatocephalus*), black drum (*Pogonias cromis*) and red drum (*Sciaenops ocellatus*) likely benefit from the presence of large expanses of mangrove forests (Lewis et al. 1985). A recent study reports that juvenile Goliath grouper prefer well-developed fringing red mangrove shorelines with high spatial complexity (Frias-Torres 2006).

The mangrove-forage association of other exploited species in South Florida is more tenuous. Species such as gray snapper (*Lutjanus griseus*), schoolmaster snapper (*L. apodus*), bluestriped grunt (*Haemulon sciurus*), and sailors choice (*H. parra*) occupy reefs as adults and also occur in those mangroves that frequently experience clear, marine waters (Ley and McIvor 2001). Stable-isotope and observational data have demonstrated that the majority of food items for these species is derived from foraging on adjacent seagrass beds at night (e.g. Rooker and Dennis 1991, Loneragan et al. 1997, de la Moriniere et al. 2003, Kieckbusch et al. 2004). Therefore, any observed growth of these species occupying mangroves during daylight hours is a result of foraging on adjacent habitats and not the mangrove habitat per se.

Assimilation of mangrove products into food webs has been shown to be minimal in a number of stable isotope studies (Sheridan and Hays 2003). For example, Fry and Smith (2002) examined stable isotopes of carbon, nitrogen, and sulfur along a salinity gradient in a riverine mangrove forest, the Shark River estuary of South Florida. Looking at mussels and barnacles, they found the strongest influence of mangrove in the food web in the middle estuary, where mixing models based on sulfur isotopes suggested that as much as 60% of filter-feeder production was mangrove-based. They concluded, however, that, overall, the food web of mangrove estuaries is based primarily on phytoplankton and benthic microalgae. In another South Florida study, Fry et al. (1999) found evidence of a mangrove diet in some pink shrimp newly recruited to the Tortugas fishing grounds; however the predominant stable isotope signature indicated a seagrass food base. While the export of dissolved and particulate materials to coastal areas may be substantial (Lee 1995), evidence of its incorporation and use in coastal waters is lacking.

The repeated observation that mangroves harbor more individuals during the day than at night is strong evidence that mangroves serve as daytime refuges from predation, and thus act as a nursery in this sense, even though some species may not feed there. It has been experimentally demonstrated that the structurally heterogeneous root habitat of mangroves reduces the effectiveness of larger-bodied predators (Primavera 1997, Laegdsgaard and Johnson 2001). Mangroves also produce shade, allowing inhabitants greater visual range than they would have in more brightly lit areas (Helfman 1981). Frias-Torres (2006) noted that shade is an important characteristic in habitat selection by goliath grouper. Because the degree of predation is dependent on light levels, the combination of root structure and inherent low light levels is an additional benefit with regard to avoiding predation (Chittaro et al. 2005).

Not all mangrove stands—even those of the same type, as defined by Gilmore and Snedaker (1993)—are the same in terms of support for fauna. Three Florida studies have compared the associated fauna of mangrove stands and found differences. In the first study, conducted in the upper reaches of northeastern Florida Bay, several distinct fish assemblages were evident within mangroves bordering basins of varying distance from freshwater and saltwater sources (Ley et al. 1999). In the second study, the fringing mangroves of the Biscayne Bay (Florida) mainland contained a significantly lower overall taxonomic richness and density of four out of five reef fishes compared to fringing forests located across the bay on the leeward side of oceanic barrier islands (Serafy et al. 2003). In the third study, density and frequency of occurrence of five reef fishes declined precipitously as a function of increasing distance from oceanic inlets, and distinct shoreline selection was exhibited (Faunce 2005). The availability of certain types of structure as microhabitat might also influence mangrove usage. For example, Frias-Torres (2006) found that juvenile goliath grouper were associated with erosional, concave shorelines of sufficient water depth (i.e., > 80 cm) containing overhangs and undercuts, as opposed to depositional shorelines without these features. Lee (2004) concluded that tidal amplitude and extent of intertidal area, rather than amount of mangrove area per se, influenced prawn catch in tropical nearshore environments across 37 countries. These results point out that the use of mangrove shorelines will be species, season, and location dependent.

Several physical features of mangroves make them especially favorable as fish habitats. Mangrove creeks and ditches, although not as well studied as fringing mangroves, are widely used by fishes. Because creek edges within fringe mangrove habitat are flooded most of the time, they provide low-water refugia during periodic dry-downs. Not surprisingly, the largest-bodied aquatic organisms, e.g., the West Indian manatee (*Trichechus manatus*), American crocodile (*Crocodyllus acutus*) American alligator (*Alligator mississippiensis*), juvenile bull sharks (*Carcharhinus leucas*), lemon sharks (*Negaprion brevirostris*), Atlantic stingray (*Dasyatis sabina*), tarpon (*Megalops atlanticus*), common snook (*Centropomus undecimalis*), and goliath grouper (*Epinephalus itajara*) have been observed within mangrove creeks and ditches (Tabb 1974, sources within Odum et al. 1982). Ley and McIvor (2001) and Faunce et al. (2004) reported a positive relationship between water depth in mangrove forests and the density of gray snapper in southeast Florida.

Mangrove creeks are important conduits between expansive coastal marshes and downstream embayments. Faunce et al. (2004) linked hydrologic regime to change in density of 12 taxonomic groups of fishes and found that the nature of the response was linked to body-size. Small bodied (< 10 cm total length) resident fishes were negatively correlated with changes in water levels within 90 days, while larger fishes, including predatory species, were positively correlated with changes over this and longer time periods (Faunce et al. 2004). The authors concluded that these results represented the concentration of small fish into the creek and their resulting exploitation by larger predators. These results highlight the importance of deepwater habitats as refugia from desiccation for forage species and as feeding areas for larger species. For prey-predator interactions to occur, both groups of fishes must have access to the same habitat.

Just as the area and depth of the creeks influence the degree to which fishes are concentrated during low water events, the flooding of basin mangrove habitats influences the amount of forage fish produced. The mangrove basin habitat (Spatial Guild V) is characterized by separation from tidal water by a berm and seasonal changes in water level and thus availability to fishery resources. The more abundant fishes found in this habitat are cyprinodontiform species such as killifish, mosquitofish, and mollies, which grow and reproduce rapidly. These "r" type species are able to quickly colonize newly flooded mangrove basin habitat during flooded periods, and their growing season is directly related to hydroperiod. In a unique long-term study, Lorenz (1999) demonstrated that basin forests that underwent longer hydroperiods possessed a greater density of demersal "prey-base" fishes than locations that experienced a shorter hydroperiod. The findings of Lorenz (1999) echoed those of similar studies conducted within the adjacent freshwater Everglades (Loftus and Eklund 1994, Trexler 2001). Because basin habitats typically cover great spatial areas, relative to other forest types, and are occupied by numerous r-type species, they have the potential to support immense biological production (biomass= area x time). The time period that adjacent basins are flooded determines the quantity of forage items that potentially can become available to higher consumers, and the rate of decline in water levels relative to the local topography (especially the slope of creek banks) enables the production to be realized by these consumers, including predatory fishes and wading birds. For this reason, both Lorenz (1999) and Faunce et al. (2004) advocated a hydroperiod of ca. 240 days followed by a dry-down of ca. 90 days.

Mangrove stands and seagrass beds and/or coral reefs may play supporting roles in providing nursery habitat for fishery species and other fish and invertebrates, and the documentation and quantification of linkages among these habitats is an emerging avenue of investigation for mangrove researchers. Approaches range from correlative analyses to elemental signatures and tagging (Gillanders et al. 2003). Skilliter et al. (2005) found that the abundance of *Penaeus plebejus* and *Metapenaeus bennettae* was significantly and consistently greater in dense seagrass proximal to mangroves than in other types of habitat. Additionally, sparse seagrass close to mangroves supported more of these species than dense seagrass farther away, indicating that the spatial arrangement of habitats was more important than structural complexity alone. Mumby et al. (2004) found that the community structure of coral reefs off Belize was influenced by the presence of mangroves in the vicinity, and the total adult biomass of several species was higher. In acknowledgement of the linkage between mangroves and adjacent habitats, research is now evolving to focus on which mangrove systems contribute most to offshore fisheries production. For example, Mumby (2006) prepared algorithms identifying the relative importance of mangrove nursery sites, the connectivity of individual reefs to mangrove nurseries, areas of nursery habitat that have unusually large importance to specific reefs, and priority sites for mangrove reforestation projects. These four algorithms should be considered for use in coastal ecosystem and fishery management and planning.

The first international symposium on mangrove habitat, organized by Joseph Serafy, NOAA, National Marine Fisheries Service, Miami, was held in Miami in spring of 2006, and peer-reviewed papers from that conference will be published within the next year, providing further information on mangroves as nurseries. The website is:
http://www.rsmas.miami.edu/conference/mangrove-fish-habitat/
A special issue of the Bulletin of Marine Science (Volume 80, Number 3, May 2007) devoted to the symposium contains keynote papers by Stephen J. M. Blaber and Ivan Nagelkerken, 19 full articles, and 4 notes. Guest editors of this special issue were Joseph E. Serafy and Rafael J. Araujo. Papers were not available for review in time for development of this mangrove section

of the FEP, therefore the volume advances the science of mangrove importance to fisheries beyond that discussed above.

3.2.3 Seagrasses

Description and Distribution

Out of the estimated 250,000 flowering plants existing on earth today, only about 50-60 species have adapted to life in the marine environment (den Hartog 1970; Hemminga and Duarte 2000; Green and Short 2003; Larkum et al. 2006). Collectively, we refer to this group of submersed aquatic vascular plants (SAV) as seagrasses. Seagrasses are clonal plants which reproduce and disperse by means of sexual and asexual reproduction. Seaweeds (macroalgae) are often mistakenly referred to as "grasses." Despite the fact that they frequently co-occur and provide similar ecological services, these two plant taxa have distinctly different growth forms and contrasting environmental requirements, the most important of which is the fact that seagrasses anchor themselves in unconsolidated sediments with an extensive root and rhizome system, thus have a very significant influence on sedimentary processes and nutrient cycling. Only one seagrass genus, *Phyllospadix*, does not require unconsolidated sediments and this species does not grow in the South Atlantic.

Taxonomically, seagrasses are divided into two families and 12 genera (den Hartog 1971; Phillips and Meinez 1988; Green and Short 2003). At least 13 species of seagrass occur in United States waters. In the south Atlantic region, with the exception of Georgia and South Carolina where highly turbid freshwater discharges, suspended sediments and large tidal amplitude combine to prevent their permanent establishment, there are 6 genera of seagrasses represented by 8 species. These species range in size from the three smallest, *Halophila decipiens* (paddle grass), *Halophila engelmannii* (star grass) and *Halophila johnsonii* (Johnson's seagrass), to the relatively larger species, *Zostera marina* (eel grass), *Ruppia maritima* (widgeon grass), *Halodule wrightii* (shoal grass), *Syringodium filiforme* (manatee grass) and *Thalassia testudinum* (turtle grass) (Figure 3.2-4).

In the South Atlantic, seagrass habitat occurs in North Carolina and Florida, with Florida having the greatest amount of seagrass habitat (Figure 3.2-5). Along the Atlantic Peninsula and South Florida regions of Florida, there are an estimated 29,769 hectares (ha) and 574,875 ha of seagrass beds, respectively (Madley et al. 2003). The South Florida total includes seagrass in Florida Bay and the continental shelf off of the Keys (Florida Straits). Seagrass estimates in the Florida Straits include areas with continuous SAV as well as areas where SAV is patchy and intermixed with hardbottom. Along the Atlantic Peninsula, seagrasses are most concentrated in the Indian River Lagoon system. This area, while only supporting approximately 3% of the total seagrass coverage along all of Florida, has the highest seagrass diversity, with all seven species present, including the federally threatened species, *Halophila johnsonii* (Johnson's seagrass) (FFWCC 2003). Over half of all seagrass habitat in Florida occurs in South Florida and Florida Bay supports the largest contiguous seagrass beds in the world. On the Atlantic side of the Florida Keys, seagrass habitat is closely associated with hardbottom, patch reefs, and mangroves (FFWCC 2003). North Carolina has the second largest seagrass distribution in the continental United States with an estimated 54,230 ha mapped (Ferguson and Wood 1994). This number includes primarily seagrasses and a small amount of visible oligohaline SAV along the western

Pamlico and Albemarle tributaries. Unlike Florida, the seagrass species growing in North Carolina, *Z. marina*, *H. wrightii* and *R. maritima*, are all found within coastal lagoons, protected inland waterways and river mouths all protected by barrier islands. A unique feature of NC seagrasses is the overlap in distribution of a temperate species (*Z. marina*) and a tropical species (*H. wrightii*). Where these species co-occur there is a bimodal seasonal abundance, which extends the total annual abundance of seagrasses for a longer period of time (Thayer et al. 1984).

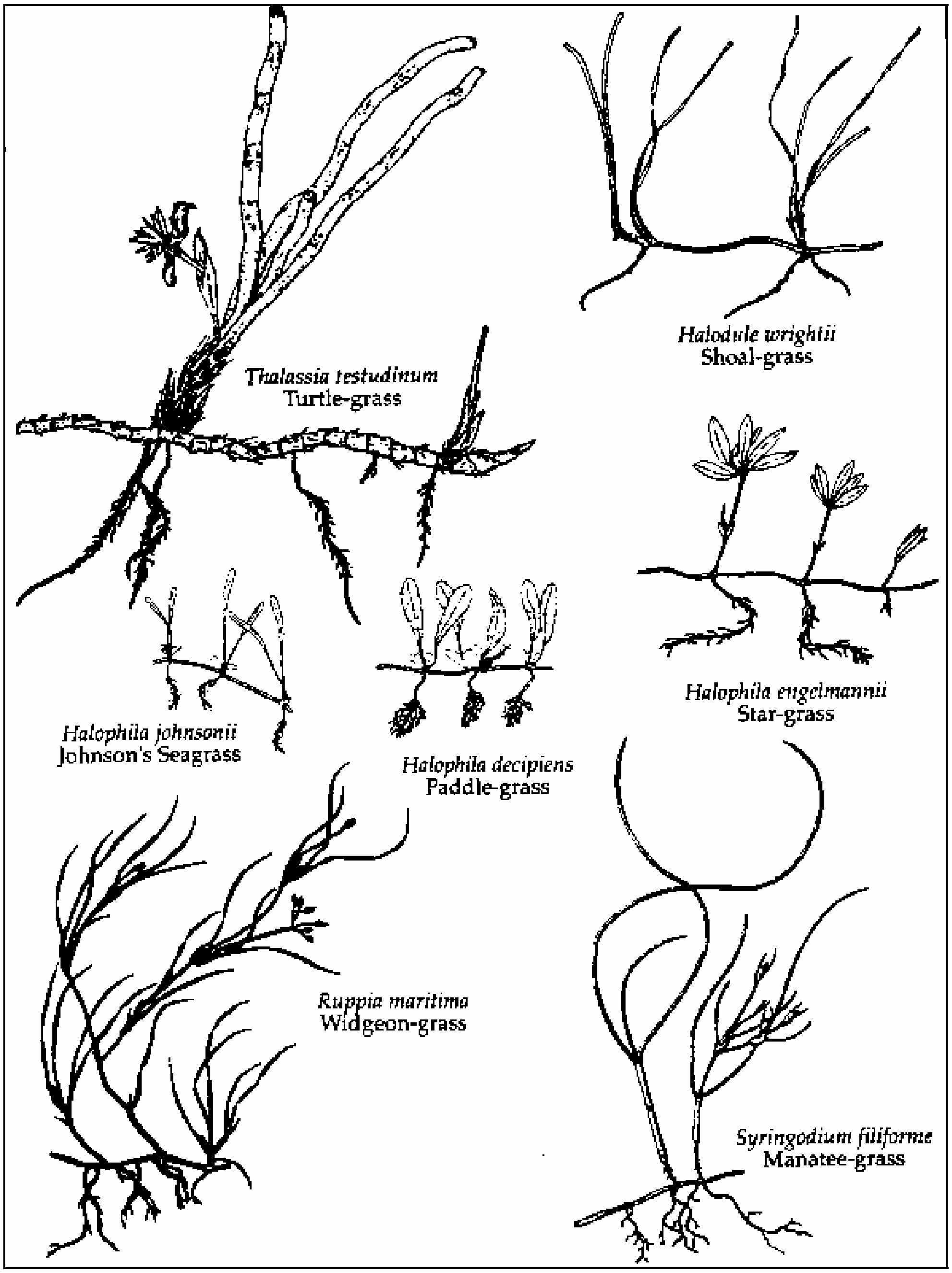
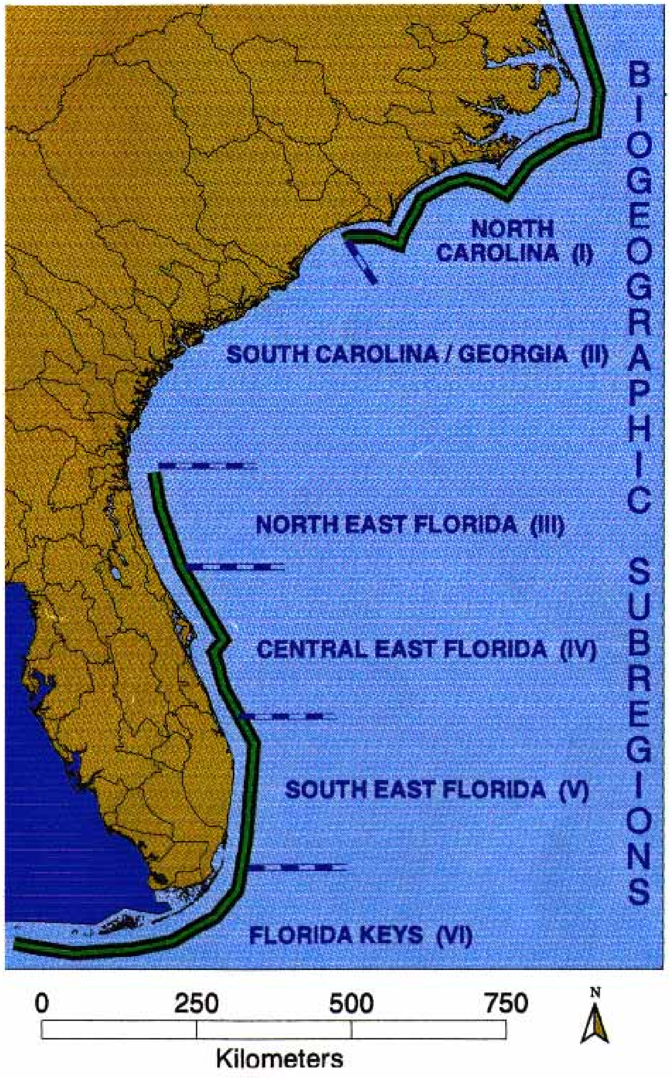


Figure 3.2-4. Illustration of seagrass species in the South Atlantic Region (Source: NMFS, 1997).

SEAGRASSES IN THE SOUTH ATLANTIC REGION



KEY

🟦 SOUTH ATLANTIC REGION

SEAGRASS DISTRIBUTION

🟫 ESTUARINE DRAINAGE AREAS

SEAGRASS SPECIES	SUBREGION I	II	III	IV	V	VI
ZOSTERA MARINA (eelgrass)	X					
RUPPIA MARITIMA (Widgeon grass)	X		X	X	X	X
HALODULE WRIGHTII (shoalgrass)	X		X	X	X	X
HALOPHILA ENGELMANNII (star grass)			X	X	X	X
SYRINGODIUM FILIFORME (manatee grass)			X	X	X	X
HALOPHILA JOHNSONII (Johnson's seagrass)					X	
THALASSIA TESTUDINUM (turtle grass)					X	X
HALOPHILA DECIPIENS (paddle grass)					X	X

Figure 3.2-5. Illustration and table of the distribution of seagrasses in the South Atlantic Region (Source: NMFS, 1998).

Mapping history in North Carolina

The majority of seagrass habitat in North Carolina was mapped by National Oceanic and Atmospheric Administration (NOAA) using photo-interpretation and groundtruthing of aerial photography taken between 1981 and 1992 (Ferguson and Wood 1994). Bogue Sound was originally mapped in 1981 by Carraway and Priddy (1982), but because of differences in scale and methodology, were not comparable to later mapping. Mapping did not include areas south of Bogue Sound. Most of the oligohaline SAV in Albemarle Sound and western Pamlico Sound tributaries were not mapped during this NOAA project. . However, since then, North Carolina Division of Water Quality (DWQ) and NC Division of Marine Fisheries (DMF) has mapped additional SAV habitat in portions of the Neuse and Pamlico rivers and Pamlico Sound tributaries using field survey techniques, and portions of Albemarle Sound have been mapped by state universities. In 2003, Elizabeth City State University remapped Back Bay, Currituck Sound and Kitty Hawk Bay using aerial photography and specifications recommended by NOAA and Virginia Institute of Marine Science (VIMS) (Finkbeiner et al. 2001; Orth et al. 2001). Although mapping of the coast is not entirely complete, the most recent map of known SAV habitat is shown in Figure 3.2-6. The SAV distribution that is depicted in the figure is a mosaic of multiple projects that used imagery ranging from 1981 to 2003, as well as some mapping conducted completely from field surveys, and includes both seagrasses and oligohaline SAV. Unmapped or inadequately mapped areas should be a high priority for future mapping.

In 2005 a North Carolina SAV Cooperative Habitat Mapping Program was established among 26 state agencies, federal agencies, universities, and non-profit organizations. The purpose of the multi-agency workgroup and 2006 Memorandum of Understanding between organizations is to enhance and accelerate mapping and monitoring efforts by pooling resources and coordinating mapping efforts. The long-term goal of the program is to manage and conserve SAV habitat in North Carolina and southern Virginia in a comprehensive manner through cooperative research, monitoring, restoration, and education (http://www.apnep.org/pages/sav.html). The Albemarle-Pamlico National Estuary Program coordinates the program and is contributing substantial funds for aerial photography so that the entire coast can be mapped in a short time period. However, there is no comprehensive monitoring program yet underway. In 2005, the NC Coastal Habitat Protection Plan (CHPP) was approved by environmental regulatory commissions. The plan summarized the ecological value and status of coastal habitats in North Carolina, including seagrass habitat, and made management recommendations including mapping and monitoring of submerged aquatic vegetation (Street et al. 2005; http://www.ncfisheries.net/habitat/chppdocs/). Through the CHPP and APNEP programs, seagrass management, that includes comprehensive monitoring, should improve over the next few years.

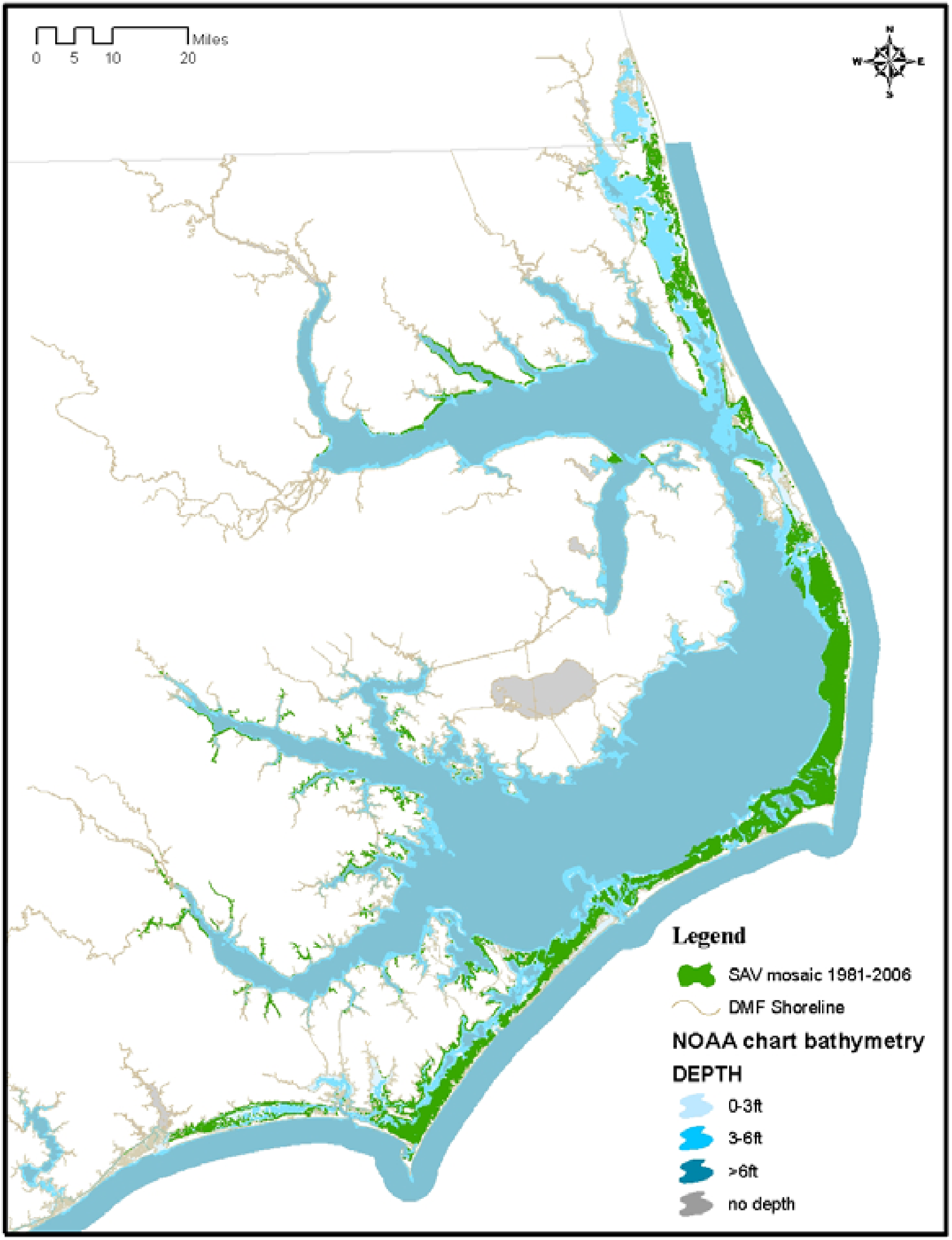


Figure 3.2-6. Distribution of seagrasses and oligohaline SAV in North Carolina (compiled by Scott Chappell, NC DMF, 2007. Published sources include Carroway and Priddy 1983; Ferguson and Wood 1994. Unpublished data sources from NC DWQ; NC DMF bottom mapping program; Elizabeth City State University; North Carolina State University).

Mapping history in Florida

Seagrass cover estimates for Florida have been based on photo-interpretation of aerial photography, mostly at a scale of 1:24,000. Sargent et al. (1995) made the first coast wide effort to summarize statewide seagrass distribution, using photography from 1982-1990. Madley et al. (2003) constructed new statewide seagrass maps using photography from 1987 to 1999 (Figures 3.2-7-3.2-13). Seagrass habitat is regularly mapped every two to three years in the Southwest, St. Johns River, and South Florida Water Management Districts. Other agencies, such as Florida Department of Environmental Protection (DEP), Florida Fish and Wildlife Conservation Commission (FFWCC), National Oceanic and Atmospheric Administration (NOAA), US Army Corps of Engineers (USACOE), US Geological Service (USGS), and US Mineral Management Service (USMMS) have mapped other local areas on a sporadic basis.

Differences in habitat classification schemes and accuracy of methods make overall comparisons difficult. However trend analysis has been done with consistent methodology in several smaller regions of Florida. Overall it appears that seagrass losses have occurred in all regions of Florida, with the largest losses occurring near highly developed areas. Along the Atlantic peninsula, comparison of estimates from recent mapping to estimates in the 1940s found little change had occurred to SAV coverage in the northern Indian River Lagoon and Banana River around the federally protected lands of NASA (FFWCC 2003). Extensive losses have occurred in the southern portion of the Indian River lagoon adjacent to highly developed shorelines. Overall, approximately 59% of what is considered potential SAV habitat (based on SAV presence in 1940 maps) in the Indian River Lagoon is vegetated with seagrass. In South Florida, mapping data has indicated significant declines in SAV coverage in highly developed areas such as northern Biscayne Bay. Seagrass habitat in Dade and Monroe counties has the greatest amount of boat-related propeller damage. Florida Bay has also experienced a large decline in seagrass coverage beginning around 1987. The die-off was attributed to reduced water clarity due to multiple factors including algal blooms, sediment sulfide toxicity, hyper-salinity due to drought, and infection by the slime mold *Labyrinthula*. Although the rate of decline has slowed in recent years, losses continue, which has in turn lead to increased turbidity, further reducing water clarity.

In Florida there are several ongoing regional seagrass management programs, primarily in subtropical portions of the peninsula (e.g., Indian River Lagoon, Florida Bay, Sarasota Bay, and Tampa Bay). To improve coordination of and increase support for seagrass monitoring and management efforts, the Florida Fish and Wildlife Conservation Commission (2003) recommended that the state develop:

- Consensus-based seagrass management strategies at the regional and statewide level;
- a methodologically consistent, statewide seagrass mapping and monitoring program;
- a schedule for reporting regional and statewide status and trends information;
- a schedule for assessing the state's management strategies and the progress made toward achieving the adopted management goals;
- a management-oriented, statewide seagrass research program; and
- a statewide, public outreach program focused on seagrass management and conservation.

In both North Carolina and Florida, more funding is needed to support comprehensive SAV mapping and management programs. Maps of SAV in Florida can also be viewed on an internet map service at http://ocean.floridamarine.org/mrgis/viewer.htm

Figure 3.2-7. Seagrass distribution along the east coast of Florida, Indian River Lagoon. (Source: P. Carlson, FFWCC 2007).

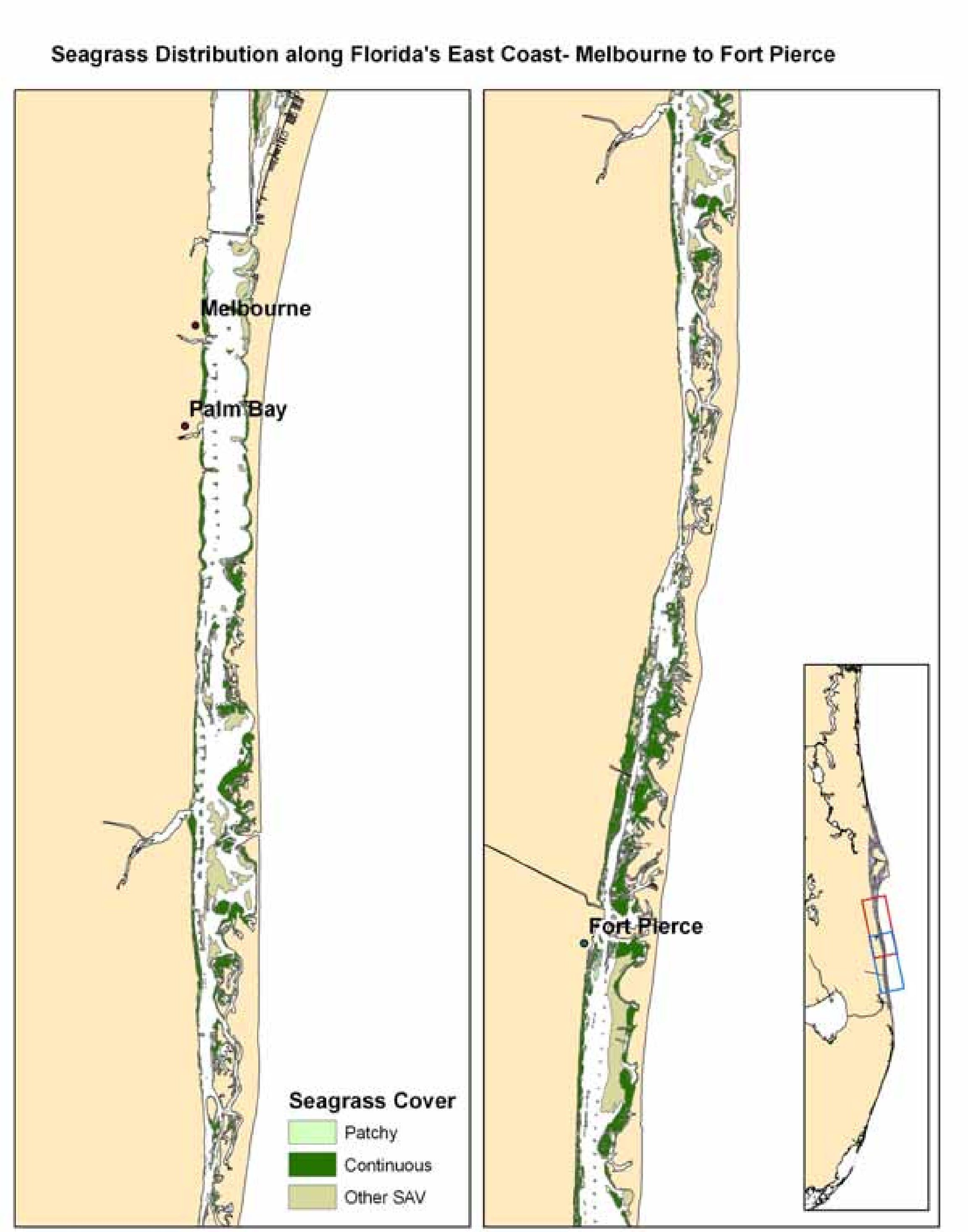


Figure 3.2-8. Seagrass distribution along Florida's east coast – Melbourne to Ft. Pierce. (Source: P. Carlson, FFWCC 2007).

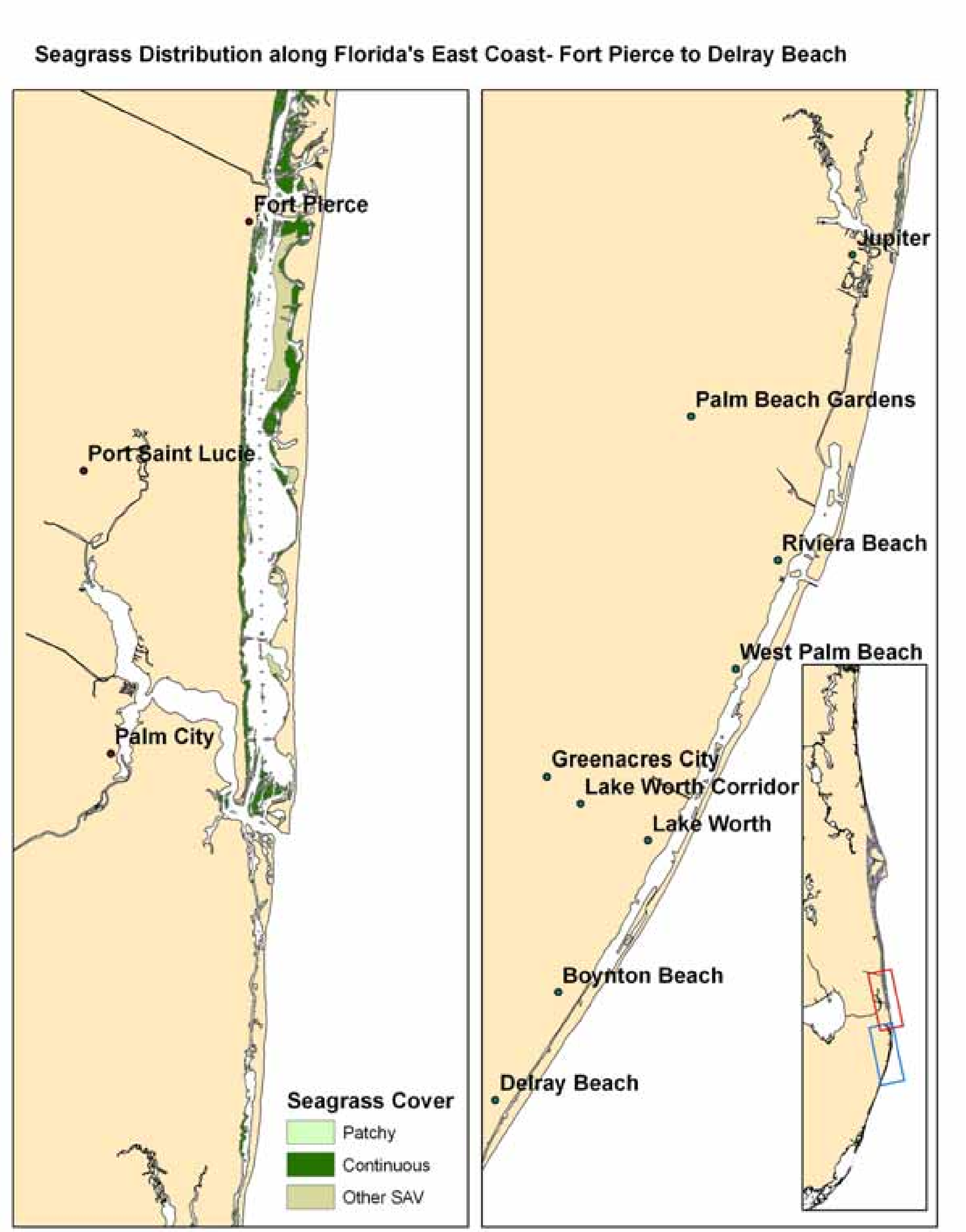


Figure 3.2-9. Seagrass distribution along Florida's east coast – Ft. Pierce to Delray Beach. (Source: P. Carlson, FFWCC 2007).

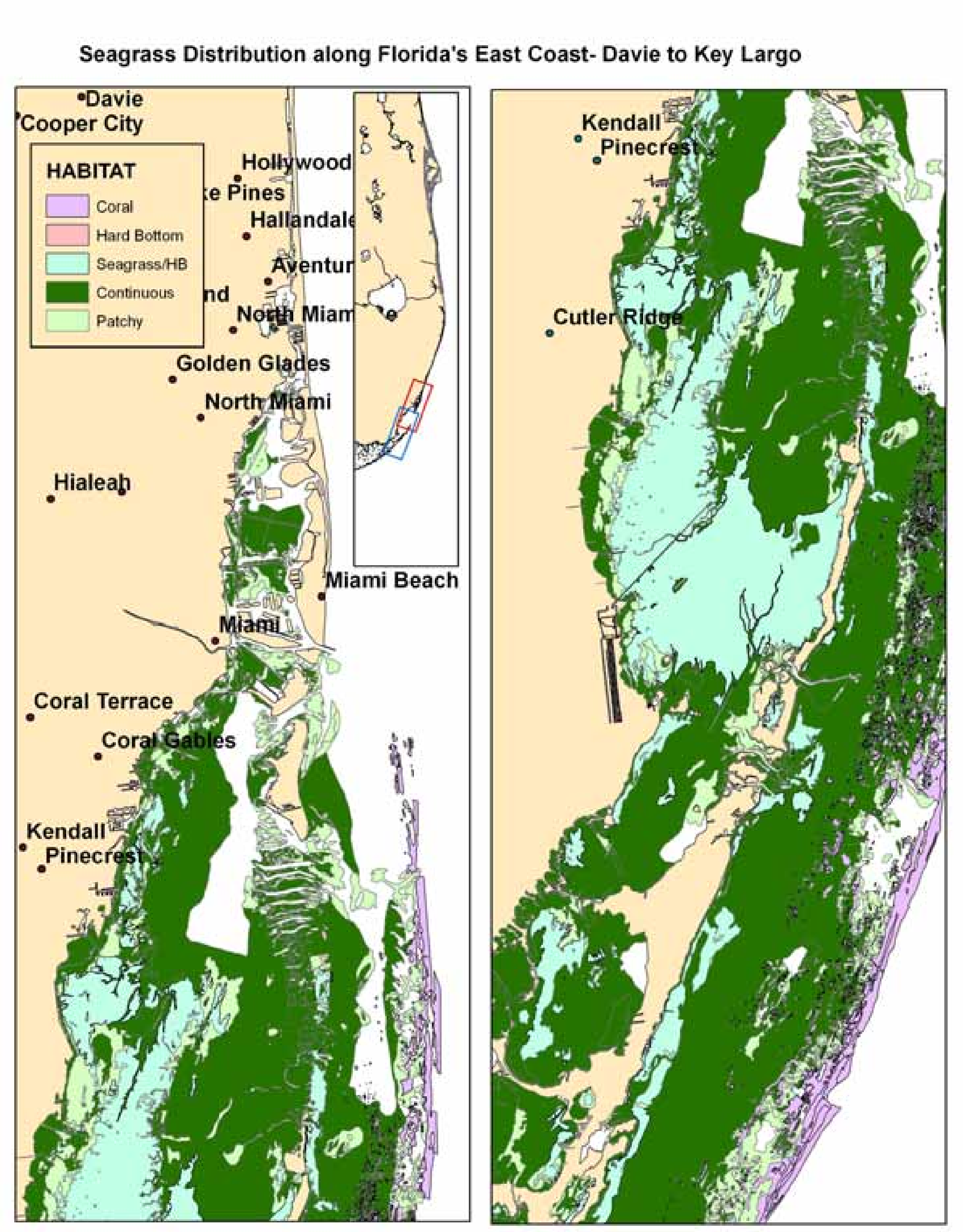


Figure 3.2-10. Seagrass distribution along Florida's southeast coast – Hollywood to Key Largo. (Source: P. Carlson, FFWCC 2007).

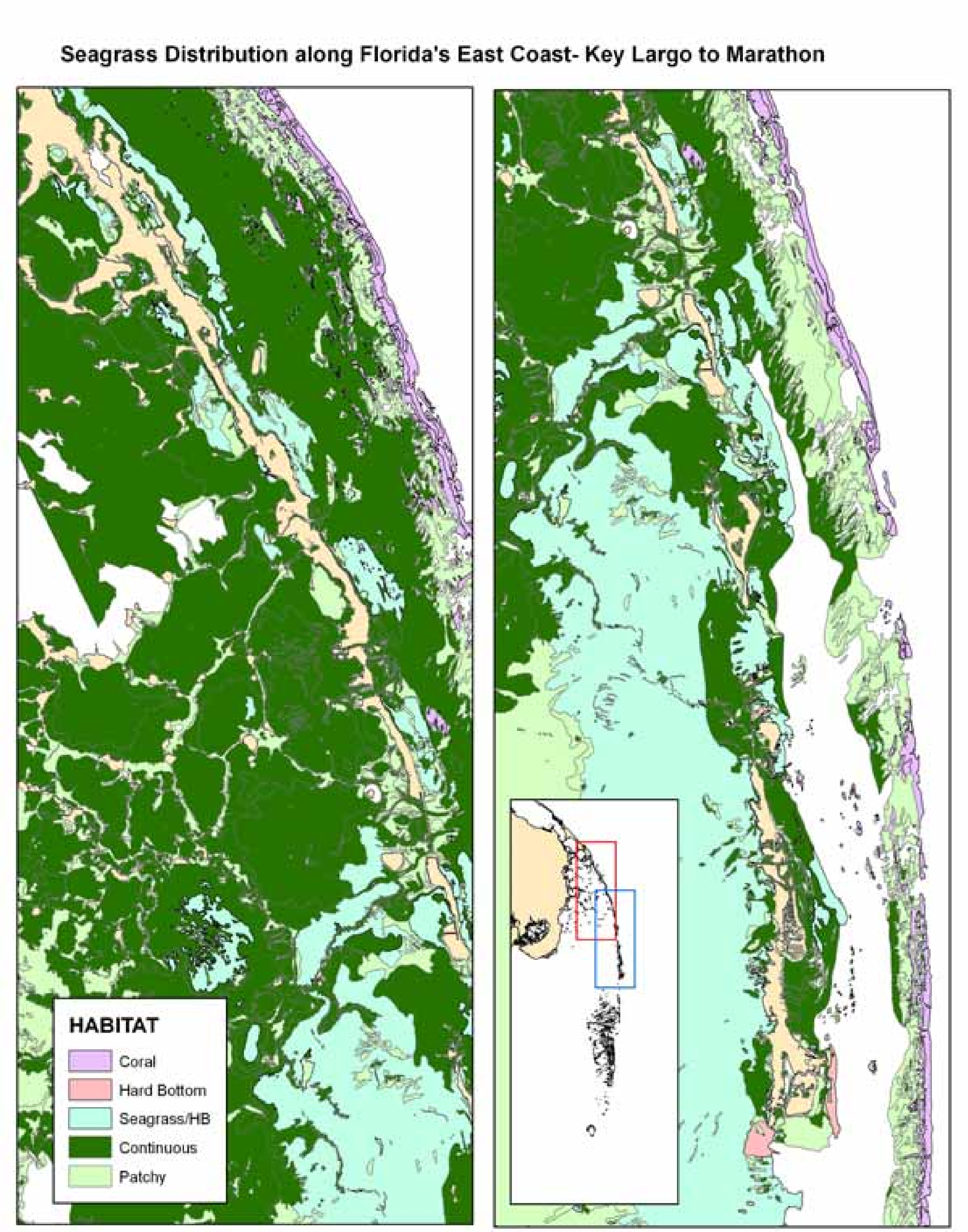


Figure 3.2-11. Seagrass distribution along the upper Florida Keys – Key Largo to Marathon. (Source: P. Carlson, FFWCC 2007).

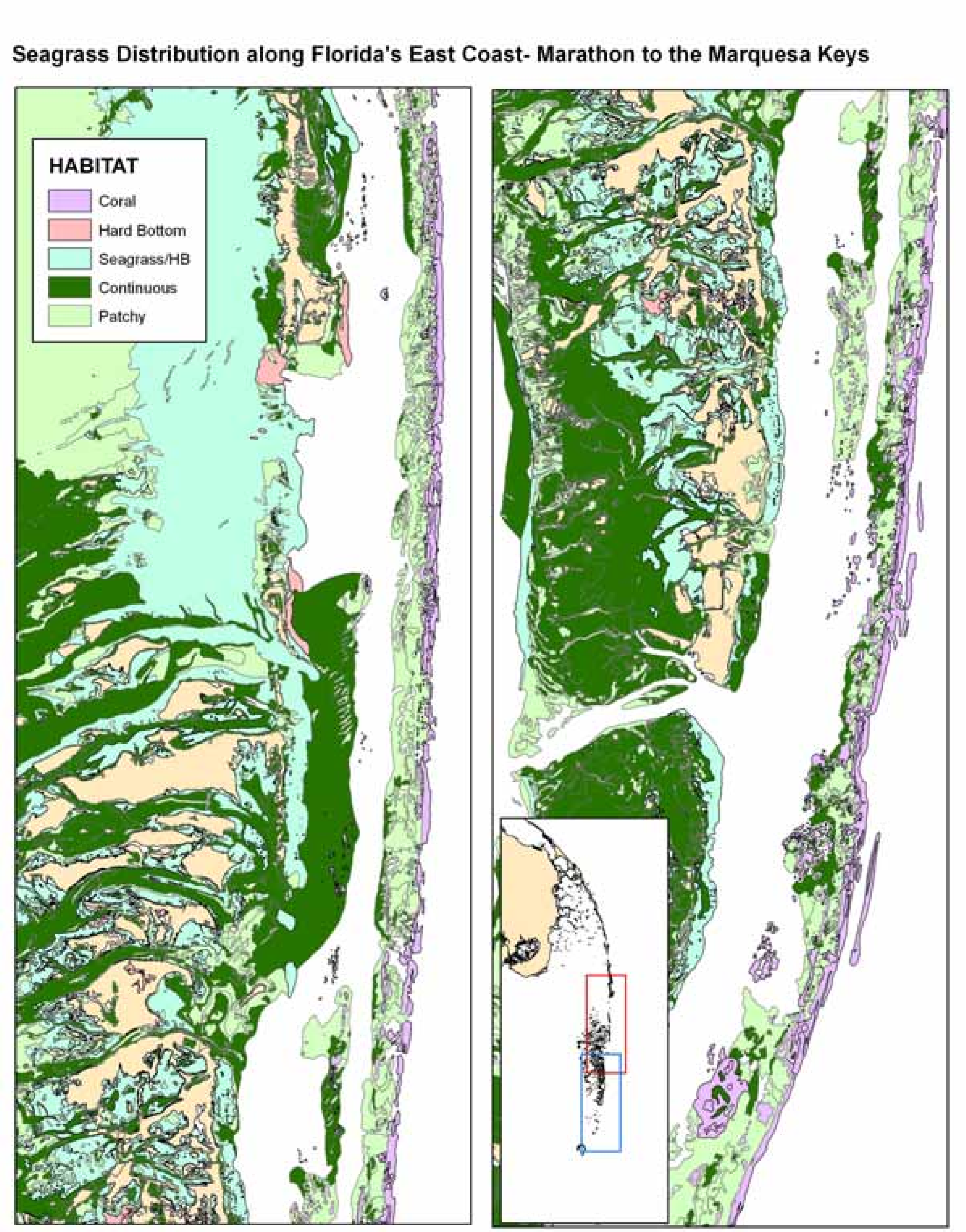


Figure 3.2-12. Seagrass distribution along the lower Florida Keys - Marathon to Marquesas. (Source: P. Carlson, FFWCC 2007)

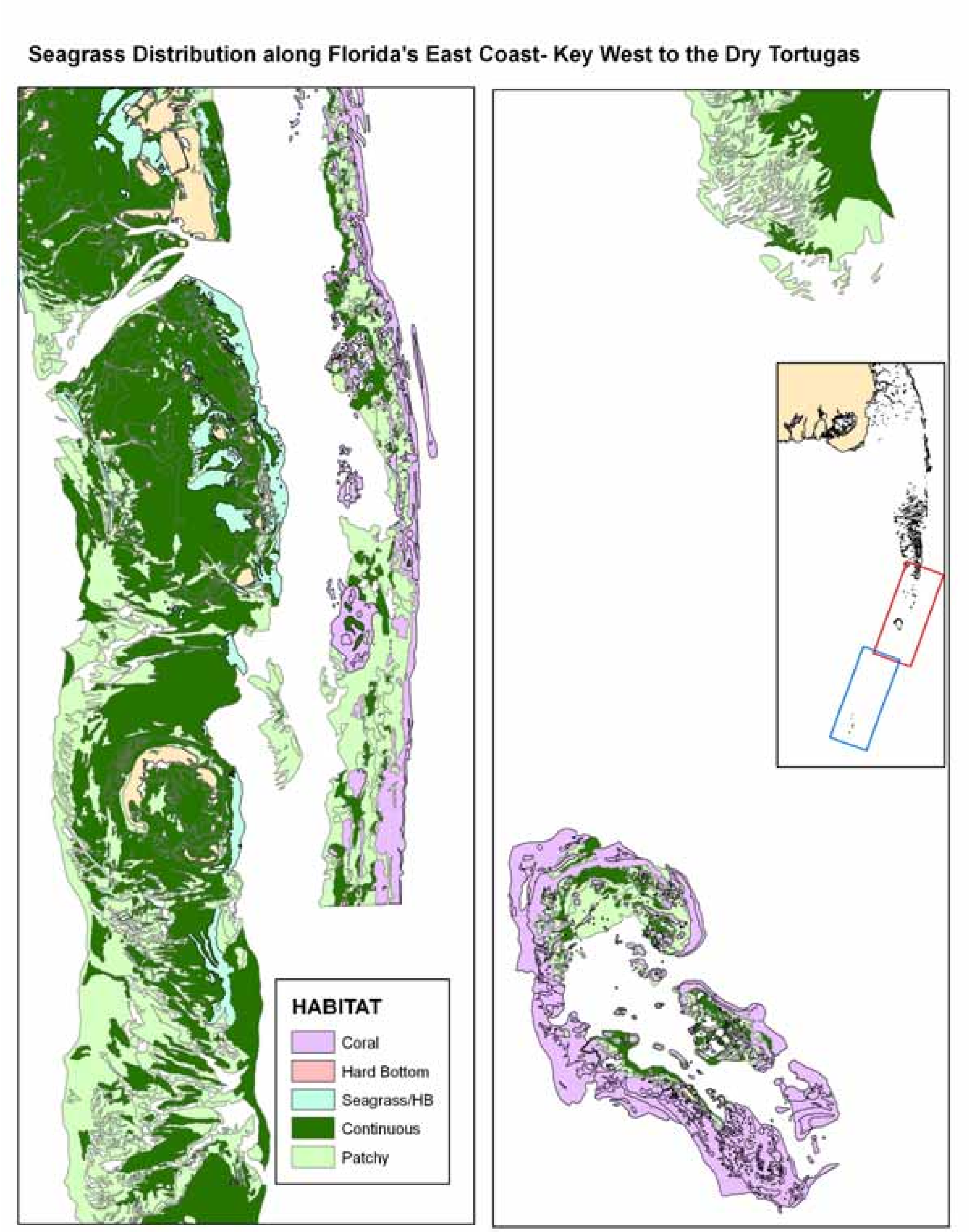


Figure 3.2-13. Seagrass distribution along lower Florida Keys - Key West to the Dry Tortugas. (Source: P. Carlson, FFWCC 2007).

General distribution of seagrass in the south Atlantic

As indicated previously, no seagrasses have been reported to occur in South Carolina and Georgia. Seven of the eight species that occur in the southeastern U.S. are found in Florida. The exception is *Z. marina* whose southern limit is north of Cape Fear, North Carolina (Thayer et al. 1984). In Florida seagrasses are distributed in protected inland waters as well as oceanic environments. In north central (approximately St. Augustine), and southeast Florida most of the seagrasses occur within protected coastal lagoons and in the Intracoastal Waterway (ICW) including; Mosquito Lagoon, Banana River, Indian River Lagoon, Lake Worth, and Biscayne Bay. The most northern distribution of *H. engelmannii* is in the Banana River at Cape Canaveral. The northern limit of *H. decipiens* and *H. johnsonii* is approximately Sebastian Inlet in the Indian River Lagoon. Beginning around the Palm Beach area and continuing south through the Florida Keys, *Halophila decipiens* is found on offshore sandy sediments between reefs down to 30m depth. Open water and oceanic meadows of *H. wrightii*, *S. filiforme* and *T. testudinum* begin just south of Virginia Key on the seaward side of Biscayne Bay and continue through the Florida Keys to the Dry Tortugas in water depths up to approximately 30-40 m. (Sargent et al. 1995)

The majority of seagrass biomass is distributed in the subtidal zone; however, all of the species, with the exception of *H. decipiens*, can be found growing in the intertidal zone where they may experience periods of exposure and desiccation. The maximum depth limits are determined by optical water quality and transparency and sometimes limited by water velocities associated with inlets, tidal channels and unstable sediments. In North Carolina maximum depths average between 1.5 and 2.5 m and are similar to the maximum depths of seagrasses in the lagoons and Intracoastal Waterway (ICW) along the east coast of Florida. In locations near inlets with clear water and stable sediments seagrasses grow to 3-5 m, while in nearshore and offshore areas of southeastern Florida and the Keys seagrasses grow to depths of 30m.

Salinity is a very important parameter in estuaries because of its potential to control physico-chemical attributes of the system that affect nutrient cycling, water transparency, floral and faunal composition, and productivity. Salinity also undergoes frequent fluctuations and may act as an important stressor. Given the fact that the south Atlantic region has extensive natural and man made fresh water sources flowing into coastal systems, salinity is a critical parameter controlling seagrass distribution and abundance (Doering and Chamberlain 1999; Estevez 1999). The spatial distribution of seagrasses in coastal systems is controlled locally by salinity, especially the upper reaches of penetration by different seagrass species (Estevez 1999). Seagrass distribution throughout an estuary can also be affected by long-term modification of freshwater inflow such as has occurred in the St. Lucie River in east central Florida.

Of the eight species of seagrass, *R. maritima*, has the widest tolerance to salinity and can grow and thrive from freshwater to hypersaline conditions (Kantrud 1991). When matched with its fecundity, these two characteristics enable *Ruppia* to occur in a wide range of estuarine conditions as well as having the ability to thrive in fluctuating environments. *Ruppia* is a very important species in marginal and transitional environments which are not as suitable for other seagrasses. *H. wrightii* is considered to be the next most tolerant species for relatively lower salinities, and similar to *Z. marina* (McMillan and Moseley 1967; Thayer et al. 1984). Both of these species are considered euryhaline and regularly reported growing at salinities ranging from very low salinities (5-10 ppt) to full strength seawater. *Thalassia* is considered euryhaline and tolerant of salinities as low as 6-10 ppt for brief periods of time; optimum salinities range from 17-36ppt (Doering and Chamberlain 1999).

The salinity tolerances of *Halopila* spp. have not been well studied, however, reports of distribution indicate they are euryhaline and found growing well upstream in estuaries experiencing low salinities and out into the open ocean (Dawes et al. 1989; Toquemada et al. 2005; Kenworthy 2000). The wide range of salinities tolerated by the species of seagrass in the South Atlantic is an important aspect of their function as essential fish habitat. Salinity tolerances enable them to be more widely distributed across the estuarine landscape and are therefore available as habitat to a broader spectrum of fishery species.

As in terrestrial grasslands, seagrass meadows may be seasonal or perennial. The meadows are usually defined by a visible boundary delineating unvegetated and vegetated substrate and vary in size from small, isolated patches of plants less than a meter in diameter to a continuous distribution of grass tens of square kilometers in area. This natural variation in grass bed morphology is related to seagrass dynamics and affects the function of seagrasses as habitat (Fonseca 1996; Murphey and Fonseca 1995; Fonseca and Bell 1998; Fonseca et al. 2002). Seagrass meadows are dynamic spatial and temporal features of the coastal landscape which actually move and can disappear and reappear periodically (den Hartog 1971; Patriquin 1975; Fonseca and Bell 1998; Fonseca et al. 1998; Fonseca et al. 2002). The presence of a seagrasses canopy does not necessarily signify whether or not a location is capable of supporting seagrass habitat. Some species are ephemeral, for example, in North Carolina, shallow *Z. marina* meadows may completely exfoliate in late summer in response to warm temperatures, leaving a signature suggesting there are no seagrasses in the area when, in many instances, the meadows recovers in winter or spring. Because of this, identification of seagrass habitat at certain times of the year can be difficult to determine from visual inspections, which complicates the ability to properly permit water dependent activities such as dredging or marina construction. Environmental characterization of SAV habitat and the better understanding of the processes driving SAV occurrence and temporal changes in distribution are needed to properly identify and protect SAV habitat.

In the South Atlantic region all seagrasses occur on unconsolidated sediments in a wide range of physical settings and different stages of meadow development leading to a variety of cover patterns, ranging from patchy to continuous. Seagrasses patches form and migrate across the sea bottom. In high current environments and areas exposed to wave turbulence, movement is considerable and beds tend to remain in a continuously patchy state. Whereas in low energy embayments and areas protected from large fetch, contiguous perennial beds will tend to form. Seagrass beds developing from seed and mature beds in relatively high energy environments may have similar patchy signatures, but very different physical and chemical characteristics (Kenworthy et al. 1982; Kenworthy 2000).

Depending on the species and the environmental conditions, a meadow may attain full development in a few months (e.g., *Z. marina and Halophila* spp.). Meadows that develop rapidly usually reproduce by seed, forming annual meadows that completely disappear during unfavorable growing conditions. For example, on the east and southeast coasts of Florida between Sebastian Inlet in the Indian River Lagoon (IRL) and North Biscayne Bay, *H. decipiens* forms annual meadows in water generally deeper than 1.5-2.0 m (Dawes et al. 1995; Kenworthy 2000). These depths are where the winter light levels cannot support the larger perennial species such as *R. maritima*, *H. wrightii*, *S. filiforme* and *T. testudinum* (Kenworthy and Fonseca 1996; Kenworthy 2000). In the relatively deeper water the smaller opportunistic *H. decipiens* is capable of germinating seeds in summer months when light levels are adequate. This life history strategy, combined with a thin leaf structure, minimal self shading, and relatively low non-photosynthetic biomass make the genus *Halophila* ideally suited for growth in fluctuating and highly disturbed environments (Kenworthy et al. 1989; Kenworthy 2000).

These dynamic features of seagrass meadows are not just restricted to the genus *Halophila*. In North Carolina annual meadows of a large bodied species, *Z. marina*, are common in shallow, protected embayments where excessively high (> 30^o C) summer water temperatures eliminate *Zostera* beds that thrive in winter and spring when water temperatures are optimal (Thayer et al. 1984). These shallow embayments are replenished annually by seed stocks of *Zostera*, whereas in North Carolina during the summer months when water temperatures exceed 25-30°C, *Zostera* thrives only in relatively deeper water or on tidal flats where water movement is nearly continuous so that the plants are insulated from lethal temperatures and desiccation. In general, whether they are found in the warm temperate coastal waters of North Carolina or the subtropical environment in southeastern Florida, seasonal fluctuations in the abundance of seagrass biomass in the subtidal is normal (Dawes et al. 1995). The range of these seasonal fluctuations tends to increase from south Florida to North Carolina. North Carolina is a special case where seasonal fluctuations may be minimized in water bodies and meadows where *Z. marina* and *H. wrightii* co-occur. These two species are at their southern (*Z. marina*) and northern (*H. wrightii*) range limits, and when one species is limited by seasonal thermal extremes the other species may be abundant.

Alternatively, meadows formed by the larger bodied species which have either limited or irregular sexual reproduction may require decades to reach full maturity. For example, the slowest growing species in the south Atlantic region, *T. testudinum*, produces relatively few fruits and seeds at irregular intervals (Tomlinson 1969; Moffler and Durako 1987; Whitfield et al. 2004). When *T. testudinum* is compared to its congeners, *H. wrightii* and *S. filiforme*, it has the slowest rate of vegetative expansion (Fonseca et al., 1987; Kenworthy et al. 2002). Depending on the environmental conditions, rates of vegetative expansion for *H. wrightii* and *S. filiforme* are normally 4 to 10 times faster than *T. testudinum* (Kenworthy et al., 2002). Thus, *T. testudinum* meadows form more slowly than any of the other species, yet if the environmental conditions allow the full development of a *T. testudinum* meadow its biomass and productivity will usually exceed any other seagrass (Zieman, 1982).

Regardless of developmental stage or species composition, small seagrass patches and entire meadows can move, the rate of which may also vary on a scale of hours to decades. These dynamic spatial and temporal features of seagrass meadows are important aspects of fishery habitats. Seagrass habitats must be recognized as including not only continuously vegetated perennial beds but also patchy environments with the unvegetated areas between patches as part of the habitat. In fact, available data show that patchy habitats provide many ecological functions similar to continuous meadows (Murphey and Fonseca 1995; Fonseca et al. 1998).

Also, it must be recognized that the absence of seagrasses in a particular location does not necessarily mean that the location is not viable seagrass habitat. It could mean that the present conditions are unfavorable for growth, and the duration of this condition could vary from months to years.

Ecological Role and Function

The ecological role and function of seagrass habitat has been described by Hemminga and Duarte (2000), Larkum et al. (2006) and Duffy (2006). For more specific information of seagrasses in the South Atlantic region we recommend two U.S. Department of Interior Community Profiles: Thayer et al. (1984) and Zieman (1982). A *Symposium on Biodiversity in the Indian River Lagoon* published in Volume 57 of the Bulletin of Marine Science (Swain et al. 1995) is an excellent compendium of the biology, ecology and biodiversity of seagrass communities on the east coast of Florida. Another important source document is the *Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States* (Durako et al. 1987). Additionally, other published books on the general biology and ecology of seagrasses have information pertaining directly to use of seagrass habitat by managed species and their food sources (McRoy and Helfferich 1977; Phillips and McRoy 1980; Larkum et al. 1989; Bortone 1999; Short and Coles 2001). Additionally, *The relationship of submerged aquatic vegetation (SAV) ecological value to species managed by the Atlantic States Marine Fisheries Commission (ASMFC): summary for the ASMFC SAV Subcommittee* by R. Wilson Laney (1997) provides detailed descriptions and literature citations of seagrass use by species managed by the ASMFC and the South Atlantic Fishery Management Council. Following is a brief summarization of the most important aspects of marine seagrasses which pertain directly to their distribution, abundance and function.

Seagrasses are rooted plants that can become nearly permanent, long-term features of coastal marine and estuarine ecosystems either as perennial or annual meadows. Because they are rooted, seagrasses directly link the sediments to the water column. No other marine plants are capable of providing this ecological service. Ecological functions provided by seagrass habitat that enhance conditions for fish species include: 1) primary productivity, 2) structural complexity, 3) modified energy regimes and stabilization of sediment and shorelines, and 4) nutrient cycling.

On a unit area basis seagrasses are among the most productive ecosystems in the world (McRoy and McMillan 1977; Hemminga and Duarte 2000). High rates of primary production lead to the formation of complex, three dimensional physical structures consisting of a canopy of leaves and a dense matt of roots and rhizomes buried in the sediments. The presence of this physical structure provides substrate for attachment of organisms, shelter from predators, frictional surface area for modification of water flow and wave turbulence, sediment and organic matter deposition, and the physical binding of sediments underneath the canopy. Linked together by nutrient absorbing surfaces on the leaves and roots, and a functional vascular system, seagrass organic matter cycles and stores nutrients, and provides both direct and indirect nutritional benefits to hundreds of species of micro-organisms, meiofauna, carnivores, herbivores and detritivores. The most important aspects of these functions are listed below.

Primary productivity

Seagrass meadows provide four important sources of primary organic matter, 1) their own tissues, 2) dissolved organic matter released from their tissues during metabolism, 3) the epiphytic microscopic and macroscopic plants that attach to the surfaces of the seagrass leaves and live among the canopy, 4) the plants that live on the sediments among the seagrass shoots, and 5) the residual organic matter which decomposes in the sediments, on the sediment surface and in the water column. The high rates of primary productivity ensure an abundant supply of organic matter available to be used as an energy source in many different food webs. In some instances a significant portion of the organic matter is exported to adjacent ecosystems (e.g., beach wrack, mangrove forests, open ocean, deep ocean canyons) where it is processed into the food chain. Some fishery organisms consume seagrasses directly (e.g., amphipods and parrot fish), but the majority of the secondary fishery production in the meadows begins with the consumption of epiphyte communities, benthic algae and the utilization of organic detritus. Thus, the food webs supported by seagrass primary production are complex and include many intermediate steps involving microorganisms, meiofauna, small invertebrates such as isopods, and amphipods, as well as the thousands of species of macroinfauna and epifauna in the sediments, on the sediment surface, and in the water column.

Structural complexity

Leaf canopies formed by seagrasses range in size from just a few centimeters (*Halophila* spp.) to more than a meter tall. Where several species co-occur, the three dimensional canopy may take on multiple layers and forms, with long (1.25 m) cylindrical stems and blade surfaces (*S. filiforme*) combined with relatively shorter strap-shaped leaves (*T. testudinum* or *H. wrightii*). No matter what species are present, the existence of leaf surfaces provides structures for attachment of smaller organisms and space between shoots for shelter from predators and adverse environmental conditions. The leaf area in a seagrass meadow may effectively increase the surface area available for colonization by an order of magnitude compared to an unvegetated substrate. While at the same time, the leaves and stems create a large volume of water column sheltered within the canopy and partially obscured by self-shading of the leaves. Within the canopy there is an enormous physico-chemical microenvironment structured and maintained by the seagrasses. This structural influence extends into the sediments where the roots and rhizomes stabilize the substrate and form a large pool of organic biomass and a matrix for meiofauna and macrofauna (Kenworthy and Thayer, 1984). The additional structure and productivity, in turn, can support a greater diversity and abundance of species. Several studies have shown significantly greater species richness and abundance in SAV beds compared to unvegetated bottom (Thayer et al. 1975; Heck et al. 1989; Ross and Stevens 1992; Irlandi 1994; ASMFC 1997; Wyda et al. 2002).

Modification of energy regimes and sediment stabilization

The leaf surfaces and the collective structure of the canopy provide frictional drag slows water motion and reduces wave turbulence (Zieman 1982). This process promotes the deposition of particles in the meadows, including but not restricted to inorganic sediments, dead organic matter and living organisms. The addition of all of these materials enhances the productivity, stability, and biodiversity of coastal systems with seagrasses. By promoting sediment deposition and stabilization, coastal habitats coupled to seagrasses meadows by water movement receive both direct and indirect benefits.

Nutrient cycling

The high rates of primary production and particle deposition make seagrass meadows important sources and sinks of nutrients. During active periods of growth the constant and high rate of leaf turnover and epiphyte growth provides nutrients for herbivores and a mechanism for nutrient export and retention. Temporary and permanent retention of nutrients within seagrass meadows is encouraged by particle deposition and burial as well as the formation of organic matter in the sediments by the roots and rhizomes.

Seagrasses are sensitive to the availability and abundance of nutrients in their surrounding environment and often retain nutrient signatures representing environmental conditions they have experienced, both spatially and temporally (Fourqurean et al. 1992). The variation in tissue nutrient composition is an important factor in fishery utilization of seagrass derived organic matter.

Species composition and community structure

Seagrass habitat supports other types of aquatic plants in addition to submerged grasses previously described. Macroalgae (benthic, drift, and floating forms) often co-occur with SAV and provide similar ecological services, but the plant taxa have distinctly different growth forms and contrasting life requirements. Macroalgae grow faster than SAV and do not require unconsolidated substrate for anchoring extensive root systems. Because of this growth pattern, macroalgae do not provide as much sediment stabilization as submerged rooted vascular plants, but do contribute to productivity and biodiversity. Macroalgal genera include salt/brackish (*Ulva*, *Codium*, *Gracilaria*, *Enteromorpha*, *Ectocarpus*, and *Cladomorpha* (Thayer et al. 1984; Mallin et al. 2000). In Florida, calcareous benthic algae, such as *Penicillus* and *Halimeda*, grow among seagrasses and contribute a significant source of calcareous sediment to the system.

Epibiota are another important component of SAV habitat. Epibiota are organisms that attach or grow on the surface of a living plant and may or may not derive nutrition from the plant itself. Micro- and macroalgae (i.e., seaweed) can grow on the leaves of SAV. Invertebrates attached to the SAV leaves include protozoans, nematodes, polychaetes, hydroids, bryozoans, sponges, mollusks, barnacles, shrimps and crabs.

Perhaps seagrass meadows are best known for their source of attachment and/or protection for invertebrates such as bay scallops (*Argopectin irradians*) and hard clams (*Mercenaria mercenaria*). Scientific evidence also indicates that blue crabs (*Callinectes sapidus*), pink and brown shrimp (*Farfantepenaeus duorarum*, *F. aztecus*), and lobster (*Panulirus argus*), just to name a few invertebrates, have a strong reliance on seagrass habitats including seagrass-supported trophic intermediaries.

The three dimensional structure provides protective cover for small resident fish and invertebrates and juvenile fish species. Because of this, the nursery role of SAV is critical for many estuarine dependent fishery species in the South Atlantic region such as gag groupers, flounders, red drum, weakfish, striped mullet, pinfish, pigfish, and silversides, just to list a few of the fish taxa documented to utilize seagrass habitats (Thayer et al. 1984; DMF 1990; ASFMC 1997). Sampling in seagrass beds in North Carolina in the 1980s documented over 150 juvenile fish and invertebrate species, of which 40 were commercially important species. In addition, at least 49 adult fish species were reported from beds in eastern Pamlico Sound (DMF 1990). ASMFC compiled a list of ASMFC managed species that utilize SAV for some portion of their life cycle. Over 30 species were documented potentially using SAV as larvae, juveniles, or adults for various functions (Table 3.2-5).

While there have been few studies dealing with larval fish settlement and use of seagrass habitats, there have been numerous publications listing juvenile and adult fishes collected in seagrass meadows. The same ecological characteristics of seagrass beds that make the habitat favorable for juveniles should also benefit larval fish and invertebrates. Seagrass beds are important for the brooding of eggs (for example, silverstripe halfbeak, *Hyporhamphus unifasciatus*) and for fishes with demersal eggs (e.g., rough silverside, *Membras martinica*). Larvae of spring-summer spawners such as anchovies (*Anchoa* spp.), gobies, (*Gobiosoma* spp.), pipefish (*Syngnathus fuscus*), weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), red drum (*Sciaenops ocellatus*), silver perch (*Bairdiella chrysoura*), rough silverside, feather blenny (*Hypsoblennius hentzi*), and halfbeaks are present and use seagrass beds.

Table 3.2-5. Ecological functions provided by seagrass habitat for various life stage(s) of ASMFC fishery species (Source: ASFMC 1997).

	Life stage documented to use SAV for function listed [1]			
SPECIES	**REFUGE/ ATTACHMENT[2]**	**SPAWNING[3]**	**FOOD[4]**	**PREY[5]**
Atlantic croaker	L,J,A		J?	J,A
Atlantic menhaden	L,J,A		J,A	
Red drum	L,J	A?		J,A
Spanish mackerel	J?			J?,A?
Spot	L,J,A			J,A
Spotted seatrout	J,A	A		L,J,A
Striped bass	J?			J?,A?
American eel	J			J,A?
Black sea bass	J			J,A?
Scup	L,J,A?	A?		L?,J,A?
Tautog	J, E[2]	E,A		L?,J,A
American lobster	J?		J?,A?	J?,A?
Atlantic herring	L?,J?			L?,J?,A?
Atlantic sturgeon	J?			J?
Bluefin	J			L?,J,A?
Northern shrimp	E?,L?[2],J?,A?	A?	J?,A?	L?,J?,A?
American shad	J?			J?,A?
Hickory shad	J?			J?,A?
Alewife	J?			J?,A?
Blueback herring	J?			J?,A?
Summer flounder	J,A			J,A
Weakfish	L,J,A	A?		L,J,A
Winter flounder	J?,A?			J?,A?
Southern flounder	J,A			J,A?
Striped mullet	J,A		J?,A?	L?,J?,A?
White mullet	L,J,A	A?	J?,A?	L?,J?,A?
Rainbow smelt	J,A?			J?,A?
Black drum	L?,J?,A?	A?	J?,A?	J?,A?
Bay scallop	E?[2],L?,J[2],A	A?	J?,A?	J,A
Brown shrimp	J,A		J,A	J,A
Pink shrimp	J,A		J,A	J,A
White shrimp	J?,A?		J,A	J?,A?
Blue crab	J,A		J,A	J,A

[1] Life stage abbreviations: E = eggs; L = larvae; J = juveniles; A = adults. ? = species overlaps with SAV geographically, but no documentation of use in literature.

[2] The species life stage uses SAV as site of physical attachment

[3] The species deposits eggs in or on SAV beds

[4] The species consumes SAV directly (herbivore) or secondarily (detritivore)

[5] The species feeds on prey that resides in or attached to SAV

In regions of North Carolina where there is often year-round cover of seagrass (either *Zostera* or *Halodule*), larval and early juvenile fishes are present in these beds during much of the year. Lists of these species are presented in referenced literature and policy statements, but it should be pointed out here that larvae and juveniles of important commercial and sportfish such as gag grouper (*Mycteroperca microlepis*), snapper (*Lutjanus griseus*), seatrout or weakfish, bluefish (*Pomatomus saltatrix*), mullet (*Mugil* spp.), spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonius undulatus*), flounder (*Paralichthys* spp.), herrings (Clupeidae), and many other species appear in seagrass beds in spring and early summer. Many of these fish reside only temporarily in grass beds to forage, spawn, or escape predation. Some species reside there until the fall when they return to the open coastal shelf waters to spawn. As is noted by the SAFMC's SAV protection policy (See FEP Volume IV, section 7.4.1), economically important species use these habitats for nursery and/or spawning grounds, including spotted seatrout (*Cynoscion nebulosus*), grunts (Haemulids), snook (*Centropomus* spp.), bonefish (*Albula vulpes*), tarpon (*Megalops atlanticus*) and several species of snapper and grouper.

For the most part, the organisms discussed above utilize the grass bed structure and trophic elements associated with the bed, but many species of herbivorous invertebrates (e.g., urchins *Lytechinus variegatus*, *Tripneustes ventricosus*), birds (e.g., black brant *Branta bernicla*), a few fish species (e.g., pinfish *Lagodon rhomboides*, parrotfish *Sparisoma radians*), the green turtle (*Chelonia mydas*) and the manatee (*Trichechus manatus*) feed directly upon coastal and estuarine seagrasses. Work on green turtles in North Carolina has shown a higher incidence of capture in pound nets set in grass beds than by nets set in unvegetated areas. Grazing can have profound effects on the system, but the consequences are neither uniform nor of similar importance in both tropical and temperate seagrasses (Thayer et al. 1984).

Seagrass as Essential Fish Habitat

Seagrasses perform several important functions in coastal ecosystems that facilitate successful spawning, feeding and growth of numerous seasonal and resident fishery species, thus serving as essential fish habitat (Heck et al. 2003; Valentine and Duffy 2006, Heck and Orth, 2006). As ecosystem engineers, SAV presence imparts unique biological, physical and chemical characteristics to water bodies which both directly and indirectly contribute to the necessary attributes of essential fish habitat (ASMFC 1997; Zieman 1982; Thayer et al. 1984). Seagrasses directly attract fish of all life stages, with the three dimensional structure of their leaf canopy offering hiding places that protect juveniles and small adults from predation by larger organisms. As such, seagrass meadows act as nurseries for juvenile fish and their food sources and affect ecological processes which enable fish to grow and mature to different ontogenetic stages, eventually reaching adult forms and emigrating to other habitats (Orth et al. 1984; Heck and Crowder 1991; Koenig and Coleman 1998; Beck et al. 2001). This concept of nursery value is one of the most important aspects of the function of seagrasses as essential fish habitat. Several studies have indicated that juvenile fishes are the most abundant age group in seagrass beds, especially in more temperate waters.

A large proportion of the seasonal residents of seagrass meadows in the south Atlantic region spawn offshore on continental shelves and reefs, enter the estuaries in late winter and early spring and take up residency until fall or until they reach a certain ontogenetic stage when they move to other habitats or offshore to renew this cycle. This process of estuarine dependency is more distinct in the northern most region of the south Atlantic (e.g., North Carolina and north and central Florida). Gag and black sea bass are two estuarine dependent reef species that utilize SAV as nurserv areas in North Carolina. Red drum, speckled trout, and weakfish spawn near inlet systems in late summer and fall and use SAV as nursery areas (Street et al. 2005). Further south in the more tropical waters of Biscayne Bay and the Florida Keys the separation in the distribution of reefs and seagrass beds is less distinct. There are also recognizable and predictable interactions where different life stages of fish move between reefs and seagrass beds on a daily basis. The best known examples in Florida are species of grunts which utilize reefs by day and seagrass beds by night. In addition to seasonal and migratory species, there are resident fish species and other fauna that utilize seagrass beds continuously (Sogard et al. 1987).

When seagrass beds are compared to unvegetated substrates, species richness and abundance of animals in seagrass beds is usually greater, implying that there is a preference for seagrass beds by some juvenile and adult species, including fish, decapods and benthic fauna (Thayer et al. 1975; Summerson and Peterson 1984; Heck et al. 1989; Ross and Stevens 1992; Irlandi 1994; ASMFC 1997; Wyda et al. 2002). Many motile species that use seagrass beds can also be found in other habitats, e.g, salt marsh, mangrove, oyster and coral reefs, and macroalgal beds, but use seagrass meadows temporarily for food and for breeding. Thus, seagrasses provide alternative sources of food and shelter and supplement the resources made available by different habitats found throughout the southeastern U.S. Furthermore, since most of the distribution of seagrasses in the southeast Atlantic region is subtidal, where almost all fish reside, seagrasses are a consistently reliable habitat. Compared to intertidal habitats, that are either regularly or irregularly flooded, seagrasses are almost always available to be used by fish. Even though subtidal seagrass beds are regularly available, environmental factors controlling reproduction and dispersal of larvae can affect the abundance of fish in seagrass beds, such that spatial and inter-annual variability is very high. It has been suggested that because most fish spawning is non-local, the abundance and diversity of fish fauna is greatly influenced by processes affecting the fate of planktonic larvae and variable settlement (Bell and Westoby 1986; Hovel et al. 2002).

With the notable exceptions of a few taxa, for example, green turtles, manatees and parrot fish, direct herbivory on seagrasses is uncommon and most of the energy flow is through detritivores, infauna, epifaunal grazers and carnivores (Zieman 1982). In general, the predominant prey items for juvenile fish are small invertebrates, mainly crustaceans, with the most important food categories being amphipods, copepods and shrimps, all of which are very common and abundant in seagrass beds and depend to a large extent on the epiphytes growing in the seagrass canopy for their energy.

Seagrasses also play a less direct but equally important role as essential fish habitat by influencing the environment they grow in as well as adjacent environments. By affecting flow velocity and turbulence within their canopies, they create an environment favorable to settlement of fish and fish food. Organic and inorganic particles settle into the meadows providing nutrients and food, enriching the environment and enhancing secondary production. In turn, the substrate is stabilized, nutrients are temporarily conserved within the meadows and water quality is improved by the presence of seagrass. These ecological services enhance the environmental conditions favoring high rates of primary and secondary production in support of healthy and abundant fish communities. Sediment stabilization by seagrasses plays an important role in protecting adjacent subtidal environments from receiving excessive sediment deposition. This is especially important for coral reefs that are very sensitive to turbidity and sedimentation. The feedback for these indirect effects is the health and secondary production of fish species residing in these adjacent habitats.

Seagrass meadows are sub-systems of larger coastal marine and estuarine ecosystems and as such they are an essential component of ecosystem based fishery management. In tropical ecosystems of the South Atlantic reefs, mangroves, unvegetated bottom and seagrasses are all physically, chemically and biologically connected. Reefs dissipate wave energy and promote physical conditions promoting the growth the seagrasses and mangroves, both of which filter sediments and protect reefs. Similar interconnectivity occurs in temperate South Atlantic estuaries, where the wetlands are represented by salt marsh and the reefs are principally shell bottom. Positive feedbacks in the context of the coastal ecosystem are critical to the diversity and abundance of fish, food and environmental quality supporting fish growth. Thus we can conclude that even though some fish species utilize or depend directly on coral and oyster reefs, mangroves, salt marshes, unvegetated substrates or intertidal flats, there are important direct and indirect dependencies on and connectivity to seagrass habitats (Duffy, 2006).

From the standpoint of essential fish habitat, being submerged most, if not all of the time, seagrasses are available to fishery organisms for extended periods. There has been a growth of research over the past 30 years trying to understand and quantify functional values of seagrass ecosystems. Experiments and observations have shown that juvenile and adult invertebrates and fishes as well as their food sources utilize seagrass beds extensively. In fact, the habitat heterogeneity of seagrass meadows, the plant biomass, and the surface area enhance faunal abundances. Predator-prey relationships in seagrass beds are influenced by canopy structure, shoot density, and surface area. Blade density interferes with the efficiency of foraging predators and the reduction of light within the leafy canopy further conceals small prey that includes young-of-the-year of many ecologically and economically important species. Additionally, some organisms can orient themselves with the seagrass blades and camouflage themselves by changing coloration. The food availability within grass beds for young stages of managed species may be virtually unlimited. These attributes are particularity beneficial to the nursery function of seagrass beds.

The seasonal patterns of reproduction and development of many temperate fishery species coincide with seasonal abundances of seagrasses (ASMFC 1997). It has been concluded in several studies that, although juvenile fish and shellfish can use other types of habitat, many estuarine species rely on seagrasses for either part of their life history or some aspect of their nutrition, and that the loss or reduction of this habitat will produce concomitant declines in juvenile fish settlement. Thus, this habitat type is essential to many species of commercial, recreational and ecologically important shellfish and finfish. In the South Atlantic, SAV was specifically designated as EFH for red drum, the snapper-grouper complex, and shrimp.

It is difficult to put an economic value to ecosystem services provided by seagrass habitat. Fl DEP estimated that each acre of seagrass has an economic value of approximately $20,500/year (equates $55.4 billion statewide) by providing essential fish habitat that supports statewide commercial fishing industry valued at over $124 billion/year, as well as recreational fishing and ecotourism activities (FFWCC 2003).

3.2.4 Oyster Reefs and Shell Banks

Description and Distribution

Reef-forming Species

In the western Atlantic, oysters, mussels, and one genus of gastropod build three-dimensional structures that are commonly called reefs (Figure 3.2-14). Wood (1998, 1999) reviews the term 'reef,' and discusses its origin and those taxa and concepts that relate to reefs. The term derives from a Norse term 'rif,' or hazardous 'rib' of sand, rock, or biologically generated substrate near the surface. Wood (1999) includes the following as extant reef producers: corals, coralline and calcareous algae, sabellariid and serpulid polychaetes, oysters, vermetid gastropods, bryozoans, sponges, and stromatolites (i.e. *Cyanophytes*). Other terms such as "bars" and "beds" also refer to reef structures that are created by the organisms themselves. Holt et al. (1998) define 'biogenic reefs' as:

> *solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms.*

The focus here includes many shellfish species (e.g., mussels, dense clam beds) that may be classified somewhere between 'non-reef' and 'reef-forming" biotopes. Holt et al. (1998) try to characterize these biotopes, but this is a difficult task. Furthermore, researchers often refer to the structure that a species generates as a 'habitat,' 'biotope' or 'biogenic reef.' We focus on species that create unique and definable areas that are different from the surrounding unstructured sediments.

Although many species typically occur on shellfish reefs, the main structural component is formed by the attachment of many individual shellfish to each other. At least three species of oysters occur along the Atlantic coast, in addition to several mussel species and other molluscs (e.g., vermetid gastropods) (Abbott 1974). Of these, only the Eastern (or American) oyster (*Crassostrea virginica*), blue mussel (*Mytilus edulis*), and horse mussel (*Modiolus modiolus*) typically form reefs along the Atlantic coast. Currently, in the Chesapeake Bay and elsewhere, there is uncertainty over whether a non-native oyster from the Pacific (*C. ariakensis*) can serve both as a 'reef builder' and suitable fisheries resource substitute for *C. virginica* (NRC 2004; Ruesink et al. 2005).

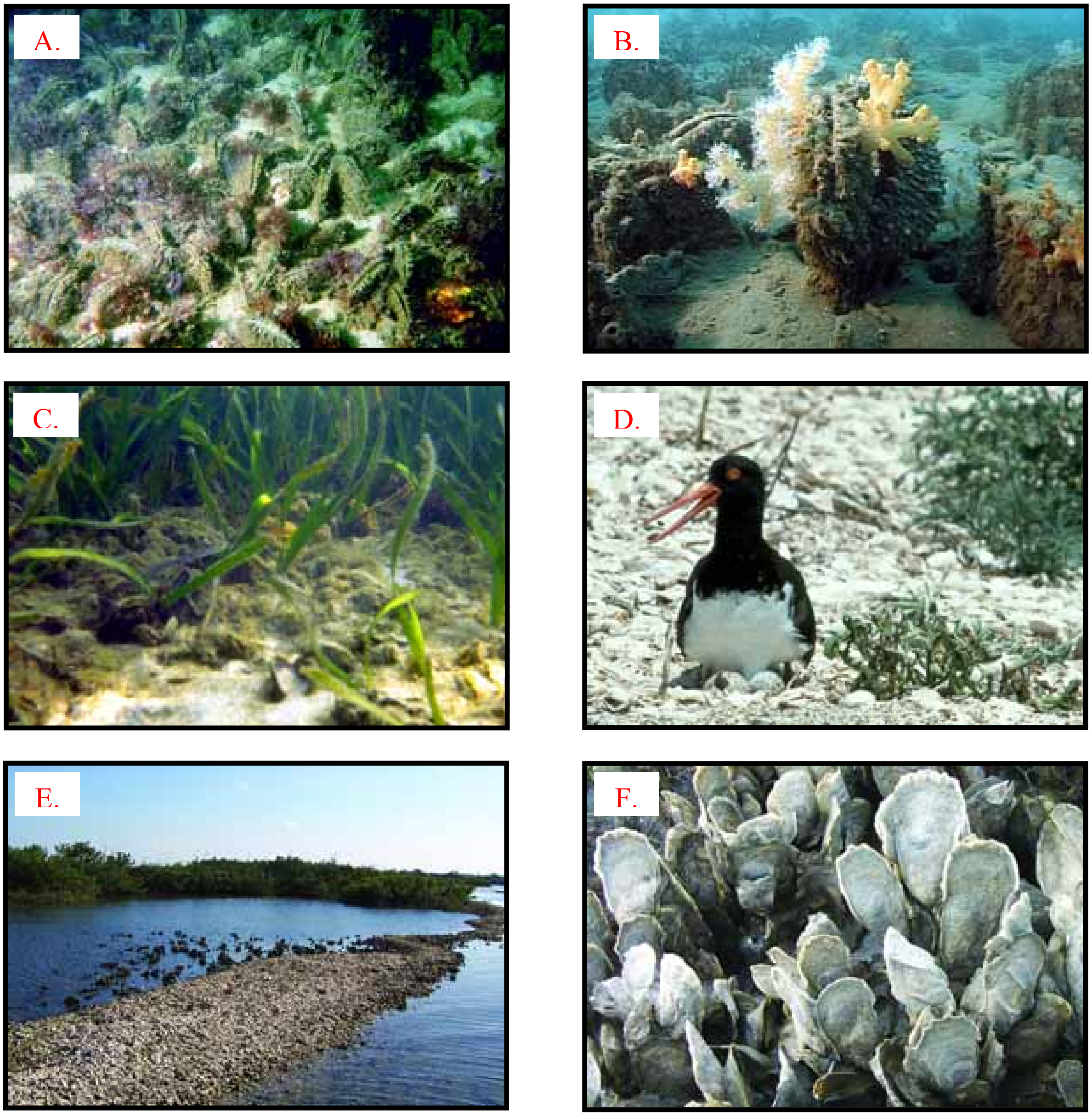


Figure 3.2-14. Examples of intertidal and subtidal shellfish habitats (Source: ASMFC, 2007). A and B: Pen shell, *Atrina zelandica*, aggregations in New Zealand (Source: Simon Thrush, National Institute of Water and Atmospheric Research, New Zealand); C: *Modiolus modiolus* reefs in St. Joe Bay, Florida (Source: Brad Peterson, State University of New York, Stony Brook); D: Nesting oyster catchers on intertidal shell accumulations along the Intracoastal Waterway (Source: Phil Wilkinson, South Carolina Department of Natural Resources); E: Intertidal oyster reefs at Canaveral National Seashore (Source: Loren Coen, South Carolina Department of Natural Resources); F: Close-up of intertidal oysters on South Carolina reefs (Source: Loren Coen, South Carolina Department of Natural Resources).

Estuarine and marine mussels

Reef-forming mussels include the *Mytilus* spp. complex (*M. edulis* and *M. trossulus*) and the horse mussel (*Modiolus modiolus*). *Mytilus* spp. (most widely recognized blue mussels) occur from Labrador to Cape Hatteras, North Carolina, on the western Atlantic coast (Abbott 1974; Suchanek 1978, 1985; Gosling 1992, 2003; Albrecht 1998; Newell 1989; Witman and Sebens 1988; Witman and Dayton 2001; Hellou and Law 2003). In many areas, *M. edulis* and *M. trossulus* are sympatric and hybridize (Riginos and Cunningham 2005). Additionally, the occurrence of *Mytilus galloprovincialis* (originally from the Mediterranean and now cultured throughout Europe and China) and a west coast species, *Mytilus californianus*, further complicate systems as invaders in many areas (McDonald and Koehn 1988; Varvio et al. 1988; Lobel et al. 1990; Seed 1992, 1995; Geller et al. 1994; Suchanek et al. 1997; Riginos and Cunningham 2005).

Gastropods of the family Vermetidae

The only habitat-forming snails on the Atlantic coast are species in the family Vermetidae. Vermetid snails cement themselves together to form dense reefs in intertidal and shallow subtidal waters from southern New England (rarely) to the tropics (Shier 1969; Safriel 1966, 1975; Abbott 1974; Safriel and Ben-Eliahu 1991; Dame et al. 2001). These uniquely cemented gastropods feed using a mucous net (video available at http://www.mbayaq.org/video/video_snailnet_feeding_qt.asp).

Worldwide vermetid snails form an often-conspicuous group of sessile gastropods living in shallow tropical and temperate reefs, commonly constructed on *Crassostrea virginica* shell accumulations. In southwestern Florida they extend intermittently as far north as Sarasota. In addition, some researchers have reported that they consider the species that was found in the Ten Thousand Islands area of southwestern Florida extinct, as the reefs were formed during the last interglacial period that drowned the beach ridges that make up the present-day islands.

There are a number of reef-forming vermetid species in Florida waters. The most common Florida species of vermetid snail, *Dendropoma corrodens*, is a small (10 mm) entrenching and encrusting species that is extremely abundant in the Florida Keys. Vermetid reef formation is restricted to the west coast of Florida, involving gastropods of the genus *Petaloconchus* (e.g., *P. macgintyi*) (less than 35 mm length). This genus is gregarious, and may form large (<1 m height) reef structures in some shallow, intertidal waters (Ortiz-Corps 1985).

In the Ten Thousand Islands area of Florida, longshore currents carry sand and shells to areas suitable for oysters to become established. These oyster reefs then provide stable substrate for mangroves, another important nursery habitat, to take hold (Lodge 1998). In some areas it has been hypothesized that vermetid gastropod reefs provide a similar substrate for mangrove initiation (Davis 1997). Unfortunately, some researchers note that vermetids appear to be in global decline (R. Bieler, Field Museum of Natural History, personal communication).

Aggregations of Living Shellfish

The term “aggregation” is used here to refer to shellfish species that are not attached to one another yet occur at densities sufficient to provide structural habitat for other organisms (Figure 3.2-14, Plate D). The term ‘bed’ is also sometimes used to refer to the same type of structure. Three groups of bivalves— scallops, pen shells, and *Rangia* —form habitat in this way (Figure 3.2-14). Although not molluscan, brachiopods also form dense aggregations that function like other molluscan species.

The major habitat-forming scallops that occur along the Atlantic and Gulf coasts are the bay scallop (*Argopecten irradians* with several recognized subspecies), calico scallop (*Argopecten gibbus*), and sea scallop (*Placopecten magellanicus*) (Bourne 1964; Shumway 1991; Blake and Graves 1995).

Pen shells (family Pinnidae) are large bivalves that bury partly into the substrate and are anchored by a substantial byssus (long, fine, silky filament). The upper portion of the shell protrudes above the substrate (often referred to as 'emergent shellfish beds'), which provides habitat for other organisms when they occur in sufficient densities (Figure 3.2-14, Plates A & B). Three species of pen shell occur along the Atlantic coast of the Americas: the saw-toothed pen shell (*Atrina serrata*), the amber pen shell (*Pinna carnea*), and the stiff pen shell (*Atrina rigida*) (Abbott 1974).

The saw-toothed pen shell, *A. serrata,* is typically found in sandy mud at depths of up to 6 m. It ranges from North Carolina to Texas and northern South America, and is relatively common in many areas in North Carolina (Abbott 1974). Several recent studies have shown that pen shells are adept at repairing damage in a short time, pointing to potentially interesting resource allocation issues (e.g., cost of shell repair) with regard to this relatively large infaunal organism (T. Alphin, University of North Carolina at Wilmington, personal communication). Many small shrimp and crab species spend their adult lives in the mantle cavity of this species and other pen shells, where they find refuge and feed on particles brought into the mantle cavity (Abbott 1974).

Although the amber pen shell, *P. carnea,* is generally found in sandy areas with depths up to 4 m, it rarely is found in the intertidal zone. It ranges from southeastern Florida to northern South America. Finally, *A. rigida* is common in sandy muds from low intertidal to 27 m in depth. It ranges from North Carolina to southern Florida and the West Indies (Abbott 1974).

Shell Accumulations

The shells of dead molluscs sometimes accumulate in sufficient quantities to provide important habitat. The term 'shell hash' refers to accumulations consisting mostly of pieces of broken shell (Anderson et al. 1979; Street et al. 2005), although this hash can also be composed of intact small bivalves and gastropod shells (e.g., Sanibel Island, FL).

Shell accumulations can occur from estuaries out to the continental slope, with several species present in each zone (Stanley and Dewitt 1983, Stanley 1985, Newell and Hidu 1986, Rice et al. 1989, MacKenzie and McLaughlin 2000, Kraeuter et al. 2003). For accumulations of smaller molluscs, we know little or nothing about their importance (W. Arnold, Florida Fish and Wildlife Research Institute, personal communication).

Accumulations of eastern oyster shells are a common feature in the intertidal zone of many southern estuaries, particularly along waterways impacted by wind and boat wakes (Figure 3.2-14, Plate D) (Anderson et al. 1979; Bahr and Lanier 1981; Grizzle et al. 2002). The dead shells of blue mussels (*Mytilus* spp.) occur intertidally in some northern estuaries. These accumulations, sometimes extending well above the high tide line, have not been well studied.

Subtidal shell accumulations, however, provide habitat for many species of commercially and recreationally important fish (Auster et al. 1991, 1995; Holt et al. 1998).

Ecological Role and Function

The ecological processes that depend on the above characteristics of shellfish habitat can be thought of as "ecosystem services." Hence, in addition to their direct habitat-related value for managed species, shellfish habitats provide important services for the ecosystem as a whole. Three of the most important of these services are discussed in more detail below: refuge, benthic-pelagic coupling, and erosion reduction (or shoreline protection).

Refuge

The term refuge is used here to describe the protective function that shellfish habitat provides for the shellfish themselves, as well as for other organisms that occur in shellfish habitat. This ecosystem service largely results from the increase in structural complexity in shellfish habitat compared to surrounding areas (particularly soft sediments). In other habitats, such as seagrasses or salt marshes, the concept of structural complexity is often associated with the notion of "nursery areas," which refer to places where juvenile invertebrates and fish are protected from predators (Lindberg and Marshall 1984; Heck et al. 1995; Benaka 1999; Halpern et al. 2001; Williams and Heck 2001; Beck et al. 2003; Heck et al. 2003; Minello et al. 2003). Shellfish habitat plays a role similar to seagrasses and other structurally complex habitats in this respect. Most of the research dealing with these topics for shellfish habitat has been done on the reef-forming species, but some information is available for shellfish aggregations and shell accumulations.

Benthic-pelagic coupling

This term refers to the transfer of materials and energy between the bottom community and the water column. It is probably most often used to refer to the overall effect of suspension feeders as they remove suspended particulates from the water column (Dame 1996). The result is a transfer of materials and energy from the water column to the benthos (Frechette et al. 1989; Meyer and Townsend 2000; Cummings et al. 2001; Dame et al. 2001; Ellis et al. 2002).

These feeding activities also typically cause a reduction in turbidity of the water column which has a positive impact on submerged aquatic vegetation (SAV), allowing more light penetration and higher rates of photosynthesis (Meyer and Townsend 2000). The shellfish release ammonia and other metabolites that are nutrients for the SAV. Therefore, SAV (Peterson and Heck 1999, 2001a, 2001b; Williams and Heck 2001; Heck and Orth 2006) and oyster reefs potentially play mutually beneficial roles (Heck 1987; Newell 1988; Dame 1996; Dame et al. 2001; Newell and Koch 2004) (also see Pomeroy et al. 2006 for a different perspective).

Oyster reefs are likely to reduce eutrophication by mediating water column phytoplankton dynamics and denitrification (Dame 1996; Newell et al. 2002; Newell 2004). A decrease in oysters in the Chesapeake Bay has led to increased phytoplankton numbers and reduced competition with zooplankton. An increase in zooplankton leads to a rise in predators, such as ctenophores and jellyfish. An increase in phytoplankton also leads to a microbial shift and anoxic conditions of deeper waters in areas such as the Chesapeake Bay (Ulanowicz and Tuttle 1992; Newell 1988) (also see Pomeroy et al. 2006 for another view). Models have shown that an increase in oyster abundance would reduce phytoplankton primary productivity and secondary gelatinous consumers (e.g., ctenophores) to historically low levels (Ulanowicz and Tuttle 1992).

Erosion reduction

Estuaries in many areas are threatened by increased coastal population growth and associated industrial, residential, and recreational development and utilization (Vernberg et al. 1999). One major area of recreational growth has been in the number of people with Class A (< 16 ft) and Class 1 (16 to 25 feet) motorized boats utilizing these waterways (NMMA 2004). Some problems related to this increase in the number of small boats have been well documented (Crawford et al. 1998; Cyr 1998; Backhurst and Cole 2000; Bauer et al. 2002; Kennish 2002). For example, increases in seagrass scarring from boat propellers and the number of marine mammal collisions are both positively correlated with increased boating activity (R. Virnstein, personal communication; Sargent et al. 1995).

However, little is known about the direct and indirect impacts of boating on other critical estuarine habitats in the landscape, such as intertidal oyster reefs (Grizzle et al. 2002; Coen and Fisher 2002; Coen and Bolton-Warberg 2003, 2005; Piazza et al. 2005; Wall et al. 2005). Those areas dominated by intertidal oyster reefs form a protective breakwater for fringing *Spartina* marshes, retarding shoreline erosion (Coen and Fischer 2002; Coen and Bolton-Warberg 2005).

Additionally, shoreline erosion in tidal channels is an issue in many states (Cyr 1998; Gabet 1998). Undercutting by wind waves and boat impacts can cause slumping (calving) of large masses of sediment embedded with *Spartina* (Gabet 1998; Chose 1999; Piazza et al. 2005). *Spartina* has been documented to be an important habitat for estuarine productivity (e.g., as a feeding ground for juvenile fishes and their prey) and is known to perform many other ecological functions, such as buffering run-off (Weinstein and Kreeger 2000).

Data collected by researchers from the South Carolina Department of Natural Resources noted significant shoreline losses at numerous study sites (n = 11) across South Carolina (Coen and Bolton-Warberg 2005). By reducing erosion, oyster reefs reduce vegetation loss and preserve other habitat types (Meyer and Townsend 2000). They also stabilize creek banks and help to reduce erosion of marshes (Meyer et al. 1997; Chose 1999; Coen and Fischer 2002; Breitburg et al. 2000; Coen and Bolton-Warberg 2003, 2005; Piazza et al. 2005), but may be easily impacted by boat wake or storm damage (Grizzle et al. 2002; Coen and Bolton-Warberg 2005).

Research on recreational boating impacts on estuarine species is surprisingly still in its infancy (Anderson 1976, 2000; Kennish 2002; Bishop 2003, 2004, 2007; Bishop and Chapman 2004). Productivity, diversity, and survival of estuaries in the southeastern United States are threatened by explosive coastal population growth and associated industrial, residential and recreational development and utilization (Vernberg et al. 1999). In spite of the potentially far excursion distances of motorboats, and the large number of boats on the water on any given day, sparse data exist to quantitatively determine the impact of boat wakes on intertidal organisms.

In conclusion, it should be noted that each of the four types of shellfish habitats differ with respect to their major characteristics and the ecosystem services they provide. Shellfish reefs typically provide the most in the way of services because they consist largely of live animals that provide a food source for many fish and invertebrates, and typically have significant vertical structure. Shellfish aggregations consist mainly of live animals but typically do not occur at densities as high, or with vertical structure as extensive, as shellfish reefs. Shellfish accumulations consist only of the dead shell remains, but they provide hard substrate and may have significant vertical structure. There is a rich literature that documents the importance of all four types of shellfish habitat to many species of fish and invertebrates, including most managed species managed.

Habitat utilization

Shell bottom provides critical fisheries habitat not only for oysters, but also for recreationally and commercially important finfish, other mollusks, and crustaceans. The ecological functions of oyster reefs related to oyster production are well known and accepted (Coen et al. 1999). These functions include aggregation of spawning stock, chemical cues for successful spat settlement, and refuge from predators and siltation. Oysters have also been described as "ecosystem engineers that create biogenic reef habitat important to estuarine biodiversity, benthic-pelagic coupling, and fishery production" (Lenihan and Peterson 1998).

Data quantifying fish use of habitats vary from presence/absence and numerical abundance, to actual fish production value. In North Carolina, 18 fishery species have been documented utilizing both natural and restored oyster reefs in Pamlico Sound, including Atlantic croaker, southern flounder, Spanish mackerel, spotted seatrout, weakfish, American eel, and black sea bass (Lenihan et al. 2001). Numerical abundance and production compared to other habitats provides additional information on the importance of habitat for fish. The species found most abundantly on oyster reefs compared to adjacent soft bottom were silver perch, sheepshead, pigfish, pinfish, toadfish, and Atlantic croaker. Southern flounder was collected on both oyster reefs and adjacent soft bottom areas, while bluefish and Atlantic menhaden were not collected near oyster reefs (Lenihan et al. 2001).

Several studies have found higher abundance and diversity of fish on shell bottom than adjacent soft bottom, particularly pinfish, blue crabs, and grass shrimp (Harding and Mann 1999; Posey et al. 1999; Lenihan et al. 2001). A study in Back Sound also found that crabs were more abundant on shell bottom than restored SAV beds (Elis et al. 1996). Breitburg (1998) concluded that the importance of shell bottom to highly mobile species is very likely underestimated, partially due to the difficulty in sampling oyster beds.

Peterson et al. (2003a) estimated the amount of fish production that shell bottom provides in addition to adjacent soft bottom habitats. Using results from numerous studies, they compared the density of fish at different life stages on oyster reefs and adjacent soft bottom habitats. The published growth rates of species were then used to determine the amount of production gained from shell bottom. The species were separated into recruitment-enhanced, growth-enhanced, and not enhanced groups. Recruitment-enhanced species are those having early life stages showing almost exclusive association with shell bottom. For other species with higher abundance in shell bottom, diet and life history studies were used to determine the fraction of their production associated with the consumption of shell bottom-enhanced species. Species consuming relatively more shell bottom-enhanced species were classified as growth-enhanced. Analysis of the studies revealed that every $10m^2$ of newly constructed oyster reef in the southeast United

States is expected to yield a benefit of an additional 2.6 kg of fish production per year for the lifetime of the reef (Peterson et al. 2003a).

Fish that utilize shell bottom can be classified into three categories: resident, transient, and facultative (Coen et al. 1999; Lowery and Paynter 2002). Resident species live on shell bottom and depend on it as their primary habitat. Transient species are wide-ranging species that use shell bottom for refuge and forage along with other habitats. Facultative species depend on shell bottom for food, but utilize other habitats with vertical relief or shelter sites.

At least seven fish species have been identified as resident species—naked goby, striped blenny, feather blenny, freckled blenny, skilletfish, and oyster toadfish (Coen et al. 1999; Lowery and Paynter 2002). These species were also considered recruitment-enhanced by Peterson et al. (2003a). Resident fish are important prey for transient and facultative predator species (Coen et al. 1999). For example, Breitburg (1998) found high densities of juvenile striped bass (15.4 individuals/m^2 of reef surface) aggregating near the reef surface feeding on naked goby larvae congregated on the down-current side of the reef. Other common predator species sampled on oyster reefs in North Carolina are red and black drum, Atlantic croaker, sheepshead, weakfish, spotted seatrout, summer and southern flounder, blue crab, and oyster toadfish. Of these species, however, only sheepshead, southern flounder, and oyster toadfish were considered shell bottom-enhanced by Peterson et al. (2003a). Production of black drum, Atlantic croaker, blue crab, and summer flounder were classified as not enhanced by shell bottom. Oyster reefs in higher salinity waters are critical habitat for predators such as juvenile gag, snappers (*Lutjanus* spp.) and stone crab (Wenner et al. 1996; Peterson et al. 2003a).

There is some variation in fish use among salinity gradients as well. Oyster reefs in higher salinity waters tend to support a greater number of associated species than reefs in lower salinity waters (Sandifer et al. 1980). Studies summarized by Coen et al. (1999), which included work in North Carolina, identified 72 facultative, resident and transient fish species in close proximity to oyster reefs. The ASMFC-managed species categorized as transient and also important to North Carolina’s coastal fisheries are American eel, Atlantic croaker, Atlantic menhaden, black sea bass, bluefish, red drum, spot, striped bass, summer flounder, tautog, and weakfish. Only black sea bass and tautog were considered shell-bottom enhanced by Peterson et al. (2003a).

A partial list of macrofaunal species observed in collections from oyster habitat is provided in Table 3.2-6. Those species that use shell bottom as spawning and/or nursery areas are identified, as are those species that forage on shell bottom habitat and/or use it as a refuge (SAFMC, 1998a; Lenihan et al., 1998; Coen et al., 1999; Grabowski et al., 2000). More than 30 species are listed in Table 2.6, and there are many more not listed, emphasizing the importance of shell bottom as fisheries habitat.

Table 3.2-6. Partial listing of finfish and shellfish species observed in collections from shell bottom in North Carolina, and ecological functions provided by the habitat (Source: Street et al. 2005).

Species*	Shell Bottom Functions [1]					Fishery [2]	Stock Status [3]
	Refuge	Spawning	Nursery	Foraging	Corridor		
ANADROMOUS & CATADROMOUS FISH							
American eel	X		X	X	X	X	U
Striped bass			**X**	**X**		**X**	**V- Albemarle Sound, Atlantic Ocean, O- Central/Southern**
ESTUARINE AND INLET SPAWNING AND NURSERY							
Anchovies (striped, bay)		**X**	**X**	**X**			
Blennies	**X**	**X**	**X**	**X**			
Black drum				**X**		**X**	
Blue crab	**X**	**X**	**X**	**X**	**X**	**X**	**C**
Oyster	**X**	**X**	**X**	**X**		**X**	**C**
Gobies	**X**	**X**	**X**	**X**			
Grass shrimp	**X**	**X**	**X**	**X**			
Hard clam	**X**	**X**	**X**	**X**		**X**	**U**
Mummichog	X	X			X		
Oyster toadfish	**X**	**X**	**X**	**X**		**X**	
Red drum	**X**		**X**	**X**	**X**	**X**	**R**
Sheepshead minnow		**X**		**X**			
Silversides				**X**			
Skilletfish	**X**		**X**	**X**			
Spotted seatrout				**X**		**X**	**V**
Stone crab	**X**		**X**	**X**		**X**	
Weakfish	X		X	X	X	X	V
MARINE SPAWNING , LOW-HIGH SALINITY NURSERY							
Atlantic croaker				X		X	C
Brown shrimp	**X**		**X**	**X**	**X**	**X**	**V**
Southern flounder				**X**		**X**	**O**
Spot	X		X	X	X	X	V
Striped mullet				X		X	C
MARINE SPAWNING , HIGH SALINITY NURSERY							
Atlantic spadefish						X	C [4]
Black sea bass	**X**		**X**	**X**	**X**	**X**	**V- north of Hatteras, O- south of Hatteras**
Gag	**X**		**X**	**X**	**X**	**X**	**V**
Gulf flounder						X	
Pigfish				**X**		**X**	
Pinfish	**X**		**X**	**X**	**X**	**X**	
Pink shrimp	**X**		**X**	**X**	**X**	**X**	**V**
Sheephead	**X**		**X**	**X**	**X**	**X**	**C** [4]
Spanish mackerel						X	V
Summer flounder	X			X	X	X	V

* Scientific names listed in Appendix I. Names in **bold** font are species whose relative abundances have been reported in the literature as being generally higher in shell bottom than in other habitats. Note that lack of bolding does not imply non-selective use of the habitat, just a lack of information.

[1] Sources: Pattilo et al. 1997; SAFMC 1998; Lenihan et al. 1998, 2001; Coen et al. 1999; Grabowski et al. 2000; Peterson et al. 2003

[2] Existing commercial or recreational fishery. Fishery and non-fishery species are also important as prey

[3] V=viable, R=recovering, C=Concern, O=overfished, U=unknown (DMF 2003a).

[4] Status of reef fish complex as a whole. Sheepshead and Atlantic spadefish have not been evaluated in NC.

Resident species, such as gobies (naked and green), Atlantic midshipman, and northern pipefish depend on shell bottom as breeding habitat (Hardy 1978a and b; Johnson 1978; Coen et al. 1999). Other species documented to spawn on shell bottom include the oyster toadfish, mummichog, sheepshead minnow, eastern oyster, grass shrimp, and hard clams (NOAA 2001). Toadfish attach their eggs to the underside of oyster shells, whereas gobies, blennies, and skilletfish place their eggs in recently dead oyster shell (Coen et al. 1999). Well-developed oyster reefs with clean oyster shells in a variety of sizes were shown to accommodate reproduction by the greatest densities of all resident species (Breitburg 1998).

Shell bottom protects oyster spat and other juvenile bivalves, finfish and crustaceans from predators. Juvenile clams, in particular, settle in shell substrate for the protection it provides (Wells 1957; MacKenzie 1977; Peterson 1982; DMF 2001b). The nursery area function of shell bottom was demonstrated by Eggleston et al. (1998) who found that juvenile blue crabs and grass shrimp were equally abundant on shell bottom and SAV in Back Sound, North Carolina. Twelve of the 18 mobile and economically important coastal fisheries species sampled by Lenihan et al. (2001) on natural and restored oyster reefs in Pamlico Sound were juveniles.

In a study where shell structure was added to mud flat reefs, juvenile fish abundance increased on the augmented reefs compared to surrounding soft bottom (Grabowski et al. 2000). The study also found that this initial increase was higher than increases that occurred when SAV and/or salt marsh were added in the same area. The ASMFC considers shell bottom as important nursery habitat for juvenile fish such as sheepshead, gag, snappers, stone and blue crabs, and penaeid shrimps (Lowery and Paynter 2002). An analysis by Peterson et al. (2003a) confirmed that sheepshead, gag, and stone crab were recruitment enhanced, as well as many non-fishery species, including anchovies, blennies, gobies, oyster toadfish, and skilletfish.

While oyster reefs are the most recognized shell bottom habitat, shell hash concentrations on tidal creek bottoms provide important nursery habitat for young fish. For example, the preferred habitat of juvenile drum species in South Carolina is high marsh areas with shell hash and mud bottoms (Daniel 1988). However, the extent of shell hash in North Carolina tidal creeks is currently unknown; known locations of shell hash include concentrations along the Intracoastal Waterway. The nursery value of designated nursery areas could be enhanced by low-density plantings of cultch material. However, the enhancement of fish stocks provided by planting could be negated if recruitment is not limiting the adult population. The recruitment enhancement provided by low-density cultch planting in nursery areas should be evaluated.

A group of important species that are largely understudied throughout their range, but includes important members of intertidal and subtidal oyster reef communities, are the grass (Caridean) shrimp species within the genus *Palaemonetes*. Grass shrimp are found in large numbers in estuarine waters along the Atlantic and Gulf coasts, where they occur from Massachusetts to Texas. They are a very common estuarine species in southeastern marshes and tidal creeks where they are usually associated with beds of submerged or emergent vegetation, oyster reef habitats, or structures such as oyster shell, fouling communities, woody debris (Ruiz et al. 1993), and docks or pilings (Coen et al. 1981). Caridean shrimp are rarely larger than 5 cm; their small size differentiates them from commercial shrimp, such as the penaieds and pendalids.

Grass shrimp are an important species from an ecological perspective because they are instrumental in transporting energy and nutrients between trophic levels in the coastal food web. Grass shrimp are consumed in large quantities by commercially important fishes and forage species, including spotted seatrout, red drum, and mummichogs (*Fundulus heteroclitus*) (Heck and Thoman 1981; Anderson 1985; Wenner et al. 1990; Posey and Hines 1991; Wenner and Archambault 1996).

Although there are no estimates of population sizes of grass shrimp, they are amongst the most widely distributed, abundant, and conspicuous of the shallow water benthic macroinvertebrates in our estuaries, often reaching hundreds to thousands per square meter (Leight et al. 2005; Coen and Luckenbach 2000; Coen et al. 2006a). Grass shrimp can inhabit very shallow areas near the margins of intertidal habitats (e.g., marsh, mudflats, oyster reefs), but have been reported at depths as great as 15 meters. In winter during temperature lows, and in summer when water temperatures approach seasonal highs, daggerblade grass shrimp may move from shallow to relatively deeper water. The extent of the movement of grass shrimp among various depths often coincides with the distribution of oyster shell substrates, which, in some waters, are preferred by both *P. vulgaris* and *P. pugio*. They are abundant in these structured estuarine and marine habitats as shellfish habitats provide abundant food and protection from predators (Thorp 1976; Coen et al. 1981; Heck and Thoman 1981; Heck and Crowder 1991).

Consequently, the association of shellfish habitats with primary producers and consumers may prove quite significant, given the importance of low trophic level species as food for managed species.

Shell bottom provides important foraging area for a variety of aquatic organisms. Fish, shrimp and crabs forage on the worms, algae, crustaceans, mollusks, and other invertebrates present on and in shell bottom habitat. Concentrations of prey organisms among the shell attract both specialized and opportunistic predators. Eggs from oysters and other organisms, and larvae from species belonging to the oyster shell bottom community, are eaten by protozoans, jellyfishes, ctenophores, hydroids, worms, mollusks, adult and larval crustaceans, and fishes (Loosanoff 1965). Blue crabs forage heavily on oyster reefs (Menzel and Hopkins 1955; Krantz and Chamberlin 1978; Mann and Harding 1997). Stomach contents of common finfish predators sampled near shell bottom in Middle Marsh, North Carolina, included fish, shrimp, tanaids, amphipods, isopods, polychaetes, bivalves, gastropods, and tunicates, as well as plant, algal and detrital material (Grabowski et al. 2000).

Grabowski et al. (2000) calculated an index of reef affinity (association) for fish species and analyzed the relative proportion of stomach contents originating from oyster reef versus non-reef habitats. Results showed:

- Pigfish and pinfish foraged more on reefs (amphipods, bivalves, gastropods and polychaetes).
- The ubiquitous spot foraged on both reef and non-reef habitats.
- Gulf and southern flounder foraged on species slightly more common on reefs.
- Blacktip sharks, spotted seatrout, and bluefish exhibited a feeding preference for oyster reef prey (fish, shrimp and crabs).
- Red drum foraged slightly more off reefs.

- Blacknose sharks rarely foraged on reef habitats.

The growth-enhanced species/groups identified in Peterson et al. (2003a) included sheepshead minnow, silversides, pigfish, southern flounder, and black sea bass. These results differ somewhat from those of Grabowski et al. (2000). The discrepancies between Peterson et al. (2003a) and Grabowski et al. (2000) could be due to regional differences in fish habitat use, or other unknown factors. Sheepshead also have an affinity for slow or sessile invertebrates found abundantly on shell bottom (Pattilo et al. 1997).

Oyster reefs are also a foraging ground for many juvenile and adult turtle species. Schmid (1998) found that both the Kemp's ridley and loggerhead sea turtles feed on organisms that inhabit the reef. Kemp's ridley turtles feed on the stone crabs (*Menippe* spp.) and blue crabs (*Callinectes sapidus*) found near the reef's surface. Loggerheads also feed on molluscs. Schmid (1998) also found that Kemp's ridleys will return to the same oyster reef for up to four years.

Another important species that utilizes intertidal and subtidal oyster reefs as foraging grounds is the blue crab, *Callinectes sapidus* (Coen et al. 1999b). Blue crabs forage heavily on oyster reefs (Mann and Harding 1997; Krantz and Chamberlin 1978), including consuming oyster spat as juveniles. A study by Menzel and Hopkins (1955) showed that juvenile blue crabs consumed as many as 19 juvenile oysters (or spat) per day.

Numerous mammals and birds directly and indirectly utilize intertidal oyster reef habitats and washed oyster shell accumulations, particularly along the IWW (Sanders et al. 2004). These include *Procyon lotor* (raccoon), and birds such as *Haematopus palliates* (American oyster catcher), *Egretta tricolor* (Tricolored Heron), *Nyctanassa violacea* (Yellow-crowned Night Heron), *Nycticorax nycticorax* (Black Heron), *Casmerodius albus* (Great Egret), *Egretta thula* (Snowy Egret), *Limosa fedoa* (Marbled Godwit), *Catoptrophorus semipalmatus* (Willet), *Pluvialis squatarola* (Black-bellied Plover), *Calidris pusilla* (Semipalmated Sandpiper), *Calidris mauri* (Western Sandpiper), *Arenaria interpres* (Ruddy Turnstone), *Tringa melanoleuca* (Greater Yellowleg), and *Tringa flavipes* (Lesser Yellowleg).

Some recent observations in SC suggest that a single oystercatcher may be able to consume over 100 adult oysters per day on intertidal reefs (F. Sanders, South Carolina Department of Natural Resources, personal communication).

Corridor and Connectivity

Shell bottom serves as a nearshore corridor to other fish habitats, such as salt marsh and SAV for finfish and crustaceans; therefore, it plays a significant ecological role in landscape-level processes (Coen et al. 1999; Micheli and Peterson 1999). Vicinity (isolation) and connectivity of intertidal oyster reefs to other fish habitats, especially SAV, are two factors that affect fish utilization of shell bottom. For example, connectivity of oyster reefs to SAV enhanced blue crab predation, whereas isolation of oyster reefs enhanced hard clam survivorship (Micheli and Peterson 1999). In Middle Marsh, North Carolina, gag, gray snapper, and spottail pinfish preferred shell bottom habitat adjacent to SAV beds (Grabowski et al. 2000), allowing access to both refuge and prey.

Species composition and community structure

Eastern oyster (*Crassostrea virginica*)

The eastern oyster's range extends from the Gulf of St. Lawrence to Key Biscayne, and south to the West Indies and the Yucatan Peninsula in Mexico (Galtsoff 1964; Burrell 1986; Kennedy 1996; MacKenzie et al. 1997a). The eastern oyster is mainly an estuarine organism, but does occur in some near-shore coastal waters. These oysters grow sub-tidally throughout most of their range, but from southern North Carolina to northeastern Florida they occur predominately in the intertidal zone (Figure 2.14) (Bahr and Lanier 1981; Kennedy 1996; Kennedy and Sanford 1999; Burrell 1986, 1997; Coen and Luckenbach 2000; Luckenbach et al. 2005). Although they occur to a depth of 30 m, the oyster's primary habitat is in shallow water less than 6 m, or intertidal (1 m to 5 m) from North Carolina to Florida. A typical feature of *C. virginica* is their extremely variable shell morphology (Galtsoff 1964; Carriker 1996; Kent 1992). Oysters have indeterminate growth; in historical times, prior to the influence of harvesting and other biological and anthropogenic factors, they often grew to sizes significantly greater than what we see today (20 cm or larger shell height).

The preferred substrate for larval settlement is oyster shell, an adaptation that assures the proximity of other oysters, which is essential for successful future reproduction. Oysters are attached to the substrate or to each other by the left valve, which tends to be thicker and more deeply cupped than the right valve (Galstoff 1964; Kennedy 1996; Soniat et al. 2004). Thus, dense reefs are formed by the setting of successive generations of oysters on the shells of their predecessors (Figure 3.2-14). In some places, oyster shell can be several meters deep or more with live animals only on the surface layer.

Long-term reef development is a complex process that involves interactions among a variety of physical and biotic factors (Bahr and Lanier 1981; Kennedy and Sanford 1999; Coen and Luckenbach 2000). In southern Atlantic waters, a reef-like structure may be achieved in three to five years, but in northern waters the process is apparently much slower. The long-term dynamics of oyster reefs have not been well studied, but some reefs in the Chesapeake Bay have persisted for millennia (Smith et al. 2003). In part because estuaries are geologically ephemeral, oysters must cope with changes in sea level, sediment, and climate. In contrast, within the past 50 years, some intertidal reefs in Florida have been completely destroyed and displaced landward by dredging and/or boat wakes (Figure 3.2-15). Hurricanes have also been implicated in a few instances; for example, in the destruction of the windrows of shell in surf troughs along the Florida coast (Livingston et al. 1999; Grizzle et al. 2002; Walters et al. in press). Elsewhere, hurricanes may have significant impacts on shellfish habitats, particularly in shallow waters (Andrews 1973; Munden 1975; Lowery 1992; Dugas et al. 1998; Livingston et al. 1999; Perret et al. 1999). Bartol and Mann (1997) observed an increase in oyster survival when oysters settled in the interstitial spaces between shells below the reef surface. Additionally, vertically growing oysters in clusters on intertidal reefs provide oysters with a way to cope with siltation, so that they are not smothered (Coen et al. 1999a; Giotta 1999).

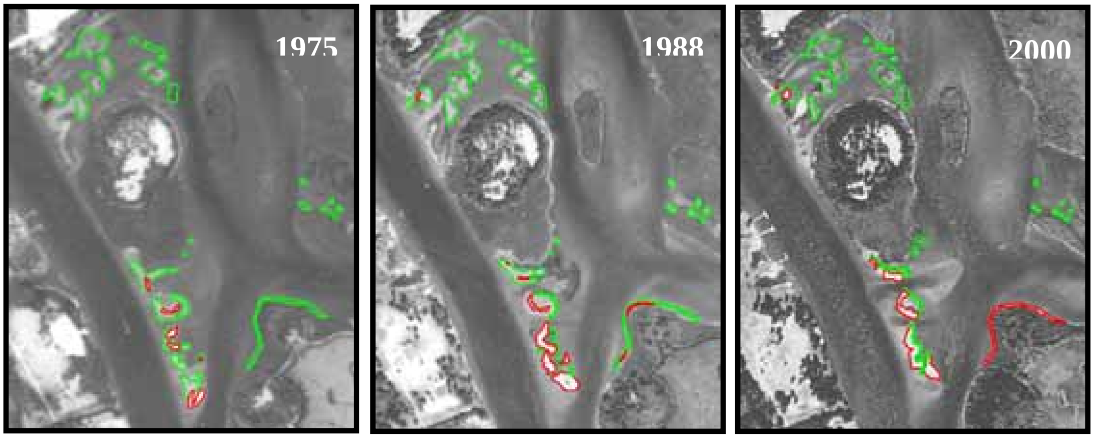


Figure 3.2-15. Time series of intertidal oyster reef changes in east-central Canaveral National Seashore (CANA), Florida (Source: ASMFC 2007). Aerial imagery showing increase in dead reef areas (red) compared to living (green) over time, most probably caused by increased boating activities (Source: Grizzle et al. 2002).

Caribbean mangrove oyster (*Crassostrea rhizophorae*)

The Caribbean mangrove oyster is restricted to the south Atlantic and Gulf coasts (Abbott 1974) and does not typically form reefs. *C. rhizophorae* is well adapted to the warmer tropical and subtropical temperatures in its native range (Bacon et al. 1991). *C. virginica* and *C. rhizophorae* oysters are closely related species (Buroker et al. 1979; Hedgecock and Okazaki 1984). Mangroves are typically the primary ‘hard’ substrate for attachment of these often common and flat oysters. Numerous other species of ‘mangrove oysters’ have been described, all in the genus *Crassostrea*. For all these species, information is extremely limited, with even less known on how they may enhance habitat complexity along the southern coast of Florida. *C. rhizophorae* is commercially important, can grow to marketable size (50 -70 mm shell height) in 4 to 8 months (Rodriguez and Frias 1992), and is currently cultivated in aquaculture facilities in the Caribbean (Littlewood 1988; Bacon et al. 1991; Newkirk and Field 1991).

Currently, there is very little information on the Caribbean mangrove oyster’s ecology (i.e. densities, filtering, etc.) or potential habitat value for other Florida mangrove-related species. However, it must be noted that the species adds considerable habitat to the recognized three-dimensional mangrove fish nurseries of the Carribbean (L. Stewart, University of Connecticut, personal communication). Presumably Caribbean mangrove oyster reefs are fouled by many different planktonic plant and animal species, thus providing a critically needed substrate for attachment.

In large part resulting from recent work on *Crassostrea ariakensis* in North Carolina (Grabowski et al. 2003, 2004; NRC 2004; Bishop et al. 2006; Carnegie et al. 2006; R. Carnegie, Virginia Institute of Marine Science, personal communication), researchers have begun to examine the dynamics of poorly studied native oyster species, such as the crested oyster (*Ostreola equestris*). Additional attention has been drawn to novel or endemic *Bonamia* spp. (newly described or observed) that may cause diseases in native or non-native species, or act as parasite reservoirs (Bishop et al. 2006; Carnegie et al. 2006; R. Carnegie, Virginia Institute of Marine Science, personal communication).

Blue mussels *(Mytilus spp.)*

Mytilus spp. occur mainly in shallow coastal waters and estuaries, and are most commonly considered a member of the fouling community because they are often found on rocks, pilings, and other hard substrates (King et al. 1990; Mathieson et al. 1991; Leichter and Witman 1997; Bertness 1999; Witman and Dayton 2001). In many areas mussels play an important role in benthic community structure (Bayne 1976; Witman 1985, 1987; Asmus and Asmus 1991; Lesser et al. 1991; Dame 1993, 1996; Hild and Günther 1999; Norén et al. 1999; Davenport et al. 2000). In some areas mussels also form dense reefs on hardbottom or on soft sediments in the intertidal and subtidal zones (Newell 1989; Nehls and Thiel 1993; Seed and Suchanek 1992; Seed 1996; Côté and Jelnikar 1999; Cranford and Hill 1999).

Blue mussel reef formation and development have not been well studied, but they are recognized as being important food and habitat providers for many species (Tsuchiya and Nishihira 1985, 1986; Witman 1985, 1987; Newell 1989; Asmus and Asmus 1991; Seed 1996; Reusch and Chapman 1997; Ragnarsson and Raffaelli 1999). Mussel consumers include crabs, lobsters, starfish, whelks, fish (e.g., tautog), and birds (e.g., ruddy turnstone, American and European oystercatchers) (Marsh 1986; Meire and Ervynck 1986; Raffaelli et al. 1990; Marsh and Wilkinson 1991; Nol and Humphrey 1994; Nagarajan et al. 2002; Sanders et al. 2004). Mussel reefs perform essentially the same functions as oyster reefs; they provide food, filtration, benthic-pelagic coupling, and physical habitat (Verwey 1952; Suchanek 1978, 1985; Wildish and Kristmanson 1984, 1997; Witman and Suchanek 1984; Dame 1996; Smaal and Hass 1997).

Horse mussel *(Modiolus modiolus)*

The horse mussel has a geographic distribution similar to the blue mussels, but occurs mainly in deeper waters on the continental shelf; however, it can be found in intertidal pools or attached to laminarian holdfasts (Holt et al. 1998). It is a widespread mussel, found throughout the northern hemisphere from the White Sea and Norway, off the Faroes and Iceland to at least as far south as the Bay of Biscay and occasionally North Africa. It is also found from Labrador to North Carolina in the Atlantic and from the Bering Sea south to Japan and California in the Pacific. It most commonly occurs partly buried in soft sediments, or attached by byssal threads to hard substrates where it forms clumps or extensive beds (or reefs) that vary in size, density, thickness, and form (Holt et al. 1998; Wildish et al. 1998).

Horse mussel recruitment is often low and may be variable in some populations (JNCC UK 1999). *M. modiolus* is a long-lived species, with some individuals living for 25 years or more. Juvenile *M. modiolus* are heavily preyed upon, especially by crabs and starfish, until they are 3 to 6 years old, at which point they normally reach a size refuge from most of their native predators.

American horse mussel *(Modiolus americanus)*

The American horse mussel is a common mussel that often forms dense associations within seagrass habitats (Figure 3.2-14, Plate C) (Peterson and Heck 1999, 2001a, 2001b). It ranges from South Carolina to the Gulf of Mexico and south to Brazil; it is also found in Bermuda. Adults can reach 100 mm shell height and they occur from the intertidal to approximately 6 m water depth. The American horse mussel can be found in densities as high as 2,000 individuals/m^2 with mean densities reaching 625 individuals/m^2 (Valentine and Heck 1993). However, these aggregations of American horse mussels are typically quite patchy (L.D. Coen, personal observation). Little is known about the broader ecological importance of the facultative mutualistic association of seagrass and shellfish, but work in St. Joe Bay, Florida in dense seagrass beds has shown a more complex interaction between these abundant filter-feeders and the *Thalassia* beds within which they reside. Specially, the mussels increase seagrass productivity through their filtering activities, changing nutrient availability through mechanisms such as biodeposition and reducing epiphyte loads on seagrasses (L. Coen, personal observation).

Ribbed mussel (*Geukensia demissa*)

The ribbed mussel is a relatively large mussel, growing to nearly 100 mm shell height. The ribbed mussel is found in coastal waters from the Gulf of St. Lawrence to Texas. It is common on both subtidal and intertidal oyster reef habitats (Van Dolah et al. 1999; Coen et al. 2004b; Luckenbach et al. 2005) and in salt marsh (Bertness 1980, 1984; Lutz and Castagna 1980; Bertness and Grosholz 1985). Unlike oysters, ribbed mussels have the ability to reattach if dislodged, which makes this species better able to adapt following a disturbance event.

The basic biology of the ribbed mussel is well understood, but little is known about its habitat value either alive or as dead articulated shells (Lent 1969; Seed 1980; Brousseau 1984; Kraus and Crow 1985; Hilbish 1987; Lin 1989a, 1989b, 1990, 1991; Wilbur and Hilbish 1989; Kemp et al. 1990; Langdon and Newell 1990; Sarver et al. 1992; Stiven and Gardner 1992; Franz 1993, 1996, 1997, 2001; Nielsen and Franz 1995; Kreeger and Newell 2000). Ribbed mussels attach by byssal threads to any hard substrate (like oyster shells and cordgrass stems) and protrude above the surface. Typically, ribbed mussels occur embedded in and amongst salt marsh sediments attached by byssal threads to each other and/or to *Spartina* spp. stalks.

Ribbed mussels occur throughout the mid- to low-intertidal regions in most southeastern estuaries. Upper intertidal limits are determined by both exposure to high temperatures and limited food availability during longer periods of tidal exposure. Lower intertidal limits are determined by the availability of effective refuge, mainly from crab predators. Although growth rates decline at higher shore levels, this is offset by increased survival (Bertness 1980; Bertness and Grosholz 1985; Stiven and Gardner 1992; Franz 2001).

A large volume of literature exists for ribbed mussels associated with salt marsh habitats on the east coast of the United States; however, much less is known about this mussel's association with oyster reefs. Researchers in South Carolina and Virginia (Coen et al. 1999a; Coen and Luckenbach 2000; Luckenbach et al. 2005) have noted large numbers of ribbed mussels often associated with intertidal and subtidal oyster reef habitats. In South Carolina, there are *G. desmissa* densities of over 500 individuals/m^2, cohabiting areas with one or more smaller (2.5 to 5 cm) mussel species (e.g., scorched mussel (*Brachidontes exustus*) and hooked mussel (*Ischadium recurvum*)). Scorched and hooked mussels can also occur at high densities, often exceeding ribbed mussel densities (L. Coen, personal observation). For example, at some restored South Carolina intertidal oyster sites, *B. exustus* densities exceeded 4,900 individuals/m^2 and *I. recurvum* densities reached 500 individuals/m^2. As a result of these high densities of individuals, mussels can be a significant nuisance species at many Gulf of Mexico oyster reef sites.

Green mussel (*Perna viridis*)

The green mussel is a recent invader to the Caribbean, Florida (Benson et al. 2001; Baker and Benson 2002), and Georgia (Power et al. 2004), reaching lengths up to 171.5 mm (J. Fajans, University of Florida, personal observation). This species should not be confused with two morphologically similar alien species, *P. perna* and *P. canaliculus* (Siddall 1980; Benson et al. 2001; Ingrao et al. 2001). Although the green mussel is overgrowing oyster reefs in Florida (Figure 3.2.16), and becoming a serious fouling problem in Florida and Georgia, it may ultimately generate a complex and important habitat not previously observed in the southeast (J. Fajans and S. Baker, University of Florida, personal communication). Recent (October 2006) collections in Charleston, South Carolina (D. Knott, South Carolina Department of Natural Resources, personal observation), collected *P. viridis*, resulting in a new northern range extension for this non-native fouling mussel species.

Figure 3.2-16. The green mussel, *Perna viridis* (Source: Jon Fajans, Keys Marine Lab, Long Key, Florida) (Source: ASMFC 2007).

Bay scallop (*Argopecten irradians*)

Bay scallops are found on the Atlantic and Gulf coasts from the north shore of Cape Cod, Massachusetts to Laguna Madre, Texas (Waller 1969; Fay et al. 1983). They can reach a maximum size of 60 to 70 mm. Seastars, wading birds, gulls, pinfish, lightning whelks, cow-nosed rays, crabs, starfish, and humans are among the numerous predators of the bay scallop (Peterson et al. 2001a). Scallops are hermaphroditic, with a single individual releasing sperm before eggs (Bricelj et al. 1987). Bay scallops reach sexual maturity within one year, spawning from August through October. The juvenile stage is reached after about 35 days post-fertilization, when they resemble a small adult in shape; their lifespan is less than two years (Peterson et al. 1989).

Bay scallops can migrate *en masse*. In many areas they have declined significantly (e.g., North Carolina). Red tides, often referred to as “harmful algal blooms,” can kill millions of adult and larval bay scallops each year. Scallops grow fastest during the warmer months when food is available. They prefer estuaries and bays where salinities are relatively high, waters are 0.3 to 0.6 m deep at low tide, and seagrasses such as eelgrass (*Zostera marina*) or shoal grass (*Halodule wrightii*) are common (Smith et al. 1988; Prescott 1990; Pohle et al. 1991; Garcia-

Esquivel and Bricelj 1993; Bologna and Heck 1999, 2002; Bologna et al. 2001). These grass beds offer protection from predators as well as sites for juvenile attachment (Pohle et al. 1991; Bologna and Heck 1999).

Atlantic calico scallop *(Argopecten gibbus)*

The Atlantic calico scallop, a relatively small scallop ranging from 25 to 60 mm shell height, is patchily distributed on the Atlantic coast from Delaware Bay south into the Caribbean Sea to about 20° N latitude. It is most commonly found from just north of Cape Hatteras, North Carolina to the Greater Antilles, and throughout the Gulf of Mexico and Bermuda (Allen and Costello 1972; Blake and Moyer 1991). Genetic and morphological similarities (Waller 1969) between Florida and North Carolina populations and coastal currents support a hypothesis that Florida may be an important larval source for North Carolina stocks (Wells et al. 1964; Krause et al. 1994). Calico scallops can be found in depths of 10 to 400 m, but have been reported from shallower waters in Biscayne Bay (Coleman et al. 1993).

Spawning occurs throughout the year, but peaks in late fall and in the spring (Arnold 1995). As with bay scallops, calicos are simultaneous hermaphrodites that release sperm and eggs. Settling calico scallops require shell or other hard substrate to provide an anchor for byssal attachment. Laboratory studies suggest that after drifting freely for 14–16 days, larvae attach to hard substrates, which are often the disarticulated shells (dead accumulations that are separated or broken) from previous generations (Ambrose and Irlandi 1992; Ambrose et al. 1992). They reach a commercial length of 47 to 53 mm in six to eight months.

The maximum life span of an Atlantic calico scallop appears to be about 24 months. Predation (Wells et al. 1964) is a major factor affecting survival during various phases of the calico scallop life cycle. Aggregations of calico scallops provide habitat for numerous species, including other types of scallops, fish, and invertebrates. Schwartz and Porter (1977) collected 111 species of fish and 60 species of macroinvertebrates, including 25 crustaceans, 12 echinoderms, 4 coelenterates, and 1 annelid. Many of the fish caught used this habitat for feeding purposes (Schwartz and Porter 1977). See section 4.1.9 in this document for more detailed information on this species.

Pen Shells

As with other filter feeders, pinnids can filter large quantities of suspended sediments and plankton out of the water column, thereby affecting phytoplankton levels and water clarity. However, high densities generate both feces and pseudofeces affecting the surrounding sediments and associated organisms (Cummings et al. 2001; Ellis et al. 2002). For example, Ellis et al. (2002) showed that sedimentation can significantly impact *Atrina* spp. populations.

All three species -- the saw-toothed pen shell (*Atrina serrata*), the amber pen shell (*Pinna carnea*), and the stiff pen shell (*Atrina rigida*) -- can occur in large numbers and protrude above the sediment's surface (Figure 3.2-14, Plates A & B). Their shells are typically covered with a diverse assemblage of fouling organisms, including barnacles and slipper shells, which create vertical structure and fish habitat (Kuhlmann 1994, 1996, 1997, 1998; Munguia 2004). Many organisms use the shells as shelter, including crabs (e.g., *Pilumnus sayi*, *Menippe* spp., *Portunus* *ordwayi*) and benthic fishes such as blennies and gobies) within seagrasses (Kuhlmann 1994). Shells can reach densities of over 13 individuals/m^2 (Kuhlmann 1994, 1996).

Additionally, the Florida blenny (*Chasmodes saburrae*), feather blenny (*Hypsoblennius hentzi*), clingfish (*Gobiesox strumosus*), and Gulf toadfish (*Opsanus beta*) use dead pen shells as nest sites (Kuhlmann 1994). Females lay a single layer of eggs on the inside of the pen shells. Similarly, Joubin's pygmy octopus (*Octopus joubini*) also lays its eggs on the inside of pen shells. Horse conchs (*Pleuroploca gigantea*) are the primary predators of pen shells (Kuhlmann 1994, 1996, 1997, 1998). Dead pen shells provide nesting sites and shelter for many fish species, but are not permanent benthic features. As the shells begin to break apart, the waves and currents sweep them away, thus changing the dynamics of the populations of the species that depend on them (Kuhlmann 1996, 1998).

The most extensive studies of pen shell communities as habitat were completed by researchers in New Zealand (Keough 1984; Cummings et al. 1998, 2001; Nikora et al. 2002; Gibbs et al. 2005). These habitats are also referred to as 'horse mussel' (*Atrina zelandica* and *Atrina novaezelandiae*) beds. Research has included fine scale boundary layer flow studies (Nikora et al. 2002), mesoscale hydrodynamic interactions (Green et al. 1998), community interactions (Keough 1984; Cummings et al. 1998, 2001), and essential fish habitat delineation for juvenile finfish species (Morrison and Carbines 2006).

Estuarine wedge clam (*Rangia cuneata*)

The estuarine wedge clam is found in Atlantic coastal and Gulf of Mexico oligohaline estuaries (Cain 1975; LaSalle and de la Cruz 1985; Abadie and Poirrier 2000), tidal rivers, and backwater bays with regular inputs of fresh water. It occurs from the upper Chesapeake Bay to Mexico, often dominating benthic biomass in low salinity areas of estuaries (Cain 1975). This clam is regarded primarily as a subtidal species found in coastal areas with a large tidal range (Estevez 2005).

The species serves as an important link in the food chain, filtering large volumes of water when at high densities and serving as a food source for fish, crabs, and ducks (LaSalle and de la Cruz 1985). In North Carolina, *Rangia cuneata* are often found within the most critical oyster habitat areas where shells accumulate over long time periods. In these areas, accumulations of estuarine wedge clam shells provide substrate for formation of oyster reefs. In a majority of cases, both living and dead *Rangia cuneata* occur together. Estuarine wedge clams are more abundant in downstream reaches and as intertidal material in upstream reaches. Interestingly, live *Rangia cuneata* in intertidal areas can be larger than those in subtidal beds (Estevez 2005).

In Lake Pontchartrain, Louisiana, individual estuarine wedge clams have an average life span of four to five years. Deposits of wedge clam shells in the lake bottom supported a shell mining industry from 1933 to 1990 (Abadie and Poirrier 2000). As with oyster shells, clam shells used to be so abundant that they were used for construction of roadways, parking lots, levees, and in the production of cement. Large (> 20 mm) *Rangia cuneata* were abundant in Lake Pontchartrain in the early 1950s, but became rare by the 1970s and 1980s. They can dominate the benthos, with densities reaching 1,896 clams/m^2 and dry weight biomass as high as 70 g/m^2.

However, clams are absent from areas that are subject to anoxia and hypoxia, or saltwater intrusions (Poirrier and Spalding 2005).

Current *Rangia cuneata* studies are seeking to document similar ecological services to oysters, in order to generate interest in its restoration (M. Poirrier, personal communication). Results indicate that increasing clam abundance by decreasing saltwater intrusion will improve water clarity; this in turn should increase submerged aquatic vegetation and add shell for mud stabilization and erosion reduction. These improvements should reduce eutrophication, improve water quality, and enhance fish habitat (M. Poirrier, personal communication).

Carolina marsh clam (*Polymesoda caroliniana*)

This brackish-water corbiculid clam (often reaching sizes over 50 mm, but typically 25- 40 mm) is often common in low salinity marshes comprised of plants such as *Juncus* sp. and near river mouths (Andrews and Cook 1951; Andrews 1977; Duobinis-Gray and Hackney 1982; Marelli 1990). The geographical range of this species is from Virginia through Florida along the Gulf of Mexico to Texas, with adult densities often exceeding 300 individuals/m^2 (Duobinis-Gray and Hackney 1982) and juvenile (<20 mm) densities at almost 2,000/m^2 (Marelli 1990). The Carolina marsh clam lives primarily in the intertidal zone (Marelli 1990), but may be found subtidally, in mud to fine sediments (Heard 1982). Some researchers have suggested competitive interactions with another common low salinity bivalve, *Rangia cuneata* (more often subtidal, as *Polymesoda* is a poor burrower in intertidal areas) (Duobinis-Gray and Hackney 1982). Early growth can be rapid (>1 mm/month) (Olsen 1973, 1976), and predation, competition, and inundation are often cited as factors controlling the distribution and abundance of this species (Andrews and Cook 1951, Andrews 1977). A related species *P. maritima*, the Florida marsh clam, is common in the Gulf coast region, and southern Florida to the Yucatan (Andrews 1977).

Little is known about the habitat value of shell accumulations or live aggregations of *Polymesoda* spp. for other organisms.

Oyster Reefs and Shell Banks as Essential Fish Habitat

The three major types of shellfish habitat (reefs, aggregations, and accumulations) differ in their combinations of habitat characteristics. However, all shellfish habitats have three major features in common that are the basis for their ecological value for managed species: hard substrate (for settlement/refuge/prey), complex vertical (3-D) structure (for settlement/refuge/prey), and food (feeding sites for larger predators).

Perhaps the most fundamental characteristic of shellfish habitat is hard substrate. The shells provide attachment surfaces for algae and sessile invertebrates, such as polychaetes (e.g., sabellids, serpulids), hydroids, bryozoans, and sponges, which in turn provide substrate for other organisms. Planktonic larvae of some shellfish species, such as oysters, need a hard substrate on which to settle in order to grow into adults (Galtsoff 1964). In many estuarine areas, oyster shell and cultch are the primary settlement material for larval oysters (Kennedy 1996; Powell et al. 2006). All three types of shellfish habitat—reefs, aggregations, and accumulations—provide suitable substrate for other shellfish and many other species that require hard substrate on which to grow.

Sufficient accumulations of hard substrate result in complex habitat structure that provides increased vertical relief and internal complexity of the structure itself. Structural complexity has historically been considered to be an important factor affecting the spatial distribution and diversity of marine and estuarine organisms (Bell et al. 1991). An increase in the physical complexity of an environment is typically correlated with an increase in microhabitat diversity (Sebens 1991). The increase in surface area provides more refuge and feeding sites, which subsequently leads to greater species richness (Bell and Galzin 1984). The interstitial spaces provide recruiting oysters with adequate water flows for growth and refuge from predators, both of which are essential for long-term maintenance of the reef structure (Bartol and Mann 1997; Bartol et al. 1999; Coen et al. 1999b; Powell et al. 2006). Oysters and other reef-forming shellfish can be considered "bioengineers" because they create habitat that allows many additional species to thrive (Jones et al. 1994, 1997).

All four shellfish habitat types provide food for other organisms, whether it is the shellfish themselves or associated organisms. Oysters and mussels are consumed by many species of fish and invertebrates. Many other species of plants and animals also occur on shell accumulations and provide food for a variety of predators. When considered in combination with the hard substrate and complex structure provided by live shellfish, their direct food value results in shellfish reefs and aggregations being uniquely valuable habitat for many managed species.

3.2.5 Intertidal Flats

Description and Distribution

This section is intended to briefly summarize the most important aspects of tidal flats which pertain directly to their function as essential fish habitat. For a more extensive and comprehensive ecological profile of tidal flats in the South Atlantic region we recommend the U.S. Department of Interior Community Profile, Peterson and Peterson (1979).

Intertidal flats are the unvegetated bottoms of estuaries and sounds that lie between the high and low tide lines. These flats occur along mainland or barrier island shorelines or can emerge in areas unconnected to dry land. Intertidal flats are most extensive where tidal range is greatest, such as near inlets and in the southern portion of the coast. Because the influence of lunar tides is minimal in the large sounds (e.g., Pamlico, Albemarle, and Currituck), true intertidal flats are not extensive, except for the area immediately adjacent to inlets (Peterson and Peterson 1979). Sediment composition on intertidal shorelines tends to shift from coarser, sandy sediment on higher portions of the shoreline, with greater wave energy, to finer, muddier sediments in the lower portion of the shoreline, with relatively less wave energy (Peterson and Peterson 1979). Conditions on intertidal flats are physically stressful for associated marine organisms. Drastic fluctuations in salinity, water and air temperature (in addition to air and wind exposure) occur during each tidal cycle. Due to physiological restraints and limited water depth, some mobile organisms are restricted to deeper waters or adjacent habitats to avoid the stressful extremes associated with low tide. However, the sediment provides a buffer from changes in temperature and salinity in the water column for benthic infauna (Peterson and Peterson 1979).

Variability in the tidal regime along the South Atlantic coast results in considerable regional variability in the distribution and character of the estimated 1 million acres (Field et al. 1991) of tidal flat habitat. Geographic patterns in sediment size on tidal flats result primarily from the interaction of tidal currents and wind energy. The coasts of North Carolina and Florida are largely microtidal (0 - 2m tidal range). In these areas wind energy has a strong affect on intertidal flats. The northern North Carolina outer banks have extensive barrier islands and relatively few inlets to extensive sound systems. South of Cape Lookout, flood-tide deltas (remnant and active) are more frequent and tidal inlets and influences on intertidal flat distribution is greater. In contrast, the coasts of South Carolina and Georgia are mesotidal (2 - 3.3m) with short barrier islands and numerous tidal inlets so that tidal currents are the primary force effecting the intertidal. In both types of systems the substrate of the intertidal flats generally becomes finer with distance from inlets due to the progressive damping of tidal currents and wave energy in the upstream direction. Exposure of flats to wave energy, which resuspends fine particles, may cause the development of sand flats in areas where the wind fetch is sufficient for the development of significant wave energy. On the microtidal coast of North Carolina sandy flats tend to develop due to the large size of the sounds and their orientation relative to prevailing winds. In contrast in Georgia and South Carolina most flats are muddy, as the sounds and estuaries are small so that the importance of wave energy is reduced. These different depositional environments result in development of varied physico-chemical environments in and on intertidal flats which in turn cause differences in the animal populations that utilize them.

Ecological Role and Function

Intertidal flats play an important role in the ecological function of South Atlantic estuarine ecosystems, particularly in regard to primary production, secondary production and water quality. Although intertidal flats are usually classified as “unvegetated,” there is actually an extremely productive microalgal community occupying the surface sediments (MacIntrye et al., 1996). The benthic microalgal community of tidal flats consists of benthic diatoms, cyanobacteria, euglenophytes and unicellular algae. Primary production of this community can equal or exceed phytoplankton primary production in the water column, and can represent a significant portion of overall estuarine primary productivity (Pinckney and Zingmark 1993; Buzzelli et al. 1999). Benthic microalgae are resuspended into the water column and transported throughout the estuary, sometimes representing over half of the chlorophyll in the water column (de Jonge and van Beusekom 1995; Tester et al. 1995). Benthic microalgae also stabilize sediments and control fluxes of nutrients (nitrogen and phosphorus) between the sediment and the water column. Autochthonous benthic microalgal and bacterial production and imported primary production in the form of phytoplankton and detritus support diverse and highly productive populations of infaunal and epibenthic animals. The primary factors controlling production by microalgae occupying these sediments include the amount of light they receive, community biomass (chl *a*), and temperature (Pinckney and Zingmark, 1993; Barranguet et al., 1998; Guarini et al., 2000).

Important benthic animals in and on the sediments include ciliates, rotifers, nematodes, copepods, annelids, amphipods, bivalves and gastropods. This resident benthos is preyed upon by mobile predators that move onto the flats with the flood tide. These predators do not always kill their benthic prey and many “nip” appendages of buried animals such as clam siphons and polychaete tentacles that can be regenerated. An important aspect of the function of these systems is the regular ebb and flood of the tide over the flats and the corresponding rhythm that exists among animals and microalgae adapted to life in the intertidal zone. The flooding tide brings food and predators onto the flat while the ebb provides residents a temporal refuge from the mobile predators.

This constantly changing system provides the following ecological functions: 1) nursery grounds for early stages of development of many benthically oriented estuarine dependent species; 2) refuges and feeding grounds for a variety of forage species and juvenile fishes; 3) significant trophic support to fish and shellfish, including oysters and clams (Riera and Richard 1996; Kreeger et al. 1997; Sullivan and Currin 2000; Page and Lastra 2003; Currin et al. 2003); 4) stabilization of sediments via the production of exopolymers (Yallop et al. 1994, 2000) and 5) modulation of sedimentary nutrient fluxes (Miller et al. 1996; Cerco and Seitzinger 1997; Sundback et al. 1991). Although it is recognized that tidal flats provide these important ecological functions, the relative contribution of intertidal flats of different types and in different locations within coastal systems is not well known.

Intertidal flats also provide habitat for a large and diverse community of infauna and epifauna, which in turn may become prey for transient fish species utilizing the intertidal flat. The faunal communites associated with intertidal flats will be described below.

Coastal development and human activities can have direct and dramatic impacts on tidal flats, although subtler impacts may occur from activities that alter current patterns, wave energy or the supply of sediment. Examples of direct impacts include on-site dredging and contaminant spills. Indirect impacts include dredging that significantly alters current patterns, dam construction that traps sediment, beach re-nourishment projects and jetty construction. Although intertidal flats are protected by the same permitting process that regulates activities impacting other estuarine habitats, the perception that flats are of minor importance relative to vegetated habitats increases pressure on intertidal flats. Flats have the same legal protection afforded vegetated intertidal areas, however; the importance of intertidal flats is not generally recognized and the relative value of intertidal flats is not understood. As a consequence permits may be more easily granted for filling/dredging tidal flats than for salt marshes and salt marsh may be planted on a natural intertidal flat when mitigation for marsh destruction is required. Increased recognition of the ecological value of tidal flats by resource managers and permitting agencies is necessary to preserve these valuable habitats, and research on the different types of intertidal flats and their relative value in coastal systems should be encouraged.

Species composition and community structure

Both plankton and benthic feeding herbivorous fish are found in abundance on intertidal flats. Schools of baitfish, small pelagic fish that tend to group together, are common over subtidal soft bottom and very abundant on shallow intertidal flats. These baitfish, such as anchovies, killifish, and menhaden, feed on the abundant supply of phyto- and zooplankton in the water column, but also consume resuspended benthic algae, microfauna, and meiofauna (Peterson and Peterson 1979). Although the majority of detritivores of the soft bottom habitat are invertebrates, striped mullet, white mullet, and pinfish also feed on detritus on subtidal bottom and intertidal flats. Other fish species use detritus as an alternate food source when preferred items are not available.

Most fish that forage on soft bottom are predaceous. Predators of benthic invertebrates include juveniles and adults of the following species (Peterson and Peterson 1979; Bain 1997):

- rays and skates,
- flatfish (southern flounder, summer flounder, hogchoker, tonguefish),
- several species of drum (spot, Atlantic croaker, red drum, kingfishes, silver perch),
- Florida pompano,
- pigfish,
- sea robins,
- lizardfish,
- spadefish,
- gobies, and
- shortnose and Atlantic sturgeons.

The compressed body forms of flatfish, rays, and skates assist in prey acquisition and predator avoidance on shallow intertidal flats (Peterson and Peterson 1979). For example, flounder forage on shallow flats by laying still, by concealing themselves under a thin layer of sediment, or by changing skin color. Small flatfish, including the bay whiff, fringed flounder, hogchoker, and tonguefish, feed mostly on copepods, amphipods, mysids, polychaetes, mollusks, and small fish. By way of comparison, summer and southern flounder primarily consume fish, such as silversides and anchovies, as well as shrimp and crabs, small mollusks, annelids, and amphipods (Peterson and Peterson 1979). Various rays excavate large pits while feeding, creating slightly deeper pockets of water that other fish and invertebrates use as refuge. Mollusks, annelids, crustaceans, and fish comprise the typical diet of rays.

To avoid predation, small fish commonly feed on open, unvegetated bottom at night and hide near structure during the day (Peterson and Peterson 1979). Larger predators that feed on smaller, benthic-feeding fish and invertebrates typically move onto the flats during high water to feed on schools of fish. These predators include sharks (sandbar, dusky, smooth dogfish, spiny dogfish, Atlantic sharpnose, scalloped hammerhead), drum (weakfish, spotted seatrout), striped bass, and estuarine dependent reef fish (black sea bass, gag grouper, sand perch, sheepshead) (Peterson and Peterson 1979; Thorpe et al. 2003).

Due to their size and shape, small baitfish and flat bodied rays, skates, and flounders have a feeding advantage over other fish in that they can forage on intertidal flats for greater amounts of time than larger fish. These fish groups are considered to be most characteristic of intertidal flats and would be most affected by habitat degradation and loss of intertidal flats from dredging, filling, bulkheading, or other anthropogenic causes (Peterson and Peterson 1979).

Fish species and age composition over soft bottom vary seasonally. Baitfish are present on shallow flats throughout the year. In the spring, large schools of baitfish are joined by juvenile fish that were spawned offshore in the winter (spot, Atlantic croaker, menhaden). In the summer, these species remain abundant on shallow unvegetated bottom; flatfish and rays also appear at this time. By fall, fish species diversity is at a maximum since summer residents and fall migrants are both present. Migratory fish feeding on the soft bottom include bluefish, striped mullet, kingfish, spotted seatrout, red drum, and many others (Peterson and Peterson 1979).

Intertidal Flats as Essential Fish Habitat

Benthic Nursery Function

Many species whose larval stages are planktonic but are benthically oriented as juveniles utilize intertidal flats as primary nursery ground. Intertidal flats are particularly suited for animals to make the shift from a pelagic to benthic existence. During this habitat shift these small animals are expected to be particularly vulnerable to adverse physical forces, predation and starvation, and flats may provide a relatively low energy environment where predation pressure is low and small benthic prey abundant. These animals may develop a tidal rhythm of behavior and move off and on the flat with the ebb and flood of the tide. This provides them an area of retention as currents over the flats are reduced, a refuge from a variety of predators due to the shallow water and excellent feeding conditions as the abundant meiofauna emerge to feed with the flooding tide. A wide variety of important fishes and invertebrates utilize intertidal flats as nurseries (Table 2.7) including the commercially important paralichthid flounders, many members of the drum family including red drum, and spotted seatrout, the mullets, gray snapper, the blue crab, and penaeid shrimps.

Table 3.2-7. Species' utilization of intertidal flats.

Species	Common name	Function	Life stage(s)
Dastatis sayi	bluntnose stingray	F	A
Rhinoptera bonasus	cownose ray	F	A
Angulla rostrata	American eel		J, A
Conger oceanicus	conger eel		A
Myrophis punctatus	speckled worm eel		J
Brevoortia tyrannus	Atlantic menhaden	R	J
Anchoa hepsetus	striped anchovy	R	J, A
Anchoa mitchilli	bay anchovy	R	J, A
Synodus foetens	inshore lizardfish	F	J, A
Urophycis regius	spotted hake	F	J
Membras martinica	rough silverside	R	J, A
Menidia menidia	Atlantic silverside	R	J, A
Centropristis striata	black seabass	R	J
Diplectrum formosum	sand perch	R	J
Mycteroperca microlepis	gag grouper	R	J
Lujanus griseus	gray snapper	N	J
Eucinostomus argenteus	spotfin mojarra	R, F	J, A
Eucinostomus gula	silver jenny	R, F	J, A
Orthopristis chrysoptera	pigfish	R	J
Archosargus probatocephalus	sheepshead	R, F	J
Lagodon rhombodies	pinfish	N, R, F	J, A
Bairdiella chrysura	silver perch		J, A
Cynocion nebulosus	spotted seatrout	N	PL, J
Cynocion regalis	weakfish		J
Leiostomus xanthurus	spot	N, R, F	PL, J, A
Menticirrhus saxatilus	southern kingfish	R, F	J
Micropogonias undulatus	Atlantic croaker	N, R, F	PL, J, A
Sciaenops ocellatus	red drum	N, R, F	PL, J, A
Mugil cephalus	striped mullet	N, R	J, A
Mugil curema	white mullet	N, R	J
Prionotus carolinus	northern searobin		J, A
Citharichthys spilopterus	bay whiff	N, R, F	PL, J, A
Etropus crossotus	fringed flounder	R, F	J, A
Paralichthys albigutta	gulf flounder	N, R, F	PL, J, A
P. dentatus	summer flounder	N, R, F	PL, J, A
P. lethostigma	southern flounder	N, R, F	PL, J, A
Scopthalmus aquosus	windowpane	F	J, A
Trinetes maculatus	hogchoker	N, R, F	PL, J, A
Symphurus plagiusa	blackcheek tonguefish	N, R, F	PL, J, A
Callinectes sapidus	blue crab	N, R, F	J, A
Penaeus aztecus	brown shrimp	N, R, F	PL, J, A
P. duorarum	pink shrimp	N, R	PL, J
P. setiferus	white shrimp	N, R, F	PL, J, A
Busycon spp.	Welk	F	A
Crassostrea virginica	eastern oyster	F	PL, J, A
Mercenaria mercenaria	hard clam	F	PL, J, A

Letter codes for function use are N=benthic nursery function, R=refuge function, and F=feeding ground function. Life stage codes are PL=post-larval, J=juvenile, and A=adult.

Refuge Function

A variety of pelagic and benthic species utilize the intertidal flats as a refuge from predation and adverse physical conditions (Table 3.2-7). Predation pressure in the subtidal, particularly in the vicinity of inlets may increase during the rising tide due to the influx of coastal predators.

Intertidal flats provide energetic advantages for animals seeking to maintain their position within the system as current velocities are generally low relative to deeper areas. Schools of planktivores including anchovies, silversides and menhaden and schools of benthic feeding juveniles such as the spot and croaker, pinfish and mojarras, move onto flats with the rising tide to take advantage of the favorable conditions flats provide. More solitary species such as black seabass and gag grouper also appear to utilize flats as a refuge during their emigration from structured estuarine nursery habitats to the sea in the fall. Flats also can provide a refuge from low oxygen levels that may develop in deeper areas of estuaries during summer months.

Feeding Ground Function
Several groups of specialized feeders utilize intertidal flats as feeding grounds (Table 3.2-7). The depositional nature of intertidal flats provide a rich feeding ground for detritivores such as mullet and predators of small benthic invertebrates such as spot and mojarra. A variety of invertebrate predators such as whelks and blue crabs feed on tidal flats as do their bivalve prey such as oysters and hard clams, important filter feeding residents of tidal flats. Another group that relies on flats as feeding grounds is predatory fishes such as rays, a wide variety of flatfishes and lizard fish whose form makes them well adapted to feed in shallow water. Other more conventionally shaped fishes whose prey concentrate on flats use these areas as feeding grounds and red drum can be found hunting blue crabs on flats. Because flats are “dry” much of the time activity is concentrated during high water making tidal flats rich feeding grounds for species adapted to shallow waters.

3.2.6 Estuarine Water Column

Description and Distribution

This habitat traditionally comprises four salinity categories: oligohaline (< 8 ppt), mesohaline (8 -18 ppt), and polyhaline waters (18 - 30 ppt) with some euhaline water (>30 ppt) around inlets. Alternatively, a three-tier salinity classification is presented by Schreiber and Gill (1995) in their prototype document developing approaches for identifying and assessing important fish habitats: tidal fresh (0-0.5 ppt), mixing (0.5-25 ppt), and sewater (>25 ppt). Saline environments have moving boundaries, but are generally maintained by sea water transported through inlets by tide and wind mixing with fresh water supplied by land runoff. Particulate materials settle from these mixing waters and accumulate as bottom sediments. Coarser-grained sediments, saline waters, and migrating organisms are introduced from the ocean, while finergrained sediments, nutrients, organic matter, and fresh water are input from rivers and tidal creeks. The sea water component stabilizes the system, with its abundant supply of inorganic chemicals and its relatively conservative temperatures. Closer to the sea, rapid changes in variables such as temperature are moderate compared to shallow upstream waters. Without periodic additions of sea water, seasonal thermal extremes would reduce the biological capacity of the water column as well as reduce the recruitment of fauna from the ocean. While nearby wetlands contain some assimilative capacity abating nutrient enrichment, fresh water inflow and tidal flushing are primarily important for circulation and removal of nutrients and wastes from the estuary.

The water column is composed of horizontal and vertical components. Horizontaly, salinity gradients (decreasing landward) strongly influence the distribution of biota, both directly (physiologically) and indirectly (e.g., emergent vegetation distribution). Horizontal gradients of nutrients, decreasing seaward, affect primarily the distribution of phytoplankton and, secondarily, organisms utilizing this primary productivity. Vertically, the water column may be stratified by salinity (fresh water runoff overlaying heavier salt water), oxygen content (lower values at the bottom associated with high biological oxygen demand due to inadequate vertical mixing), and nutrients, pesticides, industrial wastes, and pathogens (build up to abnormal levels near the bottom from lack of vertical mixing).

Typically, parameters of the following variables can be used to chemically, physically, or biologically characterize the water column: total nitrogen, total organic nitrogen, alkaline phosphatase, total organic carbon, NO^{2-}, NO^{3-}, NH^{4+}, turbidity, total phosphorus, chlorophyll a, dissolved oxygen, temperature, and salinity (see Boyer et al. 1997).

Composite signatures by these variables can be used to identify the source of the water column. Components commonly used to describe the water column are organic matter, dissolved inorganic nitrogen, dissolved oxygen, temperature, salinity, and phytoplankton. Additional physical descriptors of the water column include depth, fetch, and adjacent structure (e.g., marshes, channels, shoals). Turbidity is quantified by secchi depth, light attenuation, and NTU. Increases in turbidity, resulting from large river flow runoff or strong wind events, affect the distribution and productivity of submerged aquatic vegetation and phytoplankton through reduction of light levels necessary for photosynthesis and changes in nutrient concentrations.

The quality of our coastal waters affects fish species diversity, production, and distribution but also living fish habitats, such as submerged aquatic vegetation and oyster beds (shell bottom). Water quality in the water column is a key factor that links fish, habitat, and people. That linkage is affected by growing development pressures along our coast as well as far inland, making the protection and enhancement of water quality for fisheries resources a challenging task. Determining the best course of action for enhancing water quality requires detailed knowledge of the water quality characteristics that various species require throughout their life cycle, along with the status, trends, and threats of those characteristics.

Water column habitat is defined in this plan as “the water covering a submerged surface and its physical, chemical, and biological characteristics.” Differences in the chemical and physical properties of the water affect the biological components of the water column, including fish distribution. Water column properties that may affect fisheries resources include temperature, salinity, dissolved oxygen (DO), total suspended solids, nutrients (nitrogen, phosphorus), and chlorophyll a (SAFMC 1998a). Other factors, such as depth, pH, water velocity and movement, and water clarity, also affect the distribution of aquatic organisms.

Water column characteristics in estuaries are a dynamic mix of adjacent riverine and marine systems. Estuaries occupy the transition between freshwater and marine systems, where circulation patterns are determined by prevailing winds, buoyancy-driven flows, and lunar tides. Estuaries are important habitats for many economically important species in the South Atlantic. In North Carolina, for instance, estuarine-dependent species comprise more than 90% of commercial fisheries landings and over 60% of the recreational harvest (by weight) (from DMF annual commercial and recreational fisheries landings data).

Three salinity zones are used for simplicity and consistency with established definitions (Bulger et al. 1993):

- low-salinity (0.5-5 ppt) (also known as oligohaline)
- moderate-salinity (5-18 ppt) (also known as mesohaline)
- high-salinity (18-30 ppt) (also known as polyhaline)

Boundaries between salinity zones change in response to water flow, weather conditions, and tidal fluctuations. Flooding can result in fresh water expanding seaward over denser masses of water in the "mixing zone" (0.5 - 25 ppt). Conversely, dry weather can result in seawater advancing into typically freshwater areas. Less drastic are tidal changes resulting in periodic additions of seawater to the mixing zone. The mixing zone receives coarser-grained sediments, saline water, and migrating organisms from the flood tide, while the ebb tide brings finer-grained sediment, fresh water, nutrients, and organic matter (SAFMC 1998a). This dynamic system is mediated by a series of inlets along a chain of barrier islands separating the ocean from the adjacent estuary. Salinity in estuaries also varies in accordance with the seasonal pattern of river input depicted in Figure 3.2-17. Salinity within estuaries is generally lowest from December to early spring and highest from late spring to early fall (Orlando et al. 1994). Similarly, water temperatures are lowest during mid-winter and highest during the summer. Pilkey et al.'s (1998) analysis of North Carolina's shore and barrier islands revealed much about the variation in salinity and tidal amplitude along North Carolina's coast due to the slope of the coast.

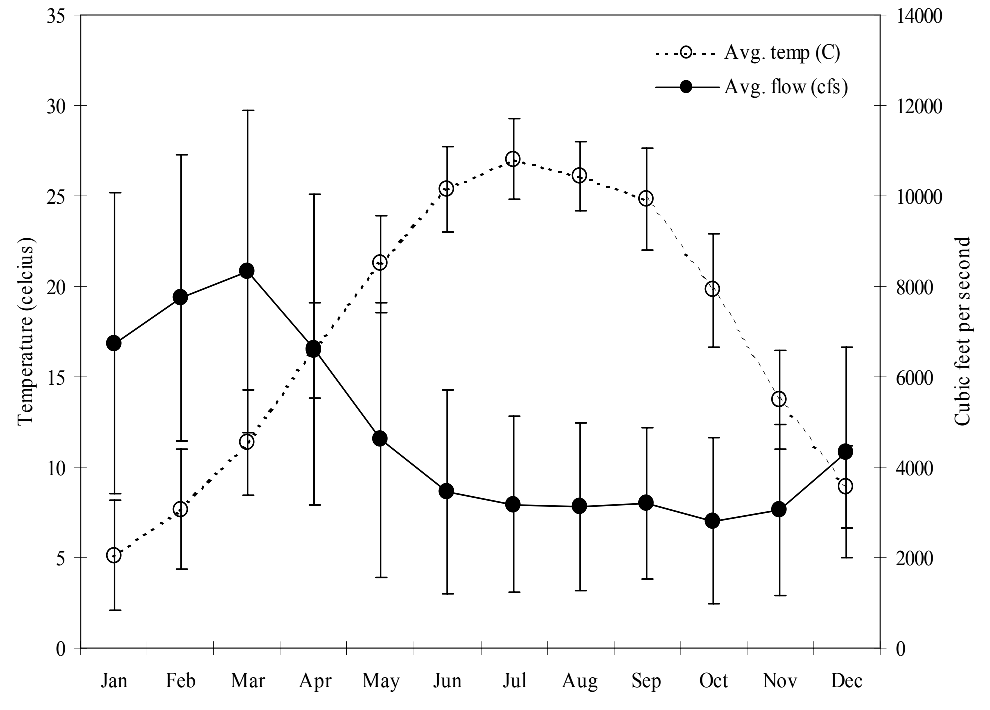


Figure 3.2-17. Average and standard deviation of monthly discharge (time period: 1969 1999, n = 1,464) and water temperature (time period: 1953-2001, data points per month = 52-123). [Source: USGS hydrologic monitoring stations on the lower Roanoke, Tar, Neuse, and Cape Fear rivers, North Carolina.

Steeper slopes with relatively short basin profiles result in less river input and greater tidal amplitude from increasing oceanic influence. In these areas, numerous inlets develop along short barrier islands, protecting narrow, back barrier sounds. Small rivers draining these areas form trunk estuaries (drowned river estuaries perpendicular to the coast) where low volumes of organic-stained fresh water mix with seawater. As a result, small trunk estuaries exhibit a distinct salinity gradient from upstream fresh waters to the ocean, while narrow back barrier sounds maintain high salinities from regular lunar tides.

Other areas have gentler slopes and relatively long basin profiles, with more river input and lower tidal amplitude from reduced seawater intrusion; such areas have few inlets and long barrier islands protecting extensive back barrier sounds with highly variable salinity. Large rivers flowing into the sounds form trunk estuaries with very low salinity.
Strong winds are a major component of water movement in large, irregularly flooded estuarine systems.

At locations relatively isolated from inlets in the Albemarle-Pamlico Sound system, the effects of lunar tides are small (a few inches at most) whereas those of wind tides can be much greater (especially during storms). A strong wind tide often floods the windward shore, exposing bottom along the leeward shore. This situation can also result in colder, nutrient-rich water welling up along the leeward shore. Wind tides also affect salinity in the estuary, by pushing high-salinity water from the ocean toward the estuary. For example, one model of the Albemarle-Pamlico system indicates that southwesterly winds cause the formation of low-salinity plumes from Oregon Inlet seaward while wedge-shaped high-salinity plumes enter Pamlico Sound from Hatteras and Ocracoke inlets (Xie and Pietrafesa 1999). This hydrodynamic model predicted the opposite effect during cold fronts, when northwesterly winds caused a wedge-shaped, high-salinity plume on the sound side of Oregon Inlet.

Circulation, by wind or lunar tide, can increase DO levels in bottom water. But while lunar-driven systems receive regular circulation, wind-driven systems depend on variable weather conditions (Luettich et al. 1999; Borsuk et al. 2001). Irregular mixing can result in stratification of the water column and hypoxia or anoxia during periods of warm, calm weather. Anoxia can also develop with light winds if a strong vertical salinity gradient is present, especially during westerly winds.

Large back barrier sounds and trunk estuaries

In North Carolina, large back barrier sounds occur north of Cape Lookout and include Albemarle, Currituck, Croatan, Roanoke, and Pamlico sounds. Large trunk estuaries flowing into these northern sounds include the Alligator, Pungo, Pamlico, and lower Neuse rivers. The Albemarle-Pamlico sound system (not including Core Sound) connects with nearshore ocean waters through Oregon Inlet in the north, and Hatteras and Ocracoke inlets in the south. These large sounds are of prime importance for North Carolina’s fishery productivity. Small tributary estuaries in west and northwest Pamlico Sound provide important fish nursery habitat. Outstanding Resource Waters within these northern estuaries include the Alligator River and an area extending offshore from Swan Quarter National Wildlife Refuge. The Alligator River is also classified as Swamp Water. Nutrient Sensitive Waters include the Pamlico, Neuse, and Pungo rivers as well as southwest Pamlico Sound.

The Albemarle-Pamlico system has a long flushing period (about 272 days) relative to the other North Carolina estuarine systems. Since the large trunk estuaries flowing into Pamlico Sound flush more rapidly than Pamlico Sound, the sound acts as a settling basin for sediments and nutrients (Giese et al. 1979). Near inlets in the Albemarle-Pamlico system, lunar tides are the dominant influence on salinity variation and water column mixing (Orlando et al. 1994). Elsewhere, wind mixing is the dominant factor.

Management of river flows can also affect salinity. Releases from Roanoke Rapids Lake and other Roanoke River reservoirs during low-flow periods are generally effective in keeping higher salinity waters out of Albemarle Sound (Giese et al. 1979), except during extreme droughts. Seasonal variation in fresh water has a major effect on salinity. Different salinity layers can occur in estuaries lacking a direct connection to the ocean, such as the Cape Fear and Northeast Cape Fear rivers (Orlando et al. 1994). Different salinity layers can also occur in Albemarle Sound during period of calm or high freshwater inflow (Steel 1991). Although the major factors driving large-scale salinity change are fairly simple in estuaries, the factors underlying smaller-scale horizontal and vertical variation can be very complex, both spatially and temporally.

Small back barrier sounds and trunk estuaries

South of Cape Lookout, back barrier sounds and trunk estuaries begin to narrow as the basin slope becomes steeper. Starting at Core Sound in the north, small back barrier sounds continue south with Bogue Sound and some very narrow sounds located between the small trunk estuaries of the New and White Oak estuaries and the more riverine lower Cape Fear River. Some of these smaller sounds are Stump Sound, Topsail Sound, Masonboro Sound, and Myrtle Grove Sound. Other small trunk estuaries include the Newport and North rivers along Bogue and Back sounds. These small back barrier and trunk estuaries contain numerous designated nursery areas and Outstanding Resource Waters. The only Nutrient Sensitive Water among small back barrier sounds and trunk estuaries is the upper New River (DWQ, unpub. data).

In Bogue and Back sounds, lunar tides are the dominant influence on salinity and water column mixing (Orlando et al. 1994) and flushing rates are faster than in the larger sounds. Winds and freshwater inflow are secondary influences on salinity variation, but may cause major seasonal differences in salinity.

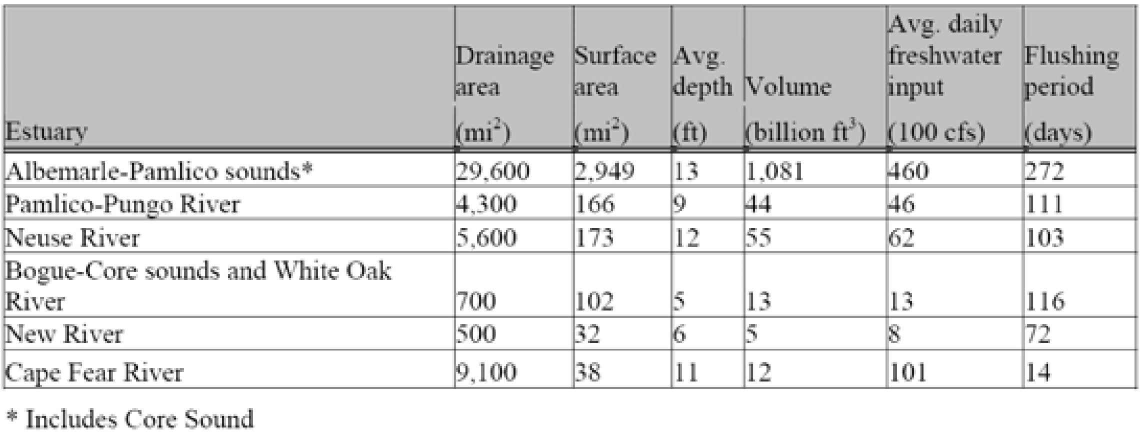
During late winter (January-March) and summer (June-August), surface and bottom salinities are only weakly stratified in Bogue Sound. Large seasonal differences in surface salinity occur. The very small back barrier sounds found in the southern estuaries have high salinities year-round. In upper sections of the New River, freshwater inflow is the dominant influence on salinity (Orlando et al. 1994). In the lower New River estuary, lunar tides have the greatest influence on salinity variation.

Cape Fear River estuary

The Cape Fear River is the only major river in North Carolina flowing directly into the ocean, making the Cape Fear River estuary unique among North Carolina estuaries. The lower river is essentially a large trunk estuary, but with a much steeper gradient in salinity than large trunk estuaries in the northern part of the coast. The upper Cape Fear estuary is composed almost entirely of low-moderate salinity fish nursery areas.

In the upper Cape Fear River estuary (north of Wilmington), seasonal patterns of freshwater inflow have the greatest influence on salinity (Orlando et al. 1994). Discharge from the principal rivers in the Cape Fear basin is three times greater during the high-flow period than during the low-flow period. Short-term increases in freshwater discharge also influence salinity in the upper estuary, displacing bottom water downstream and homogenizing the water column (Giese et al. 1979). In the lower and middle estuary, lunar tides have the dominant effect on salinity variation. Due to the relatively high discharge and low volume of the Cape Fear estuary, the flushing rate is approximately 14 days (Table 3.2-8), the most rapid turnover among major estuaries in North Carolina.

Table 3.2-8. Hydrologic and hydrodynamic characteristics of major estuaries in North Carolina. (Note: flushing period = volume / average daily freshwater input; Source: Basta et al. 1990).



Estuary	Drainage area (mi^2)	Surface area (mi^2)	Avg. depth (ft)	Volume (billion ft^3)	Avg. daily freshwater input (100 cfs)	Flushing period (days)
Albemarle-Pamlico sounds*	29,600	2,949	13	1,081	460	272
Pamlico-Pungo River	4,300	166	9	44	46	111
Neuse River	5,600	173	12	55	62	103
Bogue-Core sounds and White Oak River	700	102	5	13	13	116
New River	500	32	6	5	8	72
Cape Fear River	9,100	38	11	12	101	14

* Includes Core Sound

Ecological Role and Function

(excerpted from the NCHPP)

The water column is the lifeblood of aquatic ecosystems. It is the medium through which all other aquatic habitats are connected. As such, the water column provides a basic ecological role and function for organisms within it. The water column also provides other functions, both by itself and due to benthic-pelagic coupling. Benthic-pelagic coupling refers to the influence of the benthic community and sediments on the water column and, in turn, the influence of the water column on them, through integrated events and processes such as resuspension, settlement, and absorption (Warwick 1993).

Productivity

The potential productivity of fish and invertebrates in a system is determined by the assimilation of energy and nutrients by green plants and other life at the base of the food chain. The potential productivity of a habitat can indicate its relative value in supporting fish populations. Although productivity in the water column is derived mostly from phytoplankton, it can also come from bacterial decomposition of plants (detritus), floating plants, and macroalgae.

Historically, phytoplankton productivity in estuarine systems was thought to be relatively low compared to that of other primary producers (Peterson and Peterson 1979). For instance, Marshall (1970) estimated that phytoplankton contributed only 50 g carbon/m^2/yr to New England's subtidal shoal waters, compared to a contribution of 125 g carbon/m^2/yr for all macrophytes. In the Newport River estuary near Beaufort, North Carolina, Williams and Murdoch (1966) and Thayer (1971) estimated that phytoplankton produce about 110 g carbon/m^2/yr. Subsequent research suggested a higher contribution to overall primary production from phytoplankton (Peterson and Peterson 1979). Sellner and Zingmark (1976) found phytoplankton production as high as 350 g carbon/m^2/yr in shallow tidal creeks and estuaries of South Carolina. Various data sources for North Carolina estimate phytoplankton productivity anywhere from 67 (Beaufort Channel adjacent estuaries) to 500 g carbon/m^2/yr (Pamlico River estuary) during the growing season. Mallin et al. (2000a) found that the highest phytoplankton production is in riverine estuaries where flushing is limited by extensive barrier islands (e.g., Neuse River), whereas areas that are well flushed or unconstrained (e.g., Cape Fear River) support a much lower phytoplankton biomass and productivity. Complex, estuarine creek/salt marsh systems generally have moderate phytoplankton productivity. Lucas et al. (1999) used a depth-averaged numerical model to predict the productivity of phytoplankton in an estuary with shallow shoals, deep channels, and variable turbidity and benthic grazing. The model predicted that phytoplankton growth rate was generally greater in deeper areas when benthic grazing is high and turbidity is low. Conversely, when turbidity was high and benthic grazing was low, phytoplankton growth rate was generally greater in shallow areas.

However, phytoplankton productivity is still generally considered secondary to detritus-based production in salt marsh-dominated estuaries (Peterson and Peterson 1979; Dame et al. 2000). A study conducted on a Georgia salt marsh found a net productivity of 6,850 kcal/m^2/year from emergent vegetation and only 1,600 kcal/m^2/yr from the various algae (Teal 1962). Compared to broad, open water areas, narrow tidal creeks and their associated marsh would likely contribute more detritus than phytoplankton. However, some research suggests that much of the detrital production from emergent vegetation remains in the marsh and that phytoplankton are the major production export (Haines 1979). Planktivorous fish (e.g., menhaden) and detritivores (e.g., shrimp) can also export production from shallow marsh creeks and bays to more open waters (SAFMC 1998a).

Phytoplankton production in shallow estuaries may also be secondary to phytobenthic (microscopic plants that live on the bottom) production. In North Carolina, benthic microalgal biomass frequently exceeds phytoplankton in the nearshore ocean water column by a factor of 10 to 100 (Cahoon and Cooke 1992). Based on relative rates of primary production and nutrient cycling, Webster et al. (2002) found that phytobenthos was the dominant primary producer in a shallow estuary where light was not limiting; however, these results may not be applicable to North Carolina estuaries with higher turbidity. Net productivity for any given estuary depends on the relative proportion of wetlands, shallow soft bottom, and water column in the system.

Salinity

Salinity has a major role in the distribution of aquatic species (Szedlmayer and Able 1996). Some aquatic species are capable of tolerating large variations in salinity (e.g., blue crab), while others are capable of living in only a narrow salinity range (e.g., black sea bass).

Temperature

In general, all estuarine organisms can tolerate a very wide range of temperatures, if given adequate time to acclimate (Nybakken 1993). Organisms cannot readily adapt to a rapid increase or decrease in temperature. Early life stages of many species (e.g., clams, oysters, spot, croaker, flounder, menhaden) have a much narrower temperature tolerance than adults (Kennedy et al. 1974). If water temperature becomes too low, or falls too rapidly, there can be a fish kill of sensitive species like seatrout and red drum. Great variability in annual reported catch is typical for seatrout species and seems related to climatic conditions of the preceding winter and spring. Low catches follow severe winters; winter cold shock of juveniles and adults is cited as a primary factor in local and coast-wide declines in spotted seatrout (<http://www.ncdmf.net/stocks/spectrou.htm>, July 2003).

Dissolved oxygen

All fish and invertebrates require a minimum amount of dissolved oxygen (DO) to survive, and an even greater amount for growth and reproduction. Oxygen tolerance varies by organism type. Not accounting for mobility, fish are generally most sensitive to hypoxia (low dissolved oxygen; DO < 2 mg/l), followed by crustaceans and echinoderms, annelid worms, and mollusks (clams, oysters) (Gray et al. 2002). However, because highly mobile organisms can avoid areas of low DO, they are least affected by hypoxia. Although benthic invertebrates are fairly tolerant of low oxygen (Diaz and Rosenburg 1995), stationary invertebrates are helpless against prolonged anoxia. Therefore, DO is considered a critical factor affecting the survival of stationary benthic invertebrates and sedentary fishes and the distribution of mobile species (Seliger et al. 1985; Jordan et al. 1992; Eby et al. 2000; Buzzelli et al. 2002).

Light and water clarity

Water clarity is determined by the concentration of dissolved and suspended organic and inorganic particles in the water column. Water clarity and the resulting light availability in the water column are important to aquatic organisms for several reasons. The combination of increasing light, water velocity, and temperature during spring is the primary cue for upstream movement and spawning of anadromous fish (Klauda et al. 1991; Orth and White 1993). Extreme turbidity is known to reduce phytoplankton and submerged aquatic vegetation biomass, reduce visibility of pelagic food, reduce availability of benthic food due to smothering or bottom water hypoxia, and clog gill rakers and gill filaments (Bruton 1985). Turbidity also reduces a predator’s visual range, which therefore reduces reactive distance (Barrett et al. 1992; Gregory and Northcote 1993), volume of water searched, and feeding efficiency (Moore and Moore 1976; Vingard and O’Brien 1976; Gardner 1981).

The estuarine water column typically has relatively high loading of suspended particles (phytoplankton, detritus, and/or sediment) and reduced water clarity (Nybakken 1993). Some species are adapted to turbid conditions, and the water clarity preference of many estuarine species at various stages of their life cycle is not known (Funderburk et al. 1991). Although excessive turbidity can be problematic, moderate turbidity in estuaries can be beneficial to small or non-visually feeding fish by affording protection from visually feeding predators in shallow, food-rich areas (Ritchie 1972; Blader and Blader 1980; Boehlert and Morgan 1985; Bruton 1985; Miller et al. 1985). Because there is an increased risk of predation in clear waters, some sedentary prey use cryptic coloration, bury under sand, or seek refuge in adjacent habitats to avoid detection. Distinctive aquatic communities can thus be found in turbid and clear water bodies. While water clarity could have an effect on fish species composition, it would be difficult to separate changes in species composition due to water clarity from correlated environmental changes such as salinity, temperature, and depth.

Flow and water movement

Estuaries are mixing zones with complex water movements between fresh and salt water. The four principal factors that affect water movement in North Carolina's estuaries are: (1) rainfall (inflow), (2) wind, (3) lunar tides, and (4) density gradients (salinity and temperature) (DMF 2003b). In some freshwater rivers, flow may also be drastically affected by reservoir releases. Each creek, river, bay, or sound is uniquely different due to these four factors.

Variation in water flow occurs at a broad range of spatial scales in estuarine and marine systems. The interaction of topographic features (e.g., shoals, bays) and tidal or wind-driven circulation patterns creates large-scale (km) spatial variation (Xie and Eggleston 1999; Inoue and Wiseman 2000). At much smaller scales (<1m), topographic changes or the presence of bottom habitat structure (e.g., SAV, oyster reef, pilings, stumps, logs) can create areas of reduced and increased water velocity (Jokiel 1978; Gambi et al. 1990; Komatsu and Murakami 1994; Lenihan 1998). Temporal variation in flow is caused by regular tidal flushing or irregular circulation by the wind.

Each organism in an estuary relies upon certain circulation patterns to provide the conditions that it needs to flourish at a given life stage. Some conditions benefit one species or species' life stage more than others. The conditions needed by a species do not always occur at the same time and location each year due to variations in weather. However, the expansive nature of many South Atlantic estuaries almost assures that proper conditions for a particular species will occur somewhere, but conditions may not be optimal in all locations (NCDMF 2003b).

The aquatic organisms that flourish in estuaries rely on flow and water movement to: (1) deliver the nutrients and physical water conditions for appropriate food and nursery area development at the opportune time; (2) keep eggs and larvae of pelagic spawners in suspension to enhance survival; (3) transport and distribute eggs, larvae, and juveniles to the appropriate nursery area for optimum food availability and protection from predators; and (4) distribute sediment and affect structures that serve as habitats (i.e., shell bottom, SAV, soft bottom) for many fish species (DMF 2003b).

High flows serve as a cue for spawning activity of anadromous fish, whereas low flows correspond to the growth and recruitment period of young fish (Orth and White 1993). Successful spawning of striped bass coincides with optimal water velocities between 3.3 and 6.6 ft/s (100-200 cm/s), while adult American shad prefer water velocities between 2 and 3 ft/s (61-91 cm/s) (Fay et al. 1983d; Mackenzie et al. 1985; Hill et al. 1989). Recruitment of larval river herring in tributaries of the Chowan system is also related to flow conditions (O'Rear 1983). However, water velocity is not the only cue for anadromous fish spawning; increasing light and temperature are also important factors.

Flows have a major effect on biological interactions. Powers and Kittinger (2002) found that blue crab predation on juvenile hard clams and bay scallops decreased with increasing water velocity, while whelk predation on bay scallops increased under the same treatment. Dilution of water-borne chemical cues was likely the reason for reduced blue crab predation (Powers and Kittinger 2002). Tamburri et al. (1996) found that chemical cues successfully induced larval settlement of oysters regardless of flow conditions. In another study, Palmer (1988) showed that higher current velocities increased erosion of small animals from below the sediment surface (meiofauna) into the water column, resulting in increased predation by spot (a more non-visual feeder). Species that rely primarily on visual cues would not be affected by dilution of chemical cues. However, all mobile aquatic organisms (including visual predators) also seek to minimize the energetic cost of movement through the water column while maximizing foraging efficiency.

As fish grow and develop, flow regime requirements or preferences change (Ross and Epperly 1985). Larvae and juveniles generally prefer lower velocities than adults, enabling them to settle out and maintain their positions in the estuary. Consequently, juvenile, estuarine-dependent fish are highly abundant in shallow, side-channel habitats where velocities are low (Ross and Epperly 1985; Noble and Monroe 1991).

There is little information on flow preference of estuarine species. Hydrologic modifications can, in some situations, negatively impact optimum flow conditions for aquatic organisms.

pH

The pH of the water column is a basic chemical characteristic that affects egg development, reproduction, and the ability of fish to absorb DO (Wilbur and Pentony 1999). Among freshwater, estuarine, and marine systems, pH varies naturally, and the organisms of the aquatic community have adapted to that natural variation. However, most fish require pH >5 (Wilbur and Pentony 1999), within a possible range of 0 (extremely acidic) – 14 (extremely basic). The pH of estuaries depends on the dynamic mix of seawater and upstream fresh waters. In high-salinity estuaries with little river input, pH is near that of seawater. Fresh water has the most variable pH, depending on the buffering, or acid controlling, capacity of the water and organic matter input. Freshwater water bodies with low buffering capacity and high organic matter (e.g., swampy creeks) can have very low pH (<5).

The pH of the water is an important requirement for reproduction of estuarine organisms. For example, the optimum pH for normal egg development and larval growth of oysters occurs between 8.25 and 8.5 (Calabrese and Davis 1966; Calabrese 1972). Oysters also have an optimum pH of 7.8 for spawning and >6.75 for successful recruitment. Likewise, hard clam eggs and larvae require pH levels of 7.0-8.75 and 7.5-8.5, respectively, for the same functions (Funderburk et al. 1991). Anadromous fish species can generally tolerate fresh water with lower pH. For example, alewife eggs and larvae require pH between 5.0-8.5 pH and blueback herring eggs and larvae require pH levels between 5.7-8.5 (Funderburk et al. 1991). This pattern of pH requirements between systems also illustrates the adaptation of freshwater and estuarine organisms to their environment.

Species composition and community structure

In many South Atlantic estuaries, during spring and summer, juvenile and adult estuarine species spawned in high-salinity estuarine waters (e.g., blue crab, red drum, weakfish) or the nearshore ocean (e.g., Atlantic menhaden, Atlantic croaker, spot, southern flounder) occupy the low-salinity zone (Table 3.2-9). There are also some resident species that complete their entire life cycle in the low-salinity zone. Residents include estuarine species like bay anchovy but are dominated by freshwater species, such as white perch, yellow perch, catfishes, sunfishes, and minnows (Keefe and Harriss 1981; Copeland et al. 1983; Epperly 1984). Prominent species in this resident group include the spring-spawning white perch and white catfish (Keefe and Harriss 1981). The low-salinity zone is also occupied by the catadromous American eel.

In moderate- and high-salinity estuarine zones, the young of offshore winter and spring spawners, such as Atlantic menhaden, spot, and Atlantic croaker, predominate (Table 3.2-9). See also Essential Fish Habitat section below.

Table 3.2-9. Spawning location/strategy (“spawning guild”) and vertical orientation of some prominent coastal fish and invertebrate species. (Street et al. 2005)

Species*	Vertical orientation[1]		Fishery [3]	Stock Status [4]
	Demersal[2]	Pelagic		
ANADROMOUS FISH				
River herring (alewife and blueback herring)	**E**	**A, J, L**	**X**	**O-Albemarle Sound, U-central/southern**
American shad	**E**	**A, J, L**	**X**	**Concern**
Sturgeon (Atlantic and shortnose)	A, J, E		X[5]	Overfished
Hickory shad	**E**	**A, J, L**	**X**	**Unknown**
Striped bass	A, J	E, L	X	V- Albemarle Sound, Atlantic Ocean, O- Central/Southern
CATADROMOUS FISH				
American eel	A, J	E, L	X	
ESTUARINE AND INLET SPAWNING AND NURSERY				
Bay anchovy		**A, J, E, L**		
Bay scallop	A, J, E	L		Concern
Grass shrimps	A, J, E	L		
Hard clam	A J	E, L	X	Unknown
Mummichog	A, J, E	L		
Oyster	A, J	E, L	X	Overfished
Silversides	**E**	**A, J, L**		
Black drum	A, J	E, L	X	
Blue crab	A, J, E	L	X	Concern
Cobia		**A, J, E, L**	**X**	
Red drum	A, J	E, L	X	Recovering
Spotted seatrout	A, J	E, L	X	Viable
Weakfish	A, J	E, L	X	Viable
MARINE SPAWNING, LOW-HIGH SALINITY NURSERY				
Atlantic croaker	A, J	E, L	X	Concern
Atlantic menhaden		**A, J, E, L**	**X**	**Viable**
Shrimp	A, J, E	L	X	Viable
Southern flounder	A, J	E, L	X	Overfished
Spot	A, J	E, L	X	Viable
Striped mullet	**A**	**J, E, L**	**X**	**Concern**
MARINE SPAWNING, HIGH SALINITY NURSERY				
Black sea bass	A, J	E, L	X	O-south of Hatteras, V-north of Hatteras
Bluefish		**A, J, E, L**	**X**	**Recovering**
Florida pompano	A, J	E, L	X	
Gag	A, J	E, L	X	Viable
Gulf flounder	A, J	E, L	X	
King mackerel		**A, J, E, L**	**X**	**Viable**
Kingfish ("sea mullet")	A, J	E, L	X	Unknown
Pinfish	A, J	E, L	X	
Sheepshead	A, J	E, L	X	
Spanish mackerel		**A, J, E, L**	**X**	**Viable**
Summer flounder	A, J	E, L	X	Recovering

[1] Sources include Epperly and Ross (1986), Funderburk et al. (1991), Pattilo et al. (1997), SAFMC (1998a), NOAA (2001), USFWS species profiles (see literature cited: reference titles beginning with Species life histories and Environmental Requirements), and DMF (unpub. data).

[2] Demersal species live primarily in, on, or near the bottom while pelagic species (**bolded**) occur primarily in the water column. A=adult, J=juvenile, L=larvae, and E=egg.

[3] Existing commercial or recreational fishery. Fishery and non-fishery species are also important as prey.

[4] V = Viable, R = Recovering, C = Concern, O = Overfished, U = Unknown (DMF 2003a).

[5] Former fishery, but fishing moratorium since 1991

Estuarine Water Column as Essential Fish Habitat

The large estuaries of the South Atlantic function as settling basins where coastal rivers meet the sea. As such, the flow of water between the rivers and the estuaries, and between the estuary and the ocean, must be maintained so that settlement of transported larvae to the estuary is successful. Many fish and shellfish species occupy the estuarine water column at some point in their life cycle. Meroplankton (organisms that spend only part of their life cycle in the plankton), in particular, rely on the corridor function of the water column to transport them to favorable nursery areas.

Corridor and connectivity

The corridor function is the most basic function of the water column because the various life stages of fish species must move through it to utilize other habitats supporting other functions. The corridor function is particularly important for anadromous species such as river herring, shad, and striped bass, species that must migrate as adults from high-salinity waters, through estuarine waters, and upstream into freshwater systems to spawn in the spring. As a catadromous species, adult American eel must migrate from upstream freshwaters through estuarine waters to their spawning grounds in the Atlantic Ocean.

Spawning

Anadromous fish species such as river herring (alewife and blueback herring), striped bass, and shads (hickory and American shad) use the freshwater water column to broadcast eggs which develop as they float downstream. All of the life stages of these species use the water column as their primary habitat. Environmental conditions such as heavy rainfall, high water flow, and temperature affect anadromous fish life cycle stages and migration patterns in freshwater systems. Sufficient rainfall is needed to provide suitable current velocities for spawning. The strongest currents are required by striped bass and blueback herring. Slower current velocities are needed for American shad and alewife; alewife spawn in slow-moving oxbows and small streams, as well as fast-water sites. Adequate DO levels in slow-moving backwaters are critical to alewife spawning because the eggs require >5 mg/l DO (Funderburk et al. 1991). During their spawning migration, anadromous fish actively avoid waters with low DO and extremely high turbidity (Steel 1991).

The estuarine spawning species are mostly resident forage finfish species that spawn in shallow water during the warmer months (Table 3.2-10). This group also includes some important shellfish species (e.g., oysters, hard clams, bay scallop) and sportfish (e.g., red drum, weakfish, spotted seatrout, cobia) that spawn in deeper, flowing waters (Luczkovich et al. 1999; Powers and Gaskill 2004). Spawning for oysters, clams, and scallops is triggered primarily by increasing water temperatures during spring and/or decreasing water temperatures in fall (Fay et al. 1983c; Burrell 1986; Eversole 1987). Spotted seatrout, weakfish, and cobia spawn from spring to summer, and red drum in late summer (Table 3.2-10).

Table 3.2-10. Spawning seasons for coastal fish and invertebrate species occurring in North Carolina that broadcast planktonic or semidemersal eggs. [Sources: USFWS species profiles (see literature cited: reference titles beginning with Species life histories and Environmental Requirements), DMF fishery management plans, Funderburk et al. (1991), Pattilo et al. (1997), Luczkovich et al. (1999), NOAA (2001), and DMF (2003a)] **Black** squares indicate peak spawning. **Cross-hatched** squares indicate spawning period (Source: Street et al. 2005).

	Winter			Spring			Summer			Fall		
Species	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
ANADROMOUS FISH												
Alewife		■	■	■	■							
American shad			■	■	■	■						
Blueback herring			■	■	■							
Striped bass			■	■	■	■						
ESTUARINE AND INLET SPAWNING AND NURSERY												
Atlantic silversides			▨	▨	▨	▨						
Bay anchovy				▨	▨	▨	▨	▨	▨	▨		
Bay scallop			▨	▨					▨	■	■	▨
Blue crab				■	■	■	▨	■	■			
Black drum				▨								
Cobia					▨	▨	▨	▨				
Hard clam					▨	▨	▨	▨	▨	▨		
Inland silversides			▨	▨	▨	▨	▨	▨	▨			
Oyster					▨	▨	▨	▨	▨	▨		
Red drum								▨	▨			
Spotted seatrout				▨	▨	▨	■	▨	▨			
Weakfish				▨	■	■	▨	▨	▨			
MARINE SPAWNING, LOW-HIGH SALINITY NURSERY												
Atlantic croaker	▨	▨	▨	▨	▨				▨	■	▨	▨
Atlantic menhaden	■	▨	▨								▨	■
Brown shrimp		■	■	▨						▨	▨	
Southern flounder	■	■	▨								▨	▨
Spot	■	▨									▨	■
Striped mullet	▨	▨	▨							■	■	▨
White shrimp					▨	■	▨					
MARINE SPAWNING, HIGH SALINITY NURSERY												
Black sea bass	▨	▨	■	■	■	▨						
Bluefish			▨	▨	▨	▨	▨	▨	▨	▨	▨	
Gag		■	■									
Gulf flounder	▨	▨									▨	▨
King mackerel						▨	▨	▨	▨			
Pinfish	▨	▨	▨							▨	▨	▨
Pink shrimp				▨	▨	▨	▨					
Sheepshead			▨	▨	▨							
Spanish mackerel					▨	▨	▨	▨	▨			
Southern kingfish				▨	▨	▨	▨	▨	▨			
Summer flounder	■	▨	▨								▨	■

Nursery

Open water provides nursery habitat for most planktivorous larvae and many juvenile pelagic species (e.g., bluefish, river herring, menhaden, Spanish mackerel). The value of open water habitat for these species depends on the abundance and timing of planktonic food sources and their coincidence with required environmental conditions needed for growth during this critical time period.

The interactions of spawning locations, physical processes, environmental factors (salinity and temperature), chemical cues, and habitat preferences are determining factors for the time and place of larval settlement in estuaries (Luckenbach 1985; Peterson et al. 2000c; Brown 2002). The total nursery area for larvae of most estuarine-dependent species extends from the spawning locations to juvenile nursery habitat. For species spawned offshore in winter, the larval (primary) nursery habitat extends from the inlet water column, across primarily inshore-flowing channels, to the upper reaches of estuaries. Survival to the juvenile life stage and beyond is then dependent on the estuarine nursery areas providing the biological, physical, and chemical characteristics needed for growth.

Foraging

Within an estuary, menhaden, anchovy, silversides, striped mullet, and other pelagic species use suspended organic matter exported from the adjacent marshes, SAV, and oyster reefs without physically occupying these structured bottom habitats (SAFMC 1998a). The relative contributions of detritus and phytoplankton between the estuarine and nearshore ocean ecosystem are demonstrated by the foraging behavior of Atlantic menhaden. Lewis and Peters (1994) confirmed that the dominant food source for menhaden was detritus in shallow, estuarine systems, but phytoplankton in coastal waters.

Refuge

The water column provides a basic, but relatively minor, function as refuge for adult finfish and invertebrates. However, the water column does provide some indirect protection for forage species that need unobstructed, open water for protective schooling behavior. For example, silversides can create such dense schools that DO concentrations are low enough to repel predators (Fay et al. 1983a). Other areas of low DO can provide refuge for prey species whose predators are less tolerant of low DO. For example, copepods and zooplankton have a high tolerance for low DO, which could impact the food web in areas where the small invertebrates use low DO areas for refuge (Breitburg et al. 1997; Keister et al. 2000). Large expanses of open water can also provide protection for forage species by reducing their encounters with predators. Turbidity in the water column can provide refuge for prey species from visual predation (Bruton 1985). For example, bay anchovy may be attracted to more turbid areas for the refuge it provides (Livingston 1975). Snags from woody debris or overhanging branches extending from the shoreline provide excellent refuge for fish. Deepwater provides an important refuge from birds that feed in shallow water and protection from colder surface temperatures during winter. Deep, open-water habitats also provide refuge for fish and invertebrates during low tide (Ayvasian et al. 1992). Floating aquatic plants in fresh water such as duckweed may provide refuge for some open water fish.

3.2.7 Soft Bottom/Subtidal

Description and Distribution

(Excerpted from NC CHPP)

Soft bottom habitat is unconsolidated, unvegetated sediment that occurs in freshwater, estuarine, and marine systems. Soft bottom has only one habitat requirement – sediment supply. Environmental characteristics, such as sediment grain size and distribution, salinity, dissolved oxygen, and flow conditions, will affect the condition of the soft bottom habitat and the type of organisms that utilize it. Nevertheless, the habitat itself will persist regardless of its condition unless it becomes starved for sediment or is colonized by other organisms, transforming it into another habitat such as SAV or shell bottom. Refer to FEP Volume IV for more information on ecological impacts of alterations to soft bottom habitat.

Although soft bottom habitat is defined as "unvegetated" and lacks visible structural habitat, the surface sediments support an abundance of microscopic plants; numerous burrowing animals are hidden below the surface (Peterson and Peterson 1979). The characteristic common to all soft bottom types is the mobility of unconsolidated, uncemented soft sediment (Peterson and Peterson 1979). Soft bottom habitat can be characterized by geomorphology (the shape and size of the system), sediment type, water depth, hydrography (riverine, intertidal, or subtidal), and/or salinity regime (DENR 2000a). It is important to understand the physical and chemical properties of soft bottom habitat since these affect the benthic organisms that inhabit these areas and, in turn, their value as fish habitat. The physical and chemical character of all soft bottom is determined by the underlying geology, basin morphology, and associated physical processes (Riggs 1996).

Estuaries and sounds - intertidal flats, unvegetated shoreline and subtidal bottom

Sediment composition of soft bottoms in estuaries and sounds varies with geomorphology and position within the estuary. In North Carolina, the basin morphology of most northern estuaries is similar to a shallow, flat-bottomed dish with a small lip around the perimeter (Pilkey et al. 1998). The estuarine shoreline is a cut bank with a narrow and shallow perimeter platform (the lip) that slopes gradually away from the shoreline to approximately 3-7 ft (1.5-2 m) deep, and then more abruptly to the floor of the central basin. The central basins deepen gradually from the inner estuary to the outer estuary from about 12 – 23 ft deep (4 to 7 m). The central basins become shallow near the mouths of the estuaries due to formation of sandy bars, and behind the barrier islands due to storm overwash and transport of sand from the inlets. Coarse sands are concentrated on the shallow perimeter platforms, shoals, and inlet mouths, while fine sediments such as organic rich mud (ORM) are concentrated in the deeper central basins and downstream channels (Wells 1989; Riggs 1996; Pilkey et al. 1998). The width and thickness of ORM increase as the estuary widens and deepens in the downstream direction, since the fine sediments are easily suspended and transported away from high energy waters (Riggs 1996).

Unvegetated shorelines occur where wave energy prevents colonization by plants and there is a gently sloping area for sand to build upon (Riggs 2001). The shoreline provides an area to absorb the physical energy from waves, tides, and currents, protecting upland areas. Although unvegetated nontidal shorelines are ordinarily exposed from water, and therefore not used by fish, the dynamic processes of erosion and sediment deposition affect the composition and supply of sediment in adjacent shallow water habitats. This in turn affects the type and productivity of the benthic invertebrate community. For example, unvegetated sediment bank shorelines are generally eroding and sandy, providing a source of sand to adjacent waters (Riggs 2001). Sand deposits from inlet flood tide deltas and overwash events on back barrier islands form shallow sand flats behind the islands. In contrast, marsh or swamp forest shorelines are generally not eroding and have a high organic content, thus providing fine organic sediments to adjacent waters. Several shoreline erosion studies have been conducted along North Carolina's coast that provide information on the character and condition of intertidal, shoreline, and shallow subtidal soft bottom and were compiled and summarized in Riggs (2001).

The inlets separating North Carolina's barrier islands are part of a sand-sharing system among the islands, estuaries, and nearshore ocean. Intertidal flats or deltas form on the ebb and flood sides of inlets as sediments shift with tides and waves. Sediments in the vicinity of inlets are typically composed of coarse sands and shell fragments (Peterson and Peterson 1979). Ebb-tidal and flood-tidal deltas (i.e., the seaward and estuarine shoals of an inlet, respectively) are formed by waves and currents, and may contain large volumes of sand. Intense wave and current energy cause the flats to continually change, erode, and reform. The high instability of the ebb and flood tide deltas makes colonization by benthic invertebrates difficult (Peterson and Peterson 1979). Inlets are classified as stable, migrating, or ebb-tidal delta breaching (Fitzgerald et al. 1978). Unstable inlets may form extensive spits, tidal deltas, and sand bars, creating bathymetric complexity (or differences in water depth) in nearshore waters that attract certain fish species. The process of channel realignment and abandonment provides a mechanism for large sandbar complexes to move onto the adjacent barrier islands, supporting productive intertidal beach communities (Cleary and Marden 1999).

Ecological Role and Function

(from CHPP)

Soft bottom plays a very important role in the ecology of estuarine ecosystems as a storage reservoir of chemicals and microbes. Intense biogeochemical processing and recycling establish a filter to trap and reprocess watershed-derived natural and human-induced nutrients and toxic substances. These materials may pass through an estuary (Matoura and Woodward 1983), become trapped in the organic rich oligohaline (low salinity) zone (Sigels et al. 1982; Imberger et al. 1983), or migrate within the estuary over seasonal cycles (Uncles et al. 1988). The fate of the materials depends upon salinity gradients, which are driven by freshwater discharges, density stratification, and formation of salt wedges (Matson and Brinson 1985, 1990; Paerl et al. 1998). Density gradients (stratification) hamper mixing and oxygen exchange of sediments and water in bottom waters with overlying oxygenated waters, leading to depletion of dissolved oxygen in bottom water (Malone et al. 1988).

In North Carolina's slow-moving, expansive estuaries, nutrients and organic matter from the watershed runoff and phytoplankton production are stored in the soft bottoms. Depending upon freshwater discharge and density stratification, these materials are recycled within the sediments via microbial activities and from the sediments into the overlying waters. Increased inflows of nutrients exacerbate the process, leading to more rapid and expanding dissolved oxygen depletion. In organic enriched oligohaline zones (e.g., Pamlico and Neuse River estuaries), nutrient-induced recycling results in higher microbial activity and oxygen depletion (B.J. Copeland, NCSU, pers. com., 2004).

Although soft bottom habitat is composed of unconsolidated shifting sediments, colonization by benthic microalgae reduces the extent to which sediment is resuspended at low velocities, stabilizing bottom sediments and reducing turbidity in the water column (Holland et al. 1974; Underwood and Paterson 1993; Yallop et al. 1994; Miller et al. 1996). In spite of this, microalgae cannot stabilize sediments under intense or prolonged disturbance conditions, such as during large storm events or in the surf zone (Miller 1989). Structure from tube dwelling invertebrates also helps to bind the sediment (Peterson and Peterson 1979), while filtering activity of dense aggregations of suspension feeders (hard clams) clears significant amounts of plankton and sediment from the water column and improves water clarity (Miller et al. 1996). Yet, because of the absence of large, extensive structure, soft bottom provides relatively less stabilization benefits than other estuarine habitats.

Intertidal shorelines, flats, tidal deltas, and sand bars along the ocean shoreline buffer and modify wave energy, reducing shoreline erosion. Alterations to the ebb and flood tide deltas can result in significant changes in the adjacent barrier island shorelines. Flood-tidal deltas are an important source of sand, which allows barrier island migration to respond to sea level rise (Cleary and Marden 1999). The soft bottom associated with inlets has a great influence on overall barrier island dynamics.

Fish utilization

Like the water column, soft bottom is used to some extent by almost all native coastal fish species in North Carolina. However, certain species are better adapted to, characteristic of, or dependent on shallow unvegetated bottom. Flatfish, rays, and skates are well suited for utilization of soft bottom. Juvenile and adult fish species that forage on the rich abundance of microalgae, detritus, and small invertebrates are highly dependent on the condition of soft bottom. Table 3.2-11 summarizes important fishery and nonfishery species that are dependent on subtidal bottom for some portion of their life history and the ecological function of the soft bottom habitat.

Foraging

One of the most important functions of soft bottom habitat is as a foraging area. Members of several trophic levels in the benthic community benefit directly or indirectly from a) the high concentrations of organic matter transported to and produced on soft bottom and b) the numerically abundant, diverse invertebrate fauna associated with soft bottom – including herbivores (e.g., planktonic and benthic algal feeders), detritivores, predators of benthic invertebrates and fish (secondary consumers), and predators of those predators (tertiary consumers) (Peterson and Peterson 1979).

Spawning

Many demersal fish spawn over various areas of soft bottom habitat in North Carolina's coastal waters (Table 3.2-11). In fresh water, resident species such as largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) spawn on shallow flats where they lay eggs in bowl-shaped nests. Eggs may be dependent on the small structure available on the unvegetated bottom, such as emerging worm tubes or woody debris, to hold them in position. Since all life stages of freshwater resident fish (spawning adults, eggs, larvae, juveniles) remain near the same area of soft bottom habitat, they are relatively more vulnerable to degraded soft bottom habitat conditions than migratory species. Anadromous species, such as Atlantic and shortnose sturgeon (*Acipenser oxyrinchus oxyrinchus* and *A. brevirostrum*, respectively), spawn in upper freshwater portions of coastal rivers (Moser and Ross 1995).

Estuarine spawners include resident fish and invertebrates, as well as migratory fish that are summer estuarine spawners. Estuarine resident species include common invertebrates that occupy the intertidal flats, like hard clams, whelks, snapping shrimp, and hermit crabs. Small schooling baitfish such as mummichogs and striped killifish spawn in the marsh edges near soft bottom (Hildebrand and Schroeder 1972; Manooch 1984). Species of flatfish, including the windowpane, and hogfish have been reported to spawn on estuarine soft bottom (Hildebrand and Schroeder 1972; Manooch 1984).

Summer estuarine spawners include several species of drum. Weakfish and silver perch were documented spawning in deep estuarine channels near Pamlico Sound inlets (Ocracoke and Hatteras inlets) and in deep areas of Pamlico Sound from May to September, peaking in May and June (Luczkovich et al. 1999a). Spotted

seatrout are year-round residents of estuaries along the South Atlantic coast and spawning takes place inshore and in coastal areas (McMichael and Peters, 1989). In North Carolina, spotted sea trout spawn on the east and west sides of Pamlico Sound during a similar time period, with peak activity observed around July. Specific spawning areas for spotted sea trout identified on the west side of Pamlico Sound were Rose Bay, Jones Bay, Fisherman's Bay, and Bay River (Luczkovich et al. 1999a). In South Carolina, spotted seatrout spawn in similar habitats from April through September (Roumillat and Brouwer, 2004). Red drum were documented spawning in the mouth of the Bay River on the west side of Pamlico Sound, and in estuarine channels near Ocracoke Inlet (Luczkovich et al. 1999a). Blue crabs also spawn near inlets in summer (DMF 2000d).

Nursery

Shallow soft bottom habitat, usually adjacent to wetlands, is utilized as a nursery for many species of juvenile fish. The shallow unvegetated bottom provides an abundance of food and is inaccessible to larger predators. Shallow unvegetated flats have been documented as being particularly important nursery habitats for juvenile summer and southern flounder (Burke et al. 1991; Walsh et al. 1999). A partial list of species that use soft bottom habitat as a nursery area is included in Table 3.2-11. Studies and ongoing juvenile fish monitoring conducted by the North Carolina Division of Marine Fisheries have found that shallow unvegetated bottom supports high abundances of juvenile fish, composed of relatively few species but which have similar life histories and feeding patterns (Ross and Epperly 1985).

The dominant juvenile species utilizing shallow soft bottom estuarine nursery areas are estuarine dependent winter spawners. Most of the species spawn offshore during the winter. The larvae are transported through inlets into estuarine waters. For many species, the uppermost area of shallow creek systems corresponds to where larval settlement of winter spawned species occurs – the primary nursery areas (Weinstein 1979; Ross and Epperly 1985). However, in tributaries on the western side of Pamlico Sound, such as Neuse, Pamlico, Bay and Pungo rivers, larval settlement tends to occur in lower portions of the creeks. Unlike larval settlement in areas south of Pamlico Sound, salinity is low in the upper reaches of the Sound's tributaries and this may deter larval settlement in those areas. Abundance of juvenile species in estuarine nursery areas peaks between April and July and is correlated with water temperatures (Ross and Epperly 1985). As fish grow, they move to deeper waters and areas lower in the estuary.

In North Carolina, many areas used as nurseries by estuarine dependent fish have been designated as Primary or Secondary Nursery Areas by the Marine Fisheries Commission. However, there are other areas of soft bottom that function as nurseries but are undesignated. Benthic anadromous fish, such as Atlantic and shortnose sturgeon, use freshwater soft bottom as a nursery.

Refuge

Soft bottom habitat can provide refuge to some organisms in some locations through predator exclusion. Shallow, intertidal flats may be inaccessible to large fish predators and therefore protect small and juvenile fish and invertebrates (Peterson and Peterson 1979; Ross and Epperly 1985). Consequently, juvenile fish recruit into the shallowest portions of the estuary first. Many invertebrates, including hard clams, can avoid predation by burrowing into the sediment (Luettich et al. 1999). Flatfish, such as flounder and rays, and other small cryptic fish, like gobies, can bury slightly into the sediment, camouflaging themselves from predators (Peterson and Peterson 1979). Nonetheless, soft bottom habitat in deepwater is a vulnerable place for small fish and invertebrates that cannot burrow. For example, flounders also camouflage themselves in the sediment to ambush prey (Walsh et al. 1999). Because of this, many fish in subtidal water will venture out to feed on the open bottom only at night (Summerson and Peterson 1984).

Corridor and connectivity

Freshwater and estuarine soft bottom channels are the highways for migrating adult demersal fish species to and from other estuarine habitats and the ocean. Demersal feeding anadromous fish, such as sturgeon and striped bass, require a corridor of soft bottom to reach upstream spawning areas. Inlets act as conduits for exchange of sediment, water, and marine organisms between the estuaries and the ocean. Because large fish are less likely to be consumed as prey, they can travel relatively safely over less turbid sand flats and in channels of the middle and lower estuaries (Walsh et al. 1999). Smaller flatfish tend to be more abundant in the shallower uppermost portion of the estuary, where salinities are low, turbidity high, and sediments muddy with high detritus content (Walsh et al. 1999).

While connectivity among structured habitat patches, such as SAV, wetlands, and shell bottom, facilitates movement of blue crabs and other mobile predators through an estuary, a few meters of unvegetated bottom can act as a barrier to movement (Micheli and Peterson 1999). Such barriers can be beneficial to small invertebrates by potentially obstructing predator dispersal and reducing predation risk. Small crabs, gastropods, and infaunal bivalves, such as hard clams, were more abundant, denser, and had higher survival rates on isolated oyster beds (at least 10-15 m of unvegetated bottom between habitats) than on oyster beds adjacent to salt marsh or SAV (Micheli and Peterson 1999). Blue crab predation on infaunal bivalves was greater along vegetated edges of salt marshes and seagrass beds than in unvegetated intertidal flats (Micheli and Peterson 1999). Although structural habitat separations by unvegetated soft bottom may benefit the survival or viability of infaunal populations, fish and crustacean productivity may be enhanced by connectivity of structured estuarine habitats (Micheli and Peterson 1999). These habitat-mediated predator/prey interactions point out the importance of maintaining the integrity of an entire estuarine system.

Table 3.2-11. Partial list of common or important fish species occurring on soft bottom habitat in riverine, estuarine, and ocean waters, and ecological functions provided to hose species. Bolded species indicate relatively higher association on soft bottom habitat (Source: Street et al. 2005).

Species*	Soft bottom functions [1]					Fishery [2]	Stock status [3]
	Spawning	Nursery	Foraging	Refuge	Corridor		
ANADROMOUS SPAWNING							
Atlantic sturgeon	**X**	**X**	**X**		**X**	**X**[4]	**O**
Shortnose sturgeon	**X**	**X**	**X**		**X**	**X**[4]	**O**
ESTUARINE AND INLET SPAWNING AND NURSERY							
Blue crab	X	X	X	X		X	C
Hard clam	**X**	**X**	**X**	**X**		**X**	**U**
Hermit crab spp.	**X**	**X**	**X**				
Horseshoe crab	**X**	**X**	**X**			**X**	
Mud crab spp.	**X**	**X**	**X**				
Mummichug	**X**	**X**	**X**				
Naked goby	X	X	X				
Red drum	**X**	**X**	**X**			**X**	**R**
Sheepshead minnow	**X**	**X**	**X**				
Silver perch	X	X	X			X	
Striped killifish	X	X	X				
Whelks	X	X	X			X	
MARINE SPAWNING, LOW-HIGH SALINITY NURSERY							
Atlantic croaker		**X**	**X**			**X**	**C**
Bay whiff		**X**	**X**	**X**	**X**		
Blackcheek tonguefish	**X**	**X**	**X**	**X**	**X**		
Hogchoker	**X**	**X**	**X**	**X**	**X**		
Penaeid shrimp (brown, white, pink)		**X**	**X**	**X**	**X**	**X**	**V**
Southern flounder		**X**	**X**	**X**	**X**	**X**	**O**
Spot		**X**	**X**			**X**	**V**
Striped mullet		**X**	**X**			**X**	**C**
MARINE SPAWNING, HIGH SALINITY NURSERY							
Atlantic stingray	**X**	**X**	**X**	**X**	**X**	**X**	
Coastal sharks [5]	**X**	**X**	**X**			**X**	**O**
Cownose ray	**X**	**X**	**X**	**X**	**X**	**X**	
Florida pompano		**X**[6]	**X**			**X**	
Fringed flounder		**X**	**X**	**X**	**X**		
Gulf flounder		**X**	**X**	**X**	**X**	**X**	
Gulf kingfish		**X**[6]	**X**			**X**	**U**
Smooth dogfish	X	X	X			X	U
Spiny dogfish		X	X			X	O
Striped anchovy		**X**[6]	**X**				
Summer flounder	**X**	**X**	**X**	**X**	**X**	**X**	**V**

* Scientific names listed in Appendix I. Names in **bold** font are species whose relative abundances have been reported in the literature as being generally higher in soft bottom than in other habitats. Note that lack of bolding does not imply non-selective use of the habitat, just a lack of information.

[1] Sources: Peterson and Peterson (1979); Thorpe et al. (2003); Manooch (1984); Hildebrand and Schroeder (1972); Lippson and Moran (1974); Wang and Kernehan (1979)

[2] Existing commercial or recreational fishery. Other species important to the system as prey items.

[3] V = viable, R = recovering, C = concern, O = overfished, U = unknown (DMF 2003a)

[4] Former fishery, but fishing moratorium since 1991

[5] Incl. Atlantic sharpnose, blacknose, blacktip, bonnethead, dusky, sandbar, scalloped hammerhead, and spinner sharks

[6] Uses surf zone almost exclusively as nursery area

Species composition and community structure

Benthic microalgae are a key part of the food chain in estuarine soft bottom habitat. Benthic microalgae are microscopic photosynthetic algae that live in the top few millimeters of the surface of soft bottom (Miller et al. 1996). Because the unvegetated bottom appears barren, but is actually rich in photosynthetic algae, MacIntyre et al. (1996) referred to benthic microalgae as "The Secret Garden." Benthic microalgae on sand, mud flats, and subtidal bottom are composed primarily of benthic diatoms and blue green algae, with benthic dinoflagellates and filamentous green algae also present (Peterson and Peterson 1979). Dense mats of blue green algae sometimes form in protected higher portions of intertidal flats, giving the sediment surface a dark brown or blue-green appearance, which can form a crusty mat when dry at low tides (Peterson and Peterson 1979). Diatom mats are more abundant in the lower intertidal zone (Peterson and Peterson 1979). Benthic microalgae can either be attached to sediment particles or be mobile, migrating vertically through the sediment. Productivity depends on photosynthesis by these microalgae, which can only occur in sediments having adequate light penetration (MacIntyre et al. 1996). Photosynthetically active light generally penetrates only about 2-3 mm into the sediment, but can reach 5-20 mm in sandy, high energy environments.

Most benthic invertebrates inhabiting soft bottom live in the sediment (infauna), as opposed to the bottom's surface (epifauna), because of the high mobility of sediments (Peterson and Peterson 1979). These animals are classified by size and feeding mode. Microfauna are the very small protozoans (< 0.06 mm). Meiofauna are about 0.06 – 0.40 mm in size (the size of a sand grain), and include nematodes and copepods. Both microfauna and meiofauna are important grazers on benthic microalgae and bacteria. Macrofauna (>0.5 mm) contribute the most to infaunal biomass and include organisms such as amphipods, polychaetes, mollusks, echinoderms, and crustaceans (Peterson and Peterson 1979). These macrofauna may be deposit feeders or suspension feeders (Peterson and Peterson 1979; Miller et al. 1996). Deposit feeders ingest sediment and detrital deposits and assimilate bacteria, fungi, and microalgae from them. Compared to detritus and larger plants, microalgae may be a nutritionally richer food source for benthic invertebrates (Miller et al. 1996). Deposit feeders include mud snails, many polychaete worms, and certain bivalve clams and crustaceans.

Suspension feeders capture particles suspended in the water column. Common suspension feeders are bivalves such as the hard clam (*Mercenaria mercenaria*) and razor clam (*Tagelus plebeius*), and some polychaete worms (Miller et al. 1996). When sediment is resuspended, the benthic microalgae become available to the suspension feeders (Miller et al. 1996). A large proportion of intertidal bivalves' diet has been shown to consist of suspended benthic microalgae, particularly when chlorophyll concentrations in the water column are low (Page and Lastra 2003). While resuspended benthic microalgae can be beneficial to the invertebrate community as an additional food source, excessive suspended sediment and associated algae have been found to reduce growth rates and survival of macrofauna, such as hard clams (Bock and Miller 1995). Although the abundance of food sources affects invertebrate populations, benthic predators (such as spot and pinfish) were found to have a larger influence on soft bottom community composition and biomass relative to that of nutrient availability (Posey et al. 1995).

On submerged flats and shallow bottom, blue crab (*Callinectes sapidus*) is an important predator. Other mobile invertebrates include horseshoe crab (*Limulus polyphemus*), whelks (*Busycon* spp.), tulip snails (*Fasciolaria* spp.), moon snails (*Polinices duplicatus*), penaeid shrimp (*Farfantepenaeus* spp. and *Litopenaeus* spp.), hermit crabs (*Pagurus* spp., *Petrochirus* spp., and *Clibanarius vittatus*), sand dollars (*Mellita quinquiesperforata*), and spider crabs (*Libinia* spp.). Overall, estuarine soft bottom supports a high diversity of benthic invertebrates, with over 300 species documented in the southern portion of North Carolina (Hackney et al. 1996).

Soft Bottom/Subtidal as Essential Fish Habitat

3.3 Marine/offshore systems

3.3.1 Coral, Coral Reefs and Live/Hardbottom Habitat

3.3.1.1 Coral Reefs and Coral Communities

Description and distribution

Shallow water coral reefs and coral communities exist within the southern geographical areas under Council authority. In this document these habitats are defined as occurring in depths generally less than 40 meters. Depending upon many variables, stony corals may dominate a habitat, be a significant component, or be individual colonies within a community characterized by other fauna (e.g., sponges or macroalgae). In some areas stony corals have grown in such profusion that their old skeletons accumulate and form reef structure (e.g., coral reefs). In other areas, corals grow as a less dominant component of benthic communities on geologically derived hard substrates (e.g., coral communities). This section focuses on those ecosystems under Council authority having Scleractinians as an important member of the community. Hardbottom communities that have little or no Scleractinians are treated in the Live/Hardbottom Habitat section of this document (Section 3.3.1.2 below).

Reefs have been defined or characterized in numerous ways on the basis of rigidity, location, framework elements, sediments, and biotic diversity. To that end, Fagerstrom (1987) listed several definitive characteristics of reefs that apply to shallow coral reefs in the southeast U.S.:

- A rigid framework is present;
- Calcareous keletons or other calcareous micro-structures are abundant;
- Structures have positive topographic relief;
- Framework organisms have rapid growth rates; and
- Taxonomic diversity is high, with several ecological functional groups.

Shallow warm water coral reef and coral communities are typically, though not always, built upon coralline rock and support a wide array of corals, finfish, invertebrates, plants, and microorganisms. Hardbottoms and hard banks, found on a wider bathymetric and geographic scale, often possess high species diversity but may lack reef building corals, the supporting coralline structure, or some of the associated biota. In deeper waters, large elongate mounds called deepwater banks, hundreds of meters in length, often support a rich fauna compared to adjacent areas. Lastly are communities that may include solitary corals. This category often lacks a topographic relief as its substrate, but instead may use a sandy bottom, for example.

This section discusses coral reefs and coral communities which are habitats with corals as important contributors, and includes outer bank coral reefs, coral communities, and patch reefs (defined below). Although attempts have been made to generalize the discussion into definable types, it must be noted that the continuum of habitats includes many more than these varieties discussed below.

The following definitions of selected terminology are used throughout this Section.

<u>Stony Corals</u>: Stony corals are marine invertebrates that secrete a calcium carbonate skeleton. For the purpose of this plan, includes species belonging to the Class Hydrozoa, Family Milleporidae (fire corals) and Class Anthozoa, Order Scleractinia. The scleractinians can be hermatypic (significant contributors to the reef-building process) or ahermatypic, and may or may not contain endosymbiotic algae (zooxanthellae) (Schumacher and Zibrowius 1985). Zooxanthellate corals, host symbiotic algae from the Genus *Symbiodinium*, which provide a phototrophic contribution to the coral's energy budget, enhance calcification, and give the coral most of its color.

<u>Octocorals</u>: For the purpose of this plan, includes species belonging to the Class Anthozoa, subclass Octocorallia (soft corals and gorgonians).

Reef Habitat Types

Outer Bank Reefs

Outer bank reefs represent perhaps the geologically and ecologically oldest, most structurally complex and diverse type of coral habitat. They are located in the Florida reef tract primarily shoreward of the 18 m (60 ft) isobath. Shinn et al. (1977) and Shinn (1979) concluded that the linearity of these reefs approximately parallel to the Keys is due to underlying bedrock topography, rather than biological or water quality causes. The Florida reef tract includes approximately 96 km (52 nm) of outer bank reefs located between Fowey Rocks and the Dry Tortugas, a distance of about 270 km (146 nm) along the 20 m (66 ft.) isobath. A large portion of the reef tract is in the EEZ just beyond Florida's three-mile territorial sea.

In some areas, outer bank reefs display some characteristics of classical Caribbean reef structure and zonation such as high-relief spur and groove structures in the shallow fore-reef, a very shallow or emergent reef crest, and a rubble habitat in the leeward shadow of the reef crest. Spurs are extensions of coral reef growth seaward up to 30 m (100 ft) or more; grooves occur between adjacent spurs. Spurs and grooves are best developed in the upper and lower Keys. The middle Keys area exhibits some spur and groove formation but the orientation and development is variable (Marszalek et al. 1977). Shinn et al. (1981) found that spurs at Looe Key were constructed of *Acropora palmata* and had formed over five meters of carbonate sand. Spurs at Looe Key are no longer accreting due to the extensive die-off of *A. palmata*.

Generally, Florida reefs are smaller in area, less biologically diverse, and lack the vertical relief of most coral reefs of the Bahamas or Caribbean Sea (Marszalek et al. 1977). However, coral species diversity is still comparable to or greater than reefs bordering nearby countries.

Some areas of the outer bank reef are underdeveloped, occurring as coral reefs with sparse coral growth and no *Acropora palmata* zone. These reefs may represent relict limestone ridges in the spur and groove arrangement or relatively young reefs with immature biological zonation patterns (Marszalek et al. 1977). Long Reef in the upper Keys is an example of the relic reef case (see, for example, Shinn et al. 1977). Small stands of immature coral reef biota often bridge the gaps between more well-developed reefs.

Other areas of the outer bank reef are more developed (Marszalek et al. 1977) characterized by their "reef-flat formed of *in situ* dead encrusted elkhorn coral, *Acropora palmata*, skeletons and rubble." Colonies of *Acropora*, finger coral *Porites*, and starlet coral *Siderastrea* plus encrusting fire coral *Millepora* and dozens of benthic species form most of the live reef structure. The typical zonation pattern shows *A. palmata* colonies on the seaward face of the reef to a depth of about 4 m, with *M. complanata* and the colonial zooanthid *Palythoa* in the turbulent shallow zone and a diverse coral assemblage dominated by small star coral, *Montastraea annularis*, heads in the deeper sections (Shinn 1963). Within the Florida reef tract, Carysfort Reef and Key Largo Dry Rocks (Grecian Rocks) are examples of well developed coral reefs.

Coral Communities

Coral communities constitute a group of communities characterized by a thin veneer of live corals and other biota overlying assorted sediment types. They are usually of low relief and on the continental shelf (Bright et al. 1981); many are associated with relic reefs where the coral veneer is supported by dead corals. This grouping of coral habitat encompasses a large portion of the management area containing stony corals (Southeast Florida), especially north of the Florida Keys and south of central Florida.

Ecologically and geologically, coral communities are a diverse category. Most have a diverse assemblage of stony corals but lack the clear ecological zonation and density of frame builders typical of other coral reefs throughout the Caribbean. Diverse biotic zonation patterns vary between many of these communities because of their geologic structure and geographic location. For example the shallow water (<5m) coral communities located nearshore differ from the coral communities in deep water (>20m) in stony coral species, size distribution, and density. Coral communities are common on rocky ledges, overlying relic reefs, or on a variety of sediment types. In each case, species compositions may vary dependent upon water depth and associated parameters (light, temperature, etc.).

Coral communities in different geographical areas support different coral assemblages. Near the Florida Keys, they co-exist as underdeveloped reefs nearshore and seaward of the outer bank reef tract. North of Fowey Rocks off southeastern Florida, coral communities include all types of corals, though hermatypic species are near their northern limit (Martin County).

In the Florida Keys, coral communities of nearshore areas have been characterized by Chiappone and Sullivan (1994) and off the mainland by Nelson (1989) and Nelson and Demetriades (1992). Nearshore coral communities' characteristics differ substantially between the mainland coast of east Florida and the Florida Keys. These differences include higher wave energies, fewer corals and grasses, and coarser sediments in nearshore coral communities of mainland areas (Lindeman 1997). Additional factors complicate Keys and mainland comparisons of coral communities.

Nearshore coral communities in the Keys are distributed across more physiographically variable cross-shelf gradients with a greater potential for structural heterogeneity than on the mainland. The presence of over 6000 patch reefs in Hawk Channel (Marszalek et al. 1977), many near shallow coral communities, introduces additional inter-habitat relationships rarely found in nearshore coral communities of mainland areas.

In southeast Florida (north of the Keys), coral communities have been described by Goldberg 1973a, Moyer et al. 2003, Gilliam et al. 2007a and b, and Banks et al. 2007, and mapped using GIS and remote sensing techniques by Walker et al. *In press*. These communities have developed on relict reef tracts parallel to the shoreline in different depths separated by large expanses of sand (Banks et al 2007). The deepest community, the Outer Reef, still has many evident features of the relict reef zonation. For example, spur and groove formations dominate the eastern sides of these reefs, yet they reside in >25m depth. Even though they appear as spur and groove, they no longer function as such and do not contain an abundant population of fast-growing, frame-building corals. This is in contrast to some nearshore coral communities in the same area. Some nearshore coral communities (especially in Broward County) have a significant number of fast-growing, large, frame-building corals, yet they lack distinct zonation. There is no emergent reef crest, spur and groove fore reef, or lagoon. This community may be considered the beginnings of a new reef, however without the advantage of the Caribbean's fastest growing, frame-building coral, *Acropora palmata*, and its proximity to significant coastal development, it is unlikely to continue.

Communities containing corals from Florida north (Martin County) to North Carolina, have distinctly different assemblages than those further south. There are deep water communities dominated by a single species (*Oculina*), and shallow-water sponge or macroalgae dominated hardbottom communities where very few species of stony corals exist at low densities. These communities are covered in other sections of this document.

Patch Reefs

Patch reefs are irregularly distributed clusters of corals and associated biota located in the management area generally along the seaward (southeast) coast of the Florida Keys. Most patch reefs occur 3 to 7 km (1.6 to 3.8 nm) offshore between Miami and the Dry Tortugas on the inner shelf (less than about 15 m depth). Vertical relief ranges from less than 1 m to over 10 m. Patch reefs occur as either dome-type patches on the leeward side of outer bank coral reefs or as linear-type patches that parallel bank reefs in arcuate patterns. More than 6,000 patch reefs occur in the Florida reef tract between Miami and the Marquesas Keys, (Marszalek et al. 1977), mostly between Hawk Channel and the outer bank reefs. From above, dome patch reefs tend to be clustered. Linear-type patch reefs support flora and fauna, including elkhorn coral (*Acropora palmata*), which more nearly resemble the bank reefs. Most dome patch reefs have less than 5 m of topographic relief, but some as high as 9 m do occur. Linear-type reefs are usually situated seaward of dome-type patch reefs parallel to the outer bank reefs. In top view, linear patch reefs appear arcuate to linear, much like the outer bank coral reefs of the Florida reef tract. Hence, instead of forming clusters, these patch reefs often occur end-to-end. These linear offshore reefs are also referred to as inner line reefs and probably represent an ecologic transition form between dome patch reefs and outer bank reefs (Marszalek et al. 1977).

Patch reefs also exhibit ecological variability. Dome-type assemblages support a diverse array of stony corals and octocorals, plus numerous benthic invertebrates, algae, and fish (Marszalek et al. 1977). Except for the noticeable absence of elkhorn coral, *Acropora palmata*, the biota of dome patches resembles that of consolidated outer bank reefs, but with less coral zonation. Octocorals dominate the top interior zones whereas *M. annularis, Diploria* spp., and *Colpophyllia natans* dominate western margins. The dominant coral in this type of patch reef is the small star coral, *Montastraea annularis*, which is often present in single enormous colonies, (see also Shinn 1963). Linear-type patch reefs support corals and other marine life much like dome-types with the possible addition of *A. palmata*.

Other Habitats

Throughout much, if not all, of the management area, other bottom communities exist which include corals as a minor component of biotic diversity and abundance [for example Cairns (1979) in the Atlantic]. Although these corals contribute benthic relief and habitat to communities throughout the Council authority, they apparently comprise a minor percentage of the total coral stocks in the management area.

Ecological role and function

Coral reefs and communities serve a number of functional roles in subtropical and tropical environments of the western Atlantic, including, but not limited to: primary production, recycling of nutrients in relatively oligotrophic waters, calcium carbonate deposition yielding reef construction, refuge and foraging base for other organisms, and modification of near-field or local water circulation patterns (De Freese 1991). Coral reefs also protect shorelines, serving to buffer inshore subtidal (e.g., seagrass) and intertidal (e.g., mangroves) communities from otherwise high wave energy conditions in certain localities.

Coral reefs and communities, including associated sediments, afford organisms an incredible array of refuges (Jaap 1984). Epifauna are organisms living on the reef surface, and include mobile animals (crustaceans, echinoderms, mollusks, and fishes) and sessile animals (e.g., ascidians, sponges, corals, and bryozoans). Infauna include those animals which burrow into reef substrate, such as polychaete worms and mollusks. Meiofauna include animals associated with reef sediments. Holes and crevices in the reef structure provide shelter for echinoderms, mollusks, polychaetes, crustaceans, and fishes. In a single coral colony, for example, Grassle (1973) counted 1,441 polychaetes representing 103 species. In several coral colonies, McClosky (1970) counted 1,517 individuals representing 37 different invertebrate species. Gastropods, crustaceans, echinoderms, and fishes consume benthic algae associated with the reef structure (i.e., coral-produced substrate); these herbivores, in turn, fuel the production of higher trophic levels such as invertivores and piscivores.

Coral reefs and communities occurring in the management area, and indeed throughout the world, are markedly affected by patterns of water circulation. The most highly developed reefs in the management area are the Florida Keys reefs, generally confined to the windward or southeastern margins of the land masses (Glynn 1973; Shinn 1976). An important characteristic of coral reefs is their ability to modify the surrounding physical-chemical environment (Ginsburg and Lowenstam 1958). The reef framework controls the accumulation of sediments on and adjacent to the reef, as well as local circulation patterns (Jaap 1984). Coral reefs are an example of the ability of biological communities to affect physical circulation mechanisms, which in turn influence benthic community distribution and sedimentation. Bank reefs provide shelter for the back reef lagoon, allowing for benthic communities adapted to low-wave energy conditions, such as seagrass beds, to persist and flourish. Several studies have noted the differences in sediment and habitat characteristics between inshore and offshore environments (Enos 1977; Szmant and Forrester 1996) and associated differences in sediment nutrient characteristics. Sediments in the back reef (inner shelf margin) consist of finer grain particles with greater nutrient pools relative to sediments directly associated with reefs, such as large skeletal fragments. Benthic community distribution also differs considerably between nearshore and offshore. Seagrasses and other soft-sediment communities dominate the inner shelf margin, while reefs and bare sand slope areas dominate the outer shelf margin.

The protection offered by land from cross-platform currents (Ginsburg and Shinn 1964) is mirrored by the buffer provided to the islands by relic and/or live coral reefs. Offshore reefs help dissipate storm energies and serve to minimize impacts of storms, wave action, and other physical stresses.

Protection offered by coral reefs is crucial to the existence of other shallow-water, continental shelf communities in South Florida. Sea grass beds, mangroves, and back reef coral communities are protected from high wave energy by coral reefs in the Florida Keys. Without the buffer of coral reefs, these three important components of the coastal ecosystem would be exposed to unusually destructive forces. A loss of one of these habitats would affect the other communities as they are dependant on one another. Mangroves and beds of turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*) represent highly productive communities (Helfrich and Townsley 1965), on which numerous species such as spiny lobster (Herrnkind 1979; Davis 1979) and commercial finfish (Weinstein and Heck 1979), depend for development, recruitment, and foraging grounds. These habitats are also crucial to nutrient flows in the coastal environment and without grass beds and mangroves to assist in filtering sediments, coastal waters would deposit particulates on corals and other bottom dwellers. Therefore protection of all of these habitats is essential.

Species composition and community structure

Central Florida to North Carolina

Coral assemblages from central Florida (Stuart Inlet) north to North Carolina, are dominated by ahermatypic stony coral species and gorgonians, although some hermatypic species do occur off North Carolina (MacIntyre and Pilkey 1969) and Georgia (Hunt 1974). The very limited coral assemblages within this area are found on shallow-water hardbottom habitats ((Johnston 1976); off Georgia and South Carolina (Stetson et al. 1962; Porter 1978 personal communication; Thomas 1978 personal communication); and North Carolina (Huntsman 1984; MacIntyre and Pilkey 1969)) and deep-water banks (*Oculina* spp.). These are further described in Section 4.1.6 of this document.

Southeast Florida

This extensive coral reef and coral community system is a northward continuation of the Florida reef tract extending over 150 kilometers from northern Monroe County, through Miami-Dade, Broward, and Palm Beach Counties and into Martin County. From northern Miami-Dade

County into Palm Beach County, there are generally three reef lines, parallel to the shore and separated by sand deposits, – one that nominally crests in 3 to 4 m of water depth (Inner Reef), another in 6 to 8 m (Middle Reef), and one in 15 to 21 m depth (Outer Reef). On the shoreward side of the Inner Reef, a series of nearshore hardbottom ridges often occur (Moyer et al. 2003, Banks et al. 2007, Walker et al. *In press*).

This reef system includes over 30 species of stony corals with an average coverage of 2-3% (maximum of nearly 15%) and includes a diverse assemblage of gorgonians and sponges (Gilliam et al. 2007a and b). Nearshore, however, there are a number of *Acropora cervicornis* patches with cover approaching 30% (Gilliam et al. 2007a and b). The common stony coral species include: *Montastrea cavernosa*, *Siderastrea siderea*, *S. radians*, *Porites astreoides*, *Solenastrea bournoni*, *Meandrina meandrites*, and *Dichocoenia stokesii*.

Octocorals (gorgonians) and sponges dominate most of the communities in the system with a density of 8-10 colonies/m^2 and 11-14 colonies/m^2 and a cover of 7-20% and 2-8%, respectively (Gilliam et al. 2007a and b). Some of the common octocoral genera include: *Eunicea* spp., *Pseudopterogorgia* spp., *Muricea* spp., *Plexaurella* spp., and *Pterogorgia* spp.

The coral communities in northern Palm Beach and southern Martin Counties are a reasonable northern limit for the subtropical coral reefs on the east coast of Florida. These communities exist on hardbottom habitats with diverse assemblage of reef biota. Fewer stony coral species are present in these northern areas but several of the species common throughout the coral reef habitats south are also common and include: *Montastrea cavernosa*, *Diploria clivosa*, *Siderastrea siderea*, *Isophyllia sinuosa*, *Solenastrea bournoni*, and *Oculina diffusa*.

Nearshore Coral Communities

The nearshore coral communities extend from Key Biscayne in Central Miami-Dade County to Hillsboro Inlet in northern Broward County (Shallow Colonized Pavement and Ridges in Walker et al. *In press*). This habitat is defined as flat, low relief, solid carbonate rock with coverage of macralgae, stony coral, gorgonians, and other sessile invertebrates that are dense enough to partially obscure the underlying carbonate rock (Walker et al. *In press* adapted from Kendall et al. 2001). This habitat can have variable sand cover, which shifts according to wave-energy in response to weather. Thus, some of the colonized pavement will always be covered by shifting sand and colonization will be highly variable (Walker et al *In press*).

Portions of the nearshore coral communities contain areas of the highest stony coral cover in the region (Gilliam et al. 2007a and b). Larger stony corals in this area are abundant with 15% or higher coral coverage (compared to the more typical 1-3% coral coverage). *Montastrea cavernosa* dominates this assemblage.

This habitat also contains perhaps the most abundant population of staghorn coral, *Acropora cervicornis* in the Council management area. Cover with *A. cervicornis* patches exceeds 20% (Gilliam et. al 2007a and b) and spawning activity has been documented (Vargas-Angel et. al 2006).

The largest corals in the region have been documented on this habitat as well. Although a formal study has not been performed, an analysis of bathymetric data and subsequent field verification has identified many very large, living *Montastrea faveolata* and *M. annularis* colonies. These colonies range in size from 1 to 4 meters in diameter/height and shelter many large fishes and invertebrates. One area in particular contains over 20 *M. faveolata* colonies over 1m diameter including several >2m. Several of these large colonies throughout Broward County have been cored to identify the age of the coral and recent past living conditions. The largest known colony located off Hollywood, FL is a 2.5 m tall, 4.2m wide *M. faveolata* which was estimated at ~310 years of age in 2005 when it was cored (Helmle, pers. comm.).

Inner Reef

The Inner Reef extends from central Miami-Dade County (Key Biscayne) to northern Broward County (Hillsboro Inlet). It is composed mainly of *A. palmata* framework (Banks et al., 2007) and has many breaks and sediment pockets within and along its linear, shore-parallel morphology. The Inner Reef is not a mature reef with distinct zonation and the present lack of fast growing, reef building corals on this feature (especially *A. palmata*) suggests it is no longer aggrading (Banks et al., 2007, Walker et al. *In press*).

The Inner Reef is however a valuable coral reef community colonized by many ecologically important species. Typical sessile organisms are sponges, octocorals, and stony corals. The stony coral assemblage is quite diverse including but not limited to the following species: *M. cavernosa*, *S. siderea*, *S. radians*, *P. astreoides*, *S. bournoni*, *M. meandrites*, *D. stokesii,* and *A. cervicornis*. Some coral species, especially those with flat growth forms (*Diploria clivosa*, *Meandrina meandrites*) reach over 1m in diameter. Other ecologically important species include a diverse, abundant assemblage of octocorals and sponges, as well as colonial zoanthids (*Palythoa caribaeorum*).

The Inner Reef, and the nearshore community, appears to be an important nursery area for fishes. A recent survey recorded 169 species of fishes in this area of which recently settled juveniles (≤ 5 cm) were the dominant component (>84%), consisting primarily (>90%) of grunts (Haemulidae) (Baron et al. 2004).

Middle Reef

The Middle Reef extends from Northern Miami-Dade County (Haulover Inlet) to Southern Palm Beach County (Boca Inlet). This feature has more structural relief and is more continuous than the Inner Reef; however its composition is quite different. The Middle Reef is thought to be an ancient cemented shoreline ridge that was submerged during the latest sea level transgression (Banks et al., 2007, Walker et al. *In press*). The reef structure mostly contains a cap of mostly massive coral framework. There does appear to be some increased reef development in the northern extent of this feature, where some *A. palmata* framework has been found (Banks et al., 2007).

The present benthic coral community growing on this reef is dominated by large patches of octocorals with some areas containing 30 per m² (Gilliam et al 2007b). The octocoral assemblage is dominated by the following genera: *Eunicea* spp., *Pseudopterogorgia* spp., *Muricea* spp., *Plexaurella* spp., and *Pterogorgia* spp. An abundant and diverse stony coral assemblage also exists. This is dominated by *M. cavernosa*, *S. siderea*, and *P. astreoides*. Although coral densities can be high, coral coverage averages approximately 2-3% (Gilliam et al 2007b). Very large (>1m wide) barrel sponges, *Xestospongia muta*, are conspicuous on the Middle Reef and are quite abundant in certain areas.

Outer Reef

The Outer Reef is the most conspicuous underwater feature in Southeast Florida. It extends 128 km from southern Miami-Dade County to Central Palm Beach County. This linear, shore-parallel feature is broken by gaps of varying size caused by paleo-river drainage (Banks et al., 2007). It is composed of *A. palmata* and *A. cervicornis* framework and classic Caribbean reef morphology is evident. This believed to be a relict reef system, having "drowned" about 8000 years ago (Lighty et al., 1978; Toscano and Macintyre, 2003). This means that although the reef morphology has not changed it no longer functions the same.

Presently, the Outer Reef is capped by a coral community (Walker et al. *In press*). It has the strongest vertical relief of any of the local reef systems and exhibits a high diversity, abundance, and coverage of sessile reef organisms. Its benthic assemblages are very similar to those found on the Middle Reef. Octocorals and large barrel sponges (*Xestospongia muta*) are conspicuous and abundant. Moderate-sized stony coral colonies are also common. Coral coverage averages approximately 2-3% (Gilliam et al 2007a and b). For fishes, there is significantly greater species richness and fish abundance on the Outer Reef and Middle Reefs than the Inner Reef and nearshore hardbottom (Walker 2007 from Ferro et al., 2005).

Florida Keys/Florida Reef Tract

Within the management area, the Florida Reef Tract is perhaps the best-known coral reef area. This region has coral reef characteristics similar to many areas in the Bahamas and Caribbean Basin. The types of coral reef habitats described previously are found in the Florida Keys, the most extensive are coral communities. This is colonized by calcifying algae (e.g., *Halimda*), sponges, octocorals, and a few species of stony corals. This habitat has very wide bathymetric distribution, from the intertidal to great depths. Local environmental conditions dictate what species colonize the substrate.

The patch reef habitat is constructed by a few species of massive stony corals; most often the principal species is *Montastraea annularis*, bolder star coral. Other common foundation building species include *Colpophyllia natans* and *Siderastrea siderea*. Patch reefs are concentrated in the area off Elliott Key (Biscayne National Park), north Key Largo (John Pennekamp Coral Reef State Park, Florida Keys National Marine Sanctuary, FKNMS), and in the Hawk Channel area from Marathon to Key West (FKNMS). Stony coral species diversity and richness is highest in the patch reef habitat (Jaap et al. 2003).

The outer bank reefs are the seaward most reefs in the Florida Keys coastal ecosystem. They are the reefs most commonly visited by the diving and snorkeling charters. Their principal, unique feature is the spur and groove system (Shinn 1963). The system is a series of ridges and channels facilitating water transport from seaward to inshore. The coral most responsible for building the spurs is *Acropora palmata*, elkhorn coral (Shinn 1963). The spur and groove systems are in depths that range from a few centimeters to 10 meters. Beyond 10 meters, the spur and groove formation may or may not continue seaward as very low relief structures. Often, this habitat subunit is referred to as the fore-reef and may continue to about 30 m depth. Seaward there are sediment beds that separate the fore-reef from deeper reef formations in 40 m depth.

The Tortugas Banks are variation of the deeper reefs found in Dry Tortugas National Park. The depths are greater than 20 m and extend to 40 m. The foundation is Pleistocene karst limestone. The banks are extensive and a major grouper and snapper fishery is focused there. The most conspicuous coral is *Montastraea cavernosa*. Its growth is similar to a large toadstool: a column, capped with a hemisphere. The banks have abundant coral of a few species. Black coral (Antipatharia) are common on the outer edge of the bank.

Coral Reefs as Essential Fish Habitat

As a vital first step in understanding and managing coral reef resources, it is necessary to recognize that corals are not spread evenly over the management area. Rather, dense clusters of certain species concentrate at specific geographic locations to form coral reefs or coral communities, etc. Precise understanding of the geographic distribution of major coral habitats has been largely ignored, until recent mapping efforts (Walker et al. *In press*, Reigl et al. 2007). As these and other mapping projects are completed, expanded, and refined, they will become an important source of Essential Fish Habitat information.

Coral's most valuable contribution to the marine environment is as habitat for numerous associated organisms. As described by Jones and Endean (1973, 1976), Antonius et al. (1978), Starck (1968) Jaap (1984) Bohnsack et al. (1987) and Chiappone and Sluka (1996) and many other researchers, a coral assemblage within the management area may support rich populations of invertebrates (corals, sponges, tunicates, echinoderms, crabs, lobsters, gastropods, etc.), vertebrates (primarily fish, turtles, birds, and marine mammals), and plants (coralline algae, fleshy algae, eelgrass, turtle grass, etc.). Wells (1957) emphasized this habitat value in defining a coral reef as "... fauna and flora ... (that) ... provide the ecological niches essential to the existence of all other reef dwelling animals and plants." Undoubtedly coral is a primary provider of high quality refuge habitat for a multitude of attached and mobile organisms.

While no comprehensive quantitative inventories have been made of all of the flora and fauna associated with coral reefs, probably the best information illustrating the diversity of fauna associated with these structures is for fishes. In western Atlantic reef environments, the number of fish species directly or indirectly associated with the reef system can easily exceed 400 species (Starck 1968; Jones and Thompson 1978, Bohnsack et al. 1987; Ferro et al. 2005). The high taxonomic diversity of reef fishes indicates that many species are highly evolved, with several families generally restricted to the reef environment, among them: Chaetodontidae (butterflyfishes), Scaridae (parrotfishes), Acanthuridae (surgeonfishes), Labridae (wrasses), Holocentridae (squirrelfishes), and Pomacentridae (damselfishes) (Sale 1977; Longhurst and Pauly 1987). Many reef fishes are highly sedentary, with some species (e.g., damselfishes) actively defending territories. Even the spatial distribution of larger predatory species tends to be very reef-specific, with individuals rarely traveling more than 5 km from a home site after post-settlement, except for spawning purposes (Longhurst and Pauly 1987).

Assessments of reef fish abundances and diversity have been conducted in the Caribbean and Florida over the last four to five decades. Invariably, these studies have quantified fish populations relative to geomorphic strata or reef zonation (Ehrlich 1975; McGehee 1994; Lindeman 1997; Kendall et al. 2003; Ferro et al. 2005, Walker 2007), to substrate characteristics such as rugosity (Luckhurst and Luckhurst 1978, Walker 2007), complexity (Nunez Lara and Arias Gonzalez 1998), spatial isolation (Jordan et al. 2005), or refuge (hole) size (Hixon and Beets 1989, 1993, Sherman et al 2001). Studies have also investigated temporal variation of juvenile fish populations (Gilliam 1999; Baron et al. 2004). Numerous reef studies have described the relationship between increased habitat complexity, and increased species richness, abundance and diversity of fishes (Walker 2007). Habitat selection is seen as a trade-off between refuge from predation and access to feeding resources (Werner and Gilliam 1984, Jordan et al. 2005). Settlement to juvenile habitats is thought to reduce exposure to predators (Shulman 1984) as a way to maximize survival. Hixon and Beets (1989, 1993) showed that appropriately sized refuges could moderate predation effects and thus alter reef fish distribution patterns. At a larger scale, complete absence of particular habitats has been shown to affect fish assemblage composition if species are not able to use alternate habitats (Nagelkerken et al. 2000).

All demersal fish species under SAFMC management which can associate with coral habitats are contained within the snapper-grouper FMP. Seventy-three managed species within ten diverse families are under this plan (Section 4.1.2). Several of these families are among the most commercially and recreationally valuable fishes of the south Atlantic coast of the United States (e.g., snappers and groupers). All of these species can show some association with coral reef or community habitats during their life history. Among species, these associations differ as some coral habitat use patterns are obligate while some are facultative. In addition, temporal variations in habitat use operate at broad scales ranging from interannual to seasonal to daily (nocturnal feeding migrations). The value of coral habitats can vary accordingly. Within snapper grouper species, ontogenetic changes in habitat use lead to further variation in coral habitat use. However, the coral reef ecosystem is fundamental to the occurrence and survival of all of these species by providing direct food or shelter resources to at least some life stages of all snapper-grouper species, or providing food or shelter to their prey resources (SAFMC, 1983).

Of the ten families within the snapper-grouper plan, the three most diverse and valuable are the groupers, snappers, and grunts, with 21, 14, and 11 managed species, respectively. In groupers, the demersal life history of almost all *Epinephelus* species, several *Mycteroperca* species, and all *Centropristis* species, takes place in direct or peripheral association with coral habitats. In contrast, several species of *Mycteroperca* (gag, scamp), utilize nearshore, vegetated habitats before offshore migrations to hard structures with maturation. This latter pattern (primary use of coral structures during later ontogenetic stages) is also seen in many species of snappers and grunts. However, some species, particularly those preferring deeper water, utilize coral structures throughout their life cycle while others utilize both vegetated and hard structures opportunistically.

Similar variations in use of coral habitats are present within most of the other snapper-grouper families. For example, some managed species of triggerfish and porgy utilize coral habitats during their demersal life history, while spadefish and hogfish typically settle in vegetated, nearshore areas and use coral habitats only during later ontogenetic stages. Other patterns are also present. Most notably, jacks, although not demersal, are commonly associated with coral/ habitats as free-swimming transients. Coral habitats are primary aggregators of prey species for many species of jacks, providing habitat of essential value for the maintenance of food resources.

Due to state and Federal laws prohibiting the removal of coral much of the current economic value derived from corals in the management area comes from the non-consumptive recreational uses of coral habitats or collection of other reef resources. Throughout the management area perhaps especially in southeast Florida and the Florida Keys, dive shops, glass bottom boats, reef fishing tours, snorkel trips, boat ramps, and/or tropical specimen collecting companies, emphasize the importance of corals to many local economies. Recent studies have gone into detail describing the economic important of reef resources (Johns et al. 2001). Coastal regions depend on viable coral ecosystems therefore; extreme care must be taken to protect the long-term viability of the reef and the closely related economics of coastal counties, particularly southeast Florida and the Florida Keys.

Preservation of existing fisheries that are related to coral habitats should be of vital economic concern. Increasing fishery effort has resulted in substantial reductions in stocks of many fishery species. An analysis of fishery-independent data from 1979 to 1996 indicted that 23 analyzed reef fish species in the Florida Keys d were considered overfished with Spawning Potential Ratios below 30% Ault et al. 1998). Offshore Broward County (southeast Florida), during 667 stationary fish surveys only 2 legal-sized groupers and 219 legal-sized snappers were recorded (Ferro et al. 2005).

Complex coral reef systems usually provide greater types and quantities of habitat than more unidimensional hardbottoms. The living and nonliving components of the ecosystem are also of considerable significance in assessing value as habitat. Corals and associated benthos, such as sponges, tunicates, and algae, contribute most of the living habitat. Dead corals, perhaps parts of relic reefs, coral limestone, or lithified coral rock contribute refuge habitat and areas where the larvae of corals and sponges can settle. Regardless of the type of substrate or source of protection, the coral community offers space for organisms ranging from microscopic invertebrates to large fish. Those animals in turn contribute to the food webs of the entire ecosystem.

3.3.1.2 Live/Hardbottom Habitat

Description and distribution

Natural hardbottom consists of rock outcrops that vary in topographic relief from relatively flat and smooth to a scarped ledge with up to 10 m of vertical, sloped or stepped relief. The exposed areas of rock outcrop or relic reef are colonized to varying extent by algae, sponges, soft coral, hard coral, bryozoans, other invertebrates. Due to substantial biological, climatic, and geological differences between the temperate and tropical components of the managed area, the following summary is geographically segregated into two sections: Cape Hatteras to Cape Canaveral, and Cape Canaveral to the Dry Tortugas. Broadly, these regions represent temperate, wide-shelf systems and tropical, narrow-shelf systems, respectively, with concomitant distinctions in fish fauna (Lindeman et al., 2000). The zoogeographic break between these regions typically occurs between Cape Canaveral and Jupiter Inlet (approximately 230 km to the south). Distributions and areal amounts of hardbottom from the Florida/Georgia border to Jupiter Inlet (encompassing portions of both of the regions collated below) have been estimated from the comprehensive GIS assembly of almost all available data records (SAFMC-SA, 2001). The depth ranges covered extend from intertidal to almost 1000 m, depending on information for the varying shelf attributes of the South Atlantic Bight.

Cape Hatteras to Cape Canaveral

Major fisheries habitats on the continental shelf along the southeastern United States from Cape Hatteras to Cape Canaveral (South Atlantic Bight) can be stratified into at least five general categories: coastal, open shelf, live/hardbottom, shelf edge, and /upper slope and Blake Plateau (Figure 3.3-1) based on type of bottom and water temperature. While Figure 3.3-1 does not indicate the presence of live/hardbottom in the shallowest zone, subsequent surveys have documented extensive hardbottom habitat in this zone (SAFMC-SA, 2001). Each of these habitats harbors a distinct association of demersal fishes (Struhsaker 1969) and invertebrates. Most of the bight substrate is covered by a vast plain of sand and mud (Newton et al. 1971) underlain at depths of less than a meter by carbonate sandstone (Riggs et al. 1996; Riggs et al. 1998). The productivity of this sand- and mud-covered plain is relatively low. Scattered irregularly over the shelf, however, are zones of highly concentrated invertebrate and algal growth, usually in association with marked deviations in relief that support substantial fish assemblages (Struhsaker 1969; Huntsman and Mcintyre 1971; Wenner et al. 1983; Chester et al. 1984; Sedberry and Van Dolah 1984; Sedberry et al. 1998; Sedberry et al. 2001). Commonly called “live bottom” areas, they are usually found near outcropping shelves of sedimentary rock in the zone from 15 to 35 fathoms. High-relief rock outcrops are especially evident at the shelf break, a zone from about 55-200m where the continental shelf adjoins the deep ocean basin and is often characterized by steep cliffs and ledges (Huntsman and Manooch, 1978).

Figure 3.3-1. Selected Habitat Types on the Continental Shelf of the Southeastern United States North of Cape Canaveral (Original source: Struhsaker, 1969). Note that extensive shallow hardbottom has been revealed by recent surveys (SAFMC – SA, 2001), the term “upper slope” is now often used in place of “lower-shelf”, and additional fisheries habitat exists beyond the shelf break, on the Blake Plateau at 400-650 m depth (Sedberry et al., 2001).

The temperature regimes of the offshore shelf habitats mentioned above are strongly influenced by the Gulf Stream. The Gulf Stream plays an important role in global-scale heat, momentum, and mass flux, as well as circulation patterns throughout its length. Physical, chemical, and biological processes are influenced by the presence of the Gulf Stream. It flows generally northeastward and, with its associated pressure gradient, is responsible for transporting water along the seaward flank of the Sea Slope gyre. The conditions and flow of the Gulf Stream are highly variable on time scales ranging from two days to entire seasons. The Gulf Stream flows toward the northeast with a mean speed of 1 m/s (2 kt). The location of the Gulf Stream’s western boundary is variable because of meanders, attributable to atmospheric conditions, bottom topography, and eddies. These boundary features move to the south-southwest, and transport momentum, mass, heat, and nutrients to the vicinity of the shelf break.

All of the snapper and grouper offshore shelf habitats referred to above contain hard or live bottom areas, which provide surfaces for the growth of invertebrate organisms and the development of an ecosystem capable of supporting fishes important to commercial and recreational fisheries.

In general, the shelf demonstrates a ridge-and-swale (hill-and-valley) topography on the inner shelf and part of the outer shelf, with ridges having coarser surficial sediments than swales. At the shelf break, the topography is a discontinuous series of terraces before sloping or dropping off into steep slopes with submarine canyons, the relatively flat Blake Plateau, or deep Straits of Florida, depending on latitude.

On the shelf, the live-bottom habitats are often small, isolated areas of broken relief consisting of rock outcroppings that are heavily encrusted with sessile invertebrates such as ascidians, hydroids, bryozoans, sponges, octocorals, and hard corals. These outcrops are the ridges referred to above and are scattered over the continental shelf north of Cape Canaveral, although they are most numerous off northeastern Florida.

A study of live bottom areas from North Carolina to northern Florida (Continental Shelf Associates, 1979; Wenner et al., 1983) revealed three hardbottom habitat types: 1) emergent hardbottom dominated by sponges and gorgonian corals; 2) sand bottom underlain by hard substrate dominated by anthozoans, sponges and polychaetes, with hydroids, bryozoans, and ascidians frequently observed; and 3) softer bottom areas not underlain with hardbottom. Along the southeastern United States, most hard/live bottom habitats occur at depths greater than 27 m (90 ft), but many also are found at depths of from 16 to 27 m (54 to 90 ft), especially off the coasts of North Carolina and South Carolina, and within Gray's Reef National Marine Sanctuary off Georgia. Portions of the coastal zone off South Carolina also support extensive hardbottom habitat in depths less than 50 ft (SAFMC-SA 2001; Ojeda et al. 2004). Bottom water temperatures range from approximately 11° to 27°C (52° to 80°F). Temperatures less than 12°C may result in the death of some of the more tropical species of invertebrates and fishes.

Generally, snappers (Lutjanidae), groupers (Serranidae), porgies (Sparidae), and grunts (Haemulidae) inhabit hardbottom habitats off northeastern Florida and the offshore areas of Georgia, South Carolina, and North Carolina. The live bottom areas inshore (at depths of about 18 m; 60 ft) have cooler temperatures, less diverse populations of invertebrates, and are inhabited primarily by black sea bass, scup and associated temperate species (Sedberry and Van Dolah 1984).

The shelf edge habitat extends more or less continuously along the edge of the continental shelf at depths of 55 to 110 m (180 to 360 ft). The sediment types in this essential fish habitat zone vary from smooth mud to areas that are characterized by great relief and heavy encrustations of coral, sponge, and other predominately tropical invertebrate fauna. Some of these broken bottom areas (e.g., in Onslow Bay, North Carolina) may represent the remnants of ancient reefs that existed when the sea level was lowered during the last glacial period.

Struhsaker (1969) reported that, as a result of the proximity of the Gulf Stream, average bottom temperatures at the shelf edge are higher for a longer duration than those further inshore at other hardbottom areas. Bottom temperatures at the shelf edge habitat range from approximately 12° to 26°C (55° to 78°F). However, Miller and Richards (1980) and Sedberry et al. (2005) noted that there is a stable temperature area between 26 and 51 m (85 to 167 ft) where the temperature does not drop below 15°C (59° F). Cold water intrusions may cause the outer shelf bottom temperatures to drop (Avent et al. 1977; Mathews and Pashuk 1977; Leming 1979). Fishes that generally inhabit the shelf edge zone are more tropical, such as snappers, groupers, and porgies. Fish distribution is often diffuse in this zone, with fishes aggregating over broken bottom relief in associations similar to those formed at inshore live bottom sites. Shelf-edge reefs are important spawning grounds for many species of managed reef fish (Sedberry et al., in press).

The lower shelf habitat has a predominately smooth mud bottom, but is interspersed with rocky and very coarse gravel substrates where snowy and yellowedge groupers (*Epinephelus niveatus*, *E. flavolimbatum*) and tilefishes (Malacanthidae) are found. This habitat and its association of fishes roughly marks the transition between the fauna of the continental shelf and the fauna of the continental slope. Depths represented by this habitat zone range from 110 to 183 m (360 to 600 ft), where bottom water temperatures vary from approximately 11° to 14°C (51° to 57°F). Some species inhabiting the deeper live or hardbottom areas may be particularly susceptible to heavy fishing pressure due to limited habitat.

The continental slope off North Carolina, Georgia and Northern Florida is interrupted by the relatively flat Blake Plateau, which divides the slope into the Florida-Hatteras Slope and the Blake Escarpment. On the northern Blake Plateau are important fish habitats, including coral mounds and the Charleston Bump.

Between the 360-500 m depth contour on the Blake Plateau, and starting to the north off central North Carolina, discontinuous large mounds of deep sea coral reefs occur. While this deep coral habitat was previously described (Squires 1959; Stetson et al. 1962; Rowe and Menzies 1968), recent submersible dives have documented more information on their location and species composition (Ross 2004; See Section 3.3.1.3). The mounds consist primarily of dense thickets of the branching ahermatypic coral *Lophelia pertusa*, although other coral species have also been identified. As coral colonies die, others form on top of the mound, and extensive coral rubble accumulates to the sides of the mound. In North Carolina, two mounds have been documented off Cape Lookout and one mound off Cape Fear. The vertical height of the mounds was estimated to range from 50 to 80 m over 0.4 to 1.0 km distance. Over 43 benthic or benthopelagic fish species have been identified on these coral mounds (Ross et al. 2004).

The Charleston Bump is a deepwater rocky bottom feature on the Blake Plateau southeast of Charleston, South Carolina. It includes a shoaling ramp and ridge/trough features on which the seafloor rises from 700 m to shallower than 400 m within a relatively short distance and at a transverse angle to both the general isobath pattern of the upper slope, and to Gulf Stream currents (Brooks and Bane, 1978). The Charleston Bump includes areas of nearly vertical, 100-200-m high rocky scarps with carbonate outcrops and overhangs; other complex bottom such as coral mounds; and flat hardbottom consisting of phosphorite-manganese pavement (Popenoe and Manheim 2001; Sedberry et al. 2001). The bottom relief is important to deep reef species and supports the wreckfish (*Polyprion americanus*) fishery (Sedberry et al. 1999). It is also an important pelagic longlining area (Cramer 1996; Sedberry et al. 2001).

The feature was first described by Brooks and Bane (1978), who noted that it deflected the Gulf Stream offshore. This deflection and the subsequent downstream eddies, gyres and upwellings may increase productivity and concentrate fishes and other organisms along thermal fronts downstream from the Charleston Bump (McGowan and Richards 1985; Dewar and Bane 1985; Haney 1986; Collins and Stender 1987; Lee et al. 1991). Similar increases in productivity may occur around other deepwater bottom features. The restriction of Gulf Stream flow between the shoaling bottom and the Florida-Hatteras Slope causes swift and variable flows in the Gulf Stream, and subsequent wide-ranging and unpredictable variation in bottom temperatures (Sedberry et al. 1999; Sedberry et al. 2004). These variable oceanographic conditions and swift currents undoubtedly make life a challenge for benthic organisms, particularly sessile species. Complex bottom features, however, might provide shelter from the current for many of these, and such features could harbor a number of unique species.

Populations of economically valuable reef fishes have been in decline for at least two decades in the SAB. Such declines of top-level predators have an effect down through the food chain (Sedberry et al. 1999), and there is evidence for ecosystem overfishing on SAB reefs (McGovern et al. 1998). As a result of this overfishing and the inability of traditional methods to reverse this trend, the SAFMC has developed a series of Deepwater Marine Protected Areas (MPAs) (SAFMC, 2007). The process of siting these MPAs included obtaining input from user groups, interested parties, and the general public, along with review of existing biological and habitat data (SAFMC 2004). Of prime concern is protecting those habitats and locations that are essential to completing the life cycles of overfished species, particularly deepwater snappers and grouper populations that do not respond well to traditional managment.

Proposed MPAs include eight shelf-edge (50-100 m depth) reef sites (SAFMC 2007). This SAFMC siting process highlighted some significant problems with gaps in knowledge of distribution of habitat, species and spawning locations (see also Sale et al. 2005). These gaps include knowledge of community structure, benthic food webs, oceanographic processes that affect recruitment to and from reefs, and placement of MPA networks to maximize resource protection and production of surplus fish biomass that might spill over into adjacent fished areas. High fish biomass is known to be associated with hardbottom vs. sand bottom habitat (Wenner 1983), but additional study of distribution of individual reef fish species and spawning sites in relation to bottom habitats and faunas, and the relationship of bottom features to hydrographic features and proposed MPA sites, is needed. Oceanographic conditions, circulation patterns, chlorophyll-a concentrations, and locations of upwelling need to be mapped in relation to spawning locations and areas of juvenile recruitment. These data are needed to maximize the effectiveness of management measures such as no-take reserves. By strategic placement of MPAs in networks based on biological and oceanographic data, it is hoped that the maximum positive effect can be achieved with minimal impact on fishermen. It is imperative to collect and summarize such biological and oceanographic data, particularly data on spawning locations and recruitment pathways.

The exact extent and distribution of productive live bottom habitat on the continental shelf north of Cape Canaveral is unknown. Although a number of attempts have been made, estimations of the total area of hardbottom are confounded due to the discontinuous or patchy nature of this habitat type. Henry and Giles (1979) estimated about 4.3 percent of the Georgia Bight to be hardbottom, but this is considered an underestimate. Miller and Richards (1980) reported that live bottom reef habitat comprises a larger area of the South Atlantic Bight. The method used to determine areas of live bottom involved the review of vessel station sheets from exploratory research cruises to locate sites where reef fishes were collected. Parker et al. (1983) suggested that rock-coral-sponge (live bottom) habitat accounts for about 14 percent, or 2,040 km^2, of the substratum between the 27 m and 101 m isobaths from Cape Hatteras to Cape Fear. Live bottom constitutes a much larger percentage of the substratum at the above depths from Cape Fear to Cape Canaveral. Parker et al. (1983) estimate that approximately 30 percent, or 7,403 km^2, of the bottom in this area was composed of rock-coral-sponge substrate.

In 1992, the SEAMAP-South Atlantic Bottom Mapping Work Group of the Atlantic States Marine Fisheries Commission began an extensive effort to establish a regional database for hardbottom resources throughout the South Atlantic Bight (Van Dolah et al. 1994). The primary objectives of the effort are to identify hardbottom habitats from the beach out to a depth of 200 meters, and to summarize the information into an easily-accessible database for researchers and managers. These data are available on the Council's Internet mapping Server at www.safmc.net. In addition, the Council brought together state partmers to extend the acquisition and interpretation of bottom data from 200 to 2000 meters. This project was completed in August 2007 and data will also be available to the public via the IMS at www.safmc.net.

Moser and Taylor (1995) conducted a study on hardbottom distribution in nearshore (state-territorial) waters of North Carolina using information from local researchers, dive professionals, and fishermen. Additional sites were identified, primarily in the southern portion of Onslow Bay and northern part of Long Bay -- 20 of which were more than two meters in vertical relief. Hardbottom habitat may be concentrated seaward of inlets. Large areas of low relief hardbottom, intermittently covered with a thin layer of sand, occurs extensively off of Onslow and Brunswick Counties

In addition to the natural hard or live bottom reef habitats, wrecks and other man made structures (e.g. artificial reefs) also provide suitable substrate for the proliferation of live bottom. However, the combined area of artificial substrates will always be dwarfed compared with the total area of natural, exposed live/hardbottom. The faunal species composition on artificial reefs is similar to that identified on natural hardbottom habitat at the same depth and in the same general area (Stone et al. 1979; Stephan and Lindquist 1989; Potts and Hulbert 1994). In 1997, an assessment of the effectiveness of differently constructed artificial reefs in North Carolina (DMF 1998) found species composition to be similar on reefs constructed of different materials. However, CPUE of natural reefs was 71-85% greater than on nearby artificial reefs (DMF 1998).

Cape Canaveral to Dry Tortugas

The term hardbottom is applied in two relatively different areas of southeast Florida: the mainland and associated sedimentary barrier islands, and the coral islands and reef tract of the Florida Keys (Hoffmeister 1974). Therefore, this summary is collated by two subregions: a) mainland southeast Florida; and b) the Florida Keys. The benthic habitat characteristics of the shelf bordering the mainland are not as complex as in the Florida Reef Tract. Within both subregions, non-coralline, hardbottom habitats are present in both nearshore (<4 m) and mid- and outer-shelf areas (>4 m).

Mainland Southeast Florida

Nearshore Hardbottom

Nearshore hardbottom habitats are the primary natural reef structures at depths of 0-4 m of this subregion. These habitats are derived from large accretionary ridges of coquina mollusks, sand, and shell marl which lithified parallel to ancient shorelines during Pleistocene interglacial periods (Duane and Meisburger 1969). Currently, the majority of nearshore hardbottom reefs are within 200 m of the shore. However, they are often separated by kilometers of flat nearshore sand expanses. Nearshore hardbottom habitats on the mainland are patchily distributed among large expanses of barren, coarse sediments, commonly possess worm reefs, and show reduced coral diversities. Nelson (1990) recorded 325 species of invertebrates and plants from nearshore hardbottom habitats at Sebastian Inlet. In some areas, the hardbottom reachs heights of 2 m above the bottom and is highly convoluted. Hard corals are rare due to high turbidities and wave energy. However, hard corals that are encountered are *Siderastrea radians*, *Oculina diffusa* and *Oculina varicosa* (McCarthy, pers. com.). The habitat complexity of nearshore hardbottom is expanded by colonies of tube-building polychaete worms (Kirtley and Tanner 1968; McCarthy 2001) other invertebrates and macroalgae (Goldberg 1973; Nelson and Demetriades 1992).

A keystone contributor to the biological diversity of hardbottom habitats along the east Florida coast is the polychaete *Phragmatopoma lapidosa*, also known as *P. caudata* (Kirtley 1994; Drake et al. in review) and/or *P. lapidosa* (Pawlik 1988). Worms of this species (Family Sabellariidae) extract and glue sand together to make sand tubes, forming vast reefs in intertidal and shallow (<5 m) subtidal hardbottoms from Cape Canaveral to Key Biscayne in Florida. Their distribution continues southward to Santa Catarina, Brazil (Kirtley 1994). In Florida, the structure provided by these “worm reefs” supports a higher diversity and abundance of marine species than that of neighboring sand or hardbottom habitats. There are 8 federally and 15 State-listed species that are associated with nearshore reefs off east Florida (USFWS 1999). In particular, worm reefs are considered important sources of food and shelter for juvenile green turtles (*Chelonia mydas*) (Ehrhart et al. 1996; Wershoven and Wershoven 1988; Holloway-Adkins 2001). The reefs also provide shelter for over 325 invertebrate species (Gore et al. 1982; Nelson 1988, 1989; Nelson and Demetriades 1992) and 192 fish species (Gilmore 1977; Gilmore et al. 1981; Lindeman 1997a; Lindeman and Snyder 1999). Substantial geological evidence suggests that worm reefs are important in the maintenance and persistence of beaches and barrier islands by retention of sediment and the progradation of beaches (Kirtley 1966; Kirtley 1967; Multer and Milliman 1967; Kirtley and Tanner 1968; Gram 1968; Mehta 1973; Kirtley 1974).

Offshore Hardbottom

Several lines of offshore hardbottom reefs, derived from Pleistocene and Holocene reefs, begin in depths usually exceeding 8 m, and in bands that roughly parallel the shore (Goldberg 1973; Lighty 1977). The geologic origins and biotic characteristics of these deeper reef systems are different from the nearshore hardbottom reefs (Lighty 1977), although reefs of both depth strata are lower in relief than reefs of the Florida Reef tract.

Florida Keys and Reef Tract

Nearshore Hardbottom
Nearshore hardbottom habitats of the Florida Keys can differ both geologically and biologically from mainland areas. Florida Keys nearshore hardbottom is semi-continuously distributed among areas with high organic sediments, increased seagrasses, more corals, and reduced wave conditions. Emergent upland components of the Florida Keys are derived from ancient reefs of the Florida Reef Tract and typically do not have sizeable beaches nor a nearshore current regimefor delivery of beach-quality sediments. In contrast to the Keys, beach systems associated with sedimentary barrier islands are common in mainland areas.

Within the Keys, nearshore hardbottom is widely distributed and shows compositional differences based on proximity to tidal passes (Chiappone and Sullivan 1994). Near tidal passes, these habitats are dominated by algae, gorgonians and sponges. In the absences of strong circulation, such habitats are characterized by fleshy algae, such as *Laurencia* (Chiappone and Sullivan 1994). Hard corals are relatively uncommon in nearshore areas, presumably due to greater environmental variability in key parameters (temperature, turbidity, salinity).

Midshelf and Offshore Hardbottom
Due to the warmer water and immediate downstream positioning to the Florida Keys, these areas support a higher diversity and abundance of hard coral species. The section on Corals in the FEP document should be consulted for significant information.

Ecological role and function

The vertical relief and irregularity of hardbottom structure provides protective cover for numerous fish species and increases the surface area available for colonization by invertebrates and plants. Because of this, natural reefs can sustain greater fish stocks (270 to 5,279 kg/ha) compared to non-reef open shelf bottom (6.3 to 46.3 kg/ha) (Huntsman 1979). The abundance of fish on hardbottom and artificial reefs is related to the amount and type of structural complexity of the reef (Carr and Hixon 1997). Rocky structures with high complexity consistently supported a more abundant and diverse resident fish community than less complex structures. In addition, areas with small patches of hardbottom surrounded by sand bottom supported greater fish abundance and diversity than one large area of equal material, suggesting the importance of habitat edge and diversity to ecosystem productivity (Bohnsack et al. 1994; Auster and Langton 1999).

Most reef fish spawn in aggregations in the water column above the reef, and the eggs remain planktonic during development (Jaap 1984). Species known to spawn on nearshore hardbottom include black sea bass (*Centropristis striata*) and sand perch (*Diplectrum formosum*) between January and June (Powell and Robins 1998). Sheepshead (*Archosargus probatocephalus*), Atlantic spadefish (*Chaetodipterus faber*), and other non-fishery reef species are also thought to spawn on inshore hardbottom in North Carolina (F. Rohde, DMF, pers. com., 2001).

Nearshore and inner shelf hardbottom areas serve as important settlement and nursery habitat for immigrating larvae of many important fisheries species. Powell and Robbins (1998) collected larvae from 22 reef-associated families adjacent to hardbottom habitat in Onslow Bay. Planehead filefish, *Monacanthus hispidus*; the blenny, *Parablennius marmoreus*; the goby, *Ioglossus calliurus*; tomtate, *Haemulon aurolineatum*; white grunt, *H. plumieri*; snappers including vermilion snapper, *Rhomboplites aurorubens*; black sea bass; bank sea bass; sand perch; spottail pinfish; and whitebone porgy were commonly collected. These species are thought to have been spawned in Onslow Bay in somewhat deeper water and recruited locally to nearshore hardbottom (Powell and Robins 1998). Nearshore hardbottom also serves as intermediate nursery habitat for late juveniles emigrating out of the estuaries (Lindeman and Snyder 1999). In North Carolina, this group of fishes includes black sea bass, gag, red grouper, sheepshead, Atlantic spadefish, bank sea bass, and gray snapper, which are estuarine-dependent as early juveniles, moving offshore to hardbottom habitat as older juveniles.

In addition to providing essential functions for numerous fishery species, bio-erosion of hardbottom provides a source of new sand on the continental shelf (Riggs et al. 1985). Boring and burrowing shrimp and bivalves excavate holes chemically or mechanically, eventually weakening the rock. This process also enhances the structural complexity of hardbottom outcrops, promoting diversity of reef habitat structure.

Off Florida McCarthy (2001) suggests that worm (*Phragmatopoma lapidosa*) reefs go through predictable patterns of annual change which include high recruitment in early autumn through winter, rapid reef growth (~0.5 cm/day) resulting in maximum structure in spring and summer, and decay by early autumn (McCarthy 2001; McCarthy 2003). As recruits grow, the structure of their reef changes and these changes are important in determining the resiliency of the reefs when disturbed. Juveniles form low-lying mounds and reefs that often survive winter wave and sand disturbance (McCarthy 2001). As individuals continue to grow and accrete sand, they form large reefs that reach maximum size during the summer. Many of the intertidal colonies grow into somewhat unstable mushroom-shaped mounds whereas subtidal *Phragmatopoma lapidosa* mounds generally remain carpet-like in shape (McCarthy 2001).

Mortality of *P. lapidosa* colonies. a significant component of nearshore hardbottom in some areas of east-central Florida, increases during the summer as a result of the effects of several disturbance agents (McCarthy 2001). In the early summer, some individuals at the tops of intertidal mounds perish, leaving the tops susceptible to decay. It is likely that this mortality is caused by desiccation and/or heat stress from extreme summer temperatures. By the late summer and early autumn, wave activity from hurricanes results in maximum physical disturbance to sabellariid reefs. A large percentage of both intertidal and subtidal reefs are severely damaged at this time. Intertidal worms are more susceptible to physical destruction of their colonies, whereas subtidal worms get smothered by sand but the sand reef remains intact.

Almost simultaneously with peaks in lethal disturbance, however, larvae of *P. lapidosa* arrive in large numbers to renew the colonies by massive recruitment in cracks or atop mounds of adults (McCarthy, 2001). This process results in low lying reefs that are highly resilient and will eventually restore the structure of the reefs. Consequently, as disturbance lowers adult abundance and creates new settlement space, new individuals arrive in sufficient numbers to restore the populations. Therefore, local metapopulations may remain at fairly high abundances year after year while experiencing moderately high mortality from various agents of disturbance. When these seasonal data are integrated with those of other researchers (Gilmore 1977; Gilmore et al. 1981; Lindeman and Snyder 1999), they reveal important links between the seasonal cycle of sabellariid reef expansion and degradation, and the occupation of those reefs by juvenile and adult organisms.

Species composition and community structure

The character and extent of colonization on temperate nearshore hardbottom differs from that occurring on subtropical reefs off Florida, and varies with topography, environmental conditions and distance offshore. Studies that have documented the composition and diversity of the communities on hardbottom in North Carolina include MacIntyre and Pilkey (1969), Schneider (1976), Crowson (1980), Peckol and Searles (1984), and Kirby-Smith (1989). The dominant colonizing organisms on hardbottom in North Carolina are macroalgae (Peckol and Searles 1984), ranging from 10 to 70% of the biotic cover, and varying among seasons and years. Perennial and crustose brown and red algae were the dominant algal forms, including *Lobophora variegata*, *Lithophyllum subtenellum*, *Zonaria tournefortii*, and *Gracilaria mammillaris*. Roughly 150 species of macroalgae were identified on hardbottom in North Carolina; the majority was red algae (Rhodophyta) (Schneider 1976).

Non-mobile, attached invertebrates accounted for 10% or less of the biotic cover on hardbottom off North Carolina (Peckol and Searles 1984). The most abundant non-mobile invertebrates were the soft corals, *Titandeum frauenfeldii* and *Telesto fructiculosa*, and the hard coral, *Oculina arbuscula*. Sea urchins (*Arbacia punctulata* and *Lytechinus variegatus*) were the most common mobile invertebrates. Species composition of invertebrates occurring at hardbottom sites in South Carolina and Georgia were studied by Wenner et al. (1984). Study results using dredge and trawl samples showed that sponges, bryozoans, corals, and anemones dominated the large macroinvertebrate collection in terms of numbers and species diversity during all seasons. Sponges were the most important invertebrate group overall on the inner shelf, comprising 60–78% of the total biomass (Wenner et al. 1984). Species characteristic of the inner shelf sites included the sponges, *Homaxinella waltonsmithi*, *Spheciospongia vesparium*, *Cliona caribbaea*, and *Halichondria bowerbanki*; the echinoderms, variegated urchin (*Lytechinus variegatus*), purple sea urchin (*Arbacia punctuata*), *Encope michelini*, and *Ocnus pygmaeus*; the bryozoan, *Membranipora tenuis*; and the decapod crustacean, *Synalpheus minus*. Grab samples of small invertebrates showed that polychaetes were the most diverse and abundant group, followed by mollusks, and amphipods (Wenner et al. 1984).

Cooler and more fluctuating water temperatures limit the extent of coral colonization on hardbottom (Kirby-Smtih 1989). Two species of reef building corals that have been documented on North Carolina hardbottom are *Solenastrea hyades* and *Siderastrea siderea*. These species occurred on rock outcrops at depths of 20 to 26 m in Onslow Bay approximately 32 km offshore (MacIntyre and Pilkey 1969). Other species of coral reported for North and South Carolina include the hard corals, ivory bush coral (*Oculina arbuscula*), *Oculina varicosa*, *Astrangia danae*, *Phyllangia americana*, *Balanophyllia floridana*, and the soft corals, sea whip (*Leptogorgia virgulata*), *Telesto* spp., *Lophogorgia* spp., *Titanideum frauenfeldii*, and *Muricea pendula* (Wenner et al. 1984; Hay and Sutherland 1988).

Studies that have examined fish assemblages on natural and artificial reef habitats in North Carolina include Huntsman and Manooch (1978), Miller and Richards (1980), Grimes et al. (1982), Lindquist et al. (1989), Potts and Hulbert (1994), and Parker and Dixon (1998). Water temperature and topography are the most important factors in determining use of habitat by warm-temperate and tropical hardbottom species (Wenner et al. 1984). Lindquist et al. (1989) reported 32 species at inner shelf hardbottom sites in North Carolina, approximately five miles from shore. Commonly occurring and numerically abundant species for both natural and artificial reefs were, in order of decreasing abundance round scad (*Decapterus punctatus*), tomtate (*Haemulon aurolineatum*), spottail pinfish (*Diplodus holbrookii*), black sea bass (*Centropristis striata*), and slippery dick (*Halichoeres bivittatus*). Other common species included scup (*Stenotomus chrysops*), juvenile grunts, pigfish (*Orthopristis chrysoptera*), cubbyu (*Equetus umbrosus*), and belted sandfish (*Serranus sublgiarius*). Fish composition varied due to seasonal inshore migrations of tropical and subtropical species, fishing pressure, and microhabitat differences.

Off Florida, adult populations of the polychaete *Phragmatopoma lapidosa* dominate both intertidal and shallow subtidal habitats that can be very harsh physically in part because *P. lapidosa* can tolerate physical disturbances better than most other species (Kirtley 1966; Main and Nelson 1992; McCarthy 2001). In most areas, no other invertebrate encrusting species is as abundant as *P. lapidosa* in these habitats (McCarthy pers. com.). *P. lapidosa* can tolerate sand burial for up to three days before a significant percentage of individuals begin to die (Main and Nelson 1992). While large numbers of larvae of other encrusting species, including sponges, cnidarians, bryozoans, ascidians, bivalves and polychaetes, settle in the same intertidal and subtidal hardbottom habitats, only *P. lapidosa* settles and ultimately thrives in these habitats (McCarthy et al. 2002; McCarthy and Young, In prep).

Few quantitative characterizations of nearshore hardbottom fish assemblages are available. Based on visual censusing of three mainland southeast Florida sites over two years, 86 species from 36 families were recorded (Lindeman and Snyder 1999). Grunts (Haemulidae) were the most diverse family with 11 species recorded, more than double the species of any other family except the wrasses (Labridae) and parrotfishes (Scaridae) with seven and six species, respectively. The most abundant species were the sailor's choice, silver porgy, and cocoa damselfish. Use of hardbottom habitats was recorded for newly settled stages of over 20 species (Lindeman and Snyder 1999). Pooled early life stages (newly settled, early juvenile, and juvenile) represented over 80% of the individuals at all sites. Nearshore hardbottom fish assemblages of this subregion are characterized by diverse, tropical faunas which are dominated by early life stages.

Three studies have included sections on nearshore hardbottom fishes as part of larger project goals. Gilmore (1977) listed 105 species in association with "surf zone reefs" at depths less than two meters. Two additional species were added in later papers (Gilmore et al., 1983; Gilmore, 1992). Using visual surveys, Vare (1991) recorded 118 species from nearshore hardbottom sites in Palm Beach County. Futch and Dwinell (1977) included a list of 34 species obtained from several ichthyocide collections on "nearshore reefs." In addition to the species censused in Lindeman and Snyder (1999), 19 species were qualitatively recorded at the Jupiter and Ocean Ridge sites. Including the prior studies, over 190 species within 62 families have now been recorded in association with nearshore hardbottom habitats of mainland southeast Florida (Table 3.3-1). At least 90 species are utilized in recreational, commercial, bait, or aquaria fisheries. Nearshore hardbottom habitats typically had over thirty times the individuals per transect as natural sand habitats (Lindeman and Snyder 1999) and newly settled individuals were not recorded during any surveys of natural sand habitats.

Surveys in the Ft. Lauderdale area revelaed similarly high numbers of fishes in association with nearshore hardbottom (Baron et al. 2004). This study also found a predominance of early life stages for many taxa, with species of Haemulon to be the most abundant taxon at the generic level. During 34 visual transects over sand sites in southeast Florida, Vare (1991) recorded seven species (primarily clupeids and carangids). Approximately 15 months of sampling by seine hauls at a nearshore sand site in east-central Florida yielded a total of 22 species (Peters and Nelson 1987). One species each of engraulid and carangid comprised 70% of the total catch.

During a 4-year period, 1998 to 2002, the fishes of the three coral reef/hardbottom reef tracts count off Broward County, FL were censused (Ferro et al. 2005). A total of 86,463 fishes belonging to 208 species (52 families) was recorded. Significant differences ($p<0.05$) in total abundance, species richness and biomass were noted among the three reef tracts. In general, greater species richness and fish abundance was found on the offshore reef tract than on the middle or inshore reef tracts. The juvenile grunts, an important forage base, were significantly higher on the inshore and middle reefs, which did not differ significantly from each other, than on the offshore reef. Of management interest, the results of this census highlight a scarcity of legal size groupers (2) and snappers (198) over the entire survey.

Ault et al. (2001) describe the habitats and fish community structure within of Biscayne National Park (BNP) off Miami-Dade County, FL. Habitats were described in terms of bottom substrates, bathymetry, and seasonal salinity patterns. Analysis of community fish structure in BNP from visual census, creel census, and trawl survey databases provided spatial and temporal relationships between fishery resources and habitats.

Table 3.3-1. Species of fishes recorded from natural nearshore hardbottom habitats of mainland southeast Florida (Lindeman, 1997a), Gilmore (1977) and Vare (1991). Depths surveyed: Lindeman 1-4m; Gilmore 0-2m; Vare 4m.

Species	Lindeman	Gilmore	Vare
Rhincodontidae - Carpet Sharks			
Ginglymostoma cirratum	X	X	X
Carcharhinidae - Requiem Sharks			
Carcharhinus brevipinna	X[1]		X
Carcharhinus leucas		X	
Carcharhinus limbatus		X	
Carcharhinus plumbeus		X	
Rhinobatidae - Guitarfishes			
Rhinobatos lentiginosus			X
Dasyatidae - Stingrays			
Dasyatis americana			X
Urolophidae - Round Stingrays			
Urolophus jamaicensis			X
Muraenidae - Moray Eels			
Echidna catenata	X		
Enchelycore carychroa			X
Enchelycore nigricans[2]			
Gymnothorax funebris		X	X
Gymnothorax miliaris	X		
Gymnothorax moringa	X	X	X
Ophichthidae - Snake Eels			
Ahlia egmontis[2]			
Myrichthys breviceps	X		X
Elopidae - Tarpons			
Megalops atlanticus	X[1]		X
Clupeidae - Herrings			
Harengula clupeola	X[1]	X	
Harengula humeralis		X	
Harengula jaguana	X	X	
Opisthonema oglinum		X	X
Sardinella aurita	X[1]	X	
Clupeid sp.	X		
Engraulidae - Anchovies			
Anchoa cubana		X	
Anchoa hepsetus	X		
Anchoa lyolepis		X	
Gobiesocidae - Clingfishes			
Gobiesox strumosus		X	
Mugilidae - Mullets			
Mugil cephalus	X[1]		X
Mugil curema	X[1]		
Exocoetidae - Halfbeaks			
Hemiramphus brasiliensis	X[1]		
Hyporhamphus unifasciatus		X	
Hyporhamphus sp.		X	
Belonidae - Needlefishes			
Strongylura marina			X
Atherinidae - Silversides			
Membras martinica		X	
Menidia peninsulae		X	
Scorpaenidae - Scorpionfishes			
Scorpaena plumieri	X	X	X
Holocentridae - Squirrelfishes			
Holocentrus adscensionis			X
Holocentrus rufus	X		
Pomacentridae - Damselfishes			
Abudefduf saxatilis	X	X	X
Abudefduf taurus	X		
Microspathodon chrysurus			X
Pomacentrus fuscus	X		X

Table 3.3-1. continued.

Pomacentrus leucostictus	X	X	X
Pomacentrus partitus	X		X
Pomacentrus planifrons			X
Pomacentrus variabilis	X	X	X
Serranidae - Sea Basses & Groupers			
Centropristis striata		X	X
Diplectrum formosum			X
Epinephelus adscensionis			X
Epinephelus itajara		X	
Epinephelus morio	X		
Mycteroperca bonaci	X[1]		X
Mycteroperca microlepis		X	
Serranus subligarius		X	
Grammistidae - Soapfishes			
Rypticus maculatus	X	X	
Rypticus saponaceus			X
Lutjanidae - Snappers			
Lutjanus analis		X	X
Lutjanus apodus	X	X	X
Lutjanus chrysurus	X	X	X
Lutjanus griseus	X	X	X
Lutjanus jocu		X	X
Lutjanus mahogoni		X	
Lutjanus synagris	X	X	X
Haemulidae - Grunts			
Anisotremus surinamensis	X	X	X
Anisotremus virginicus	X	X	X
Haemulon album		?	
Haemulon aurolineatum	X	X	X
Haemulon carbonarium	X	X	X
Haemulon chrysargyreum	X	X	X
Haemulon flavolineatum	X	X	X
Haemulon macrostomum	X		X
Haemulon melanurum	X	X	X
Haemulon parra	X	X	X
Haemulon plumieri	X	X	X
Haemulon sciurus	X		X
Haemulon striatum			?
Orthopristis chrysoptera			?
Inermiidae - Bogas			
Inermia vittata			?
Apogonidae - Cardinalfishes			
Apogon binotatus	X		
Apogon maculatus	X	X	X
Apogon pseudomaculatus		X	
Astrapogon stellatus[2]			
Phaeoptyx conklini[2]			
Pomatomidae - Bluefishes			
Pomatomus saltatrix		X	
Carangidae - Jacks and Pompanos			
Caranx bartholomaei	X	X	X
Caranx crysos	X	X	X
Caranx hippos	X[1]	X	X
Caranx latus		X	X
Caranx ruber	X	X	X
Chloroscombrus chrysurus	X[1]	X	
Decapterus punctatus	X		
Oligoplites saurus	X[1]	X	X
Selar crumenopthalmus	X[1]		
Selene setapinnis	X		
Selene vomer		X	
Seriola dumerili		X	
Trachinotus carolinus	X[1]		
Trachinotus falcatus	X[1]		
Trachinotus goodei			X

Table 3.3-1. continued.

Mullidae - Goatfishes			
Mulloidichthys martinicus	X		X
Pseudupeneus maculatus	X	X	X
Centropomidae - Snooks			
Centropomus undecimalis	X[1]		X
Sparidae - Porgies			
Archosargus probatocephalus	X	X	X
Calamus bajonado	X	X	
Diplodus argenteus	X	X	
Diplodus holbrooki		X	X
Coryphaenidae - Dolphins			
Coryphaena equiselis		X	
Sciaenidae - Drums			
Bairdiella sanctelucia		X[3]	
Equetus acuminatus	X	X	X
Equetus lanceolatus			X
Equetus umbrosus	X		
Odontoscion dentex	X	X	X
Umbrina coroides	X	X	
Gerreidae - Mojarras			
Eucinostomus argenteus	X?	X	X
Eucinostomus gula	X?	X	
Eucinostomus sp.	X		
Gerres cinereus	X	X	X
Echeneidae - Remoras			
Echeneis naucrates			X
Priacanthidae - Bigeyes			
Priacanthus arenatus			X
Pempheridae - Sweepers			
Pempherus schomburgki	X	X	X
Aulostomidae - Trumpetfishes			
Aulostomus maculatus		X[4]	
Fistularidae - Cornetfishes			
Fistularia tabacaria			X
Ephippidae - Spadefishes			
Chaetodipterus faber		X	X
Chaetodontidae - Butterflyfishes			
Chaetodon capistratus			X
Chaetodon ocellatus	X		X
Chaetodon sedentarius			X
Chaetodon striatus		X	
Pomacanthidae - Angelfishes			
Holacanthus bermudensis	X		X
Holacanthus ciliarus		X	
Pomacanthus arcuatus	X	X	X
Pomacanthus paru	X		X
Labridae - Wrasses			
Bodianus rufus	X		X
Doratonotus megalepis		X	
Halichoeres bivittatus	X	X	X
Halichoeres garnoti			X
Halichoeres maculipinna	X	X	X
Halichoeres poeyi	X	X	
Halichoeres radiatus	X	X	X
Hemipteronotus splendens			X
Hemipteronotus sp.	X[1]		
Lachnolaimus maximus	X		X
Thalassoma bifasciatum	X	X	X
Scaridae - Parrotfishes			
Scarus coelestinus	X		
Scarus guacamaia	X		
Scarus taeniopterus			X
Scarus vetula	X		
Sparisoma atomarium		X	
Sparisoma aurofrenatum	X		

Table 3.3-1. continued.

Sparisoma chrysopterum		X				X
Sparisoma radians				X		
Sparisoma rubripinne		X		X		X
Sparisoma viride		X				X
Scarid sp.		X				
Synodontidae - Lizardfishes						
Synodus intermedius						X
Sphyraenidae - Barracudas						
Sphyraena barracuda		X		X		X
Sphyraena guachancho				X		
Kyphosidae - Sea Chubs						
Kyphosus incisor		X?		X		
Kyphosus sectatrix		X?		X		X
Kyphosus sp.		X				
Scombridae - Mackerels						
Scomberomorus regalis		X[1]				X
Opistognathidae - Jawfishes						
Opistognathus macro.				X		
Dactyloscopidae - Sand Stargazers						
Dactyloscopus crossotus				X		
Platygillellus rubrocinctus[2]						
Uranoscopidae - Stargazers						
Astroscopus y-graecum				X		
Ogcocephalidae - Batfishes						
Ogcocephalus radiatus						X
Labrisomidae - Clinids						
Labrisomus bucciferus		X				
Labrisomus gobio		X				
Labrisomus nuchipinnis		X		X		X
Malacoctenus macropus		X		X		
Malacoctenus triangulatus		X		X		
Paraclinus nigripinnis				X		
Starksia ocellata		X				
Blenniidae - Combtooth Blennies						
Entomacrodus nigricans				X		
Parablennius marmoreus		X				X
Scartella cristata		X		X		
Gobiidae - Gobies						
Coryphopterus glaucofrenum		X				
Gobiosoma oceanops		X[1]				X
Nes longus		X				
Eleotridae - Sleepers						
Erotelis smaragdus				X		
Triglidae - Searobins						
Prionotus ophryas				X		
Acanthuridae - Surgeonfishes						
Acanthurus bahianus		X		X		X
Acanthurus chirurgus		X		X		X
Acanthurus coeruleus	X		X		X	
Bothidae - Lefteye Flounders						
Bothus lunatus						X
Balistidae - Triggerfishes						
Balistes capriscus				X		
Balistes vetula						X
Canthidermis sufflamen						X
Monacanthidae - Filefishes						
Aluterus scriptus		X				X
Cantherhines pullus		X				X
Monacanthus hispidus				X		
Ostraciidae - Boxfishes						
Lactophrys triqueter		X		X		X
Lactophyrs quadricornis		X				X
Tetraodontidae - Pufferfishes						
Canthigaster rostrata		X				X
Sphoeroides spengleri						X

Table 3.3-1. continued.

Diodontidae - Porcupinefishes		
Diodon holocanthus		X
Diodon hystrix	X	X

[1] - Observed, but not censused in Lindeman (1997a).
[2] - Reported only by Futch and Dwinell (1977).
[3] - Reported in Gilmore (1992).
[4] - Reported in Gilmore et al. (1983).
? - Reported, but identification questionable.

The tropical invertebrate fauna of several of the mid-shelf reefs off east Florida are described by Goldberg (1973) and Blair and Flynn (1989). No quantitative examinations of the fish assemblages of these habitats are published. Qualitative characterizations exist in Herrema (1974) and Courtenay et al. (1974, 1980). Using various collecting gears and literature reviews, Herrema (1974) recognized the occurrence of 206 “primary reef” fishes off the mainland southeast coast of Florida. Emphasis was placed on the similarities between this fauna and the reef fish fauna characterized at Alligator Reef in the Florida Keys (Starck 1968). Lutjanids, haemulids and many other families were represented in both subregions on almost a species by species basis (Herrema 1974). This information was not contradicted by the faunal characterizations in Courtenay et al. (1974, 1980). Based primarily on offshore records, Perkins et al. (1997) identified 264 fish taxa from the shelf of mainland Florida as hardbottom obligate taxa.

Chiappone and Sluka (1996) identified only one study that had quantitatively focused on fishes of nearshore hardbottom areas in the Florida Keys. This work was based on strip transect surveys at two sites in the middle Keys and recorded a total of 30 species within 18 families. In Jaap’s (1984) review of Keys reefs, Tilmant compiled a list of 47 fish species occurring on nearshore hardbottom. In contrast, 192 species have been compiled for mainland areas (Lindeman 1997). The paucity of fish studies on nearshore hardbottom habitats of both the mainland and the Florida Keys render definitive comparisons premature at this stage. Several additional factors further complicate Keys and mainland comparisons. First, nearshore hardbottom in the Keys is distributed across more physiographically variable cross-shelf strata with a greater potential for structural heterogeneity than on the mainland. Second, the presence of over 6000 patch reefs in Hawk Channel (Marszalek et al. 1977), many near shallow hardbottom habitats, introduces additional inter-habitat relationships rarely found in nearshore hardbottom of mainland areas. Characterizing the fish assemblages of the heterogenous nearshore areas of the Keys may be more problematic than for the relatively homogeneous nearshore hardbottom areas of mainland Florida. In both regions, some ecotones and attributes of vertical relief (e.g., sand-hardbottom interfaces and ledges) appear to aggregate some taxa. However, the microhabitat-scale distributions of fishes within nearshore hardbottom habitats remain unquantified.

In Chiappone and Sluka (1996), no studies of fishes from hardbottom areas of the outer reef tract or the intermediate Hawk Channel area were identified. Most studies of offshore fish faunas in the Florida Keys have focused on reef formations derived primarily from hermatypic corals. Such areas may contain bedrock outcroppings properly termed hardbottom, however, this is typically not discriminated in the literature. Therefore, characterizations of offshore hardbottom ichthyofauna are not available and literature focused on coral reef fish assemblages of Hawk Channel and the Florida Reef Tract must be consulted. This document does not attempt to summarize the literature on offshore harbottom of the Florida Keys. Significant recent references on carbonate bank geology include Mallinson et al. (2003).

Bohnsack et al. (1999) provide a summary of a 20 year historical data base that will form the baseline for assessing future changes in reef fish communities in the Florida Keys National Marine Sanctuary. A total of 263 fish taxa from 54 families were observed from 118 coral reef/hardbottom sites in the Florida Keys from 6,673 visual stationary samples from 1979 through 1998. The ten most abundant species accounted for 59% of all individuals observed. Ten species had a frequency-of-occurrence in samples greater than 50% and only ten species accounted for 55% of the total observed biomass.

Live/hardbottom as Essential Fish Habitat

The live bottom areas constitute essential habitat for warm-temperate and tropical species of snappers, groupers, and associated fishes. Exploratory surveys for reef fishes has yielded 119 species representing 47 families of predominately tropical and subtropical fishes off the coasts of North Carolina and South Carolina (Grimes et al., 1982; Lindquist et al 1989; Table 3.3-2). Recently, Parker and Dixon (1998, 2002) identified 119 species of reef fish representing 46 families during underwater surveys 44 km off Beaufort, North Carolina (Table 2.18). Twenty-nine tropical fishes and a basket sponge were new to the study area. Distinct faunal assemblages were associated with two habitats: live/hardbottom on the open shelf; and at the shelf edge.

Table 3.3-2. List of fishes occurring at reef and rock outcropping habitats on the outer continental shelf of North Carolina and South Carolina (Source: Grimes et al. 1982; Lindquist et al. 1989).

Species	Common name	Collection	Habitat type
Carcharhinidae			
Carcharhinus falciformis	Silky shark	HL	SE, ILB
Sphyrnidae			
Sphyrna lewini	Scalloped harmmerhead	GN	SE
Rajidae			
Raja sp.	Skate	TWL	SE
Dasyatidae			
Dasyatis sp.	Stingray	TWL	SE
Muraenidae			
Gymnothorax nigromarginatus	Blackedge moray	HL	SE, ILB
Muraena retifera	Reticulate moray	HL	SE
Ophichthidae			
Ophictus ocellatus	Palespotted eel	HL, SC	SE, ILB
Congridae			
Conger oceanicus	Conger eel	HL, T	SE
Paraconger caudilimbatus	Margintail conger	HL	SE
Engraulidae			
Anchoa sp.	Anchovy	SC	ILB

Synodontidae			
Synodus foetens	Inshore lizardfish	HL	ILB
S. synodus	Red lizardfish	TWL	SE
Trachinocephalus myops	Snakefish	HL, TWL	SE, ILB
Batrachoididae			
Opsanus pardus	Leopard toadfish	T	ILB
Antennaridae			
Antennarius ocellatus	Ocellated frogfish	T	ILB
Ogcocephalidae			
Halieutichthys aculeatus	Pancake batfish	TWL	SE
Ogcocephalus sp.	Batfish	TWL, SC	SE
Gadidae			
Urophycis earlii	Carolina hake	HL	ILB
Ophidiidae			
Rissola marginata	Striped cusk-eel	SC, TWL	ILB
Holocentridae			
Holocentrus ascensionis	Squirrelfish	HL	ILB
H. rufus	Longspine squirrelfish	HL	SE
Fistulariidae			
Fistularia villosa	Red cornetfish	HL	SE
Sygnathidae			
Hippocampus erectus	Lined seahorse	SC	SE, ILB
Sygnathus sp.	Pipefish	SC	SE, ILB
Serranidae			
Centropristis ocyurus	Bank sea bass	HL, TWL	ILB
C. striata	Black sea bass	HL, T, SC	ILB
Dermatolepis inermis	Marbled grouper	HL	ILB
Diplectrum formosum	Sand perch	HL, SC, TWL	ILB
Epinephelus adscensionis	Rock hind	HL	ILB
E. drummondhayi	Speckled hind	HL	ILB
E. flavolimbatus	Yellowedge grouper	HL	SE
E. fulva	Coney	HL	ILB
E. guttatus	Red hind	HL	ILB
E. morio	Red grouper	HL	SE
E. mystacinus	Misty grouper	HL	SE
E. nigritus	Warsaw grouper	HL	SE
E. niveatus	Snowy grouper	HL	SE
Mycteroperca microlepis	Gag	HL	SE, ILB
M. phenax	Scamp	HL	SE, ILB
M. venenosa	Yellowfin grouper	HL	ILB
Ocyanthias martinicensis	Roughtongue bass	TWL	SE
Petrometopon cruentatum	Graysby	HL	ILB
Paranthias furcifer	Creolefish	HL	SE
Serranus phoebe	Tattler	AC	SE
S. subligarius	Belted sandfish	D	ILB
Grammistidae			
Rypticus saponaceous	Greater soapfish	T	ILB
Priacanthidae			
Pristigenys alta	Short bigeye	TWL	ILB
Priacanthus cruentatus	Glasseye snapper	TRP	ILB

Apogonidae			
Apogon pseudomaculatus	Twospot cardinalfish	TWL	ILB
Branchiostegidae			
Caulolatilus microps	Gray tilefish	HL	SE
C. chrysops	Atlantic golden tilefish	HL	SE
Malacanthidae			
Malacanthus plumieri	Sand tilefish	HL	SE
Rachycentridae			
Rachycentron canadum	Cobia	HL	SE
Carangidae			
Alectis crinitus	African pompano	T	ILB
Caranx ruber	Bar jack	D	ILB
Decapterus punctatus	Round scad	SC, TWL	ILB
Seriola dumerili	Greater amberjack	HL	SE, ILB
S. rivoliana	Almaco jack	HL	SE, ILB
Ephippidae			
Chaetodipterus faber	Atlantic spadefish	D	ILB
Lutjanidae			
Lutjanus cyanopterus	Cubera snapper	HL	SE
L. buccanella	Blackfin snapper	HL	SE
L. campechanus	Red snapper	HL	SE, ILB
L. synagris	Lane snapper	TWL	ILB
L. vivanus	Silk snapper	HL	SE
Ocyurus chrysurus	Yellowtail snapper	HL	ILB
Rhomboplites aurorubens	Vermilion snapper	HL	SE, ILB
Pomadasyidae			
Haemulon aurolineatum	Tomtate	SC, HL, TWL	SE, ILB
H. melanurum	Cottonwick grunt	HL	ILB
H. plumieri	White grunt	HL, TWL	ILB
Orthopristis chrysoptera	Pigfish	D	ILB
Balistidae			
Aluterus schoepfi	Orange filefish	SC	ILB
Balistes capriscus	Gray triggerfish	HL	SE, ILB
B. vetula	Fringed filefish	TWL	ILB
Monacanthus hispidus	Planehead filefish	TWL	ILB
Tetraodontidae			
Sphoeroides dorsalis	++Marbled puffer	TWL	ILB
S. spengleri	++Bandtail puffer		
Sparidae			
Diplodus holbrookii	Spottail pinfish	D	ILB
Archosargus probatocephalus	Sheepshead	D	ILB
Calamus leucosteus	Whitebone porgy	D	ILB
Stenotomus chrysops	Scup	D	ILB
Sciaenidae			
Equetus umbrosus	Cubbyu	D	ILB
Labridae			
Haliachoeres bivittatus	Slippery dick	D	ILB

HL=hook and line, T= trap, TWL=trawl, GN=gill net, SC=stomach contents, D=observed by divers, AC= ???
SE=shelf edge, ILB=inshore live bottom

++ indicated species not recorded by Struhsaker (1969)

Table 3.3-3. Number of dives during which fishes and sponges were observed from October 1975 through March 1980[1,2] and April 1990 through August 1993[1] (of a total of 48 and 31 dives, respectively) on the “210 Rock” off Beaufort, North Carolina (Parker and Dixon (1998; 2002).

Species	**1975-1980**	**%**	**1990-1993**	**%**
Rhincodontidae				
Ginglyostoma cirratum, nurse shark[3]	2	4.2		
Odontaspididae				
Odontaspis taurus, sand tiger			1	2.1
Carcharhinidae				
Carcharhinus leucas, bull shark			1	2.1
C. obscurus, dusky shark			1	3.2
Galeocerdo cuvier, tiger shark			1	2.1
Rhizoprionodon terraenovae, Atlantic sharpnose shark	5	10.4		
Sphyrnidae				
Sphyrna sp., hammerhead			1	2.1
Dasyatidae				
Dasyatis sp., stingray	3	6.3	2	6.5
Muraenidae				
Gymnothorax moringa, spotted moray (S)	5	10.4	5	16.1
G. saxicola, blackedge moray (S)			1	2.1
Muraena retifera, reticulate moray (S)			3	6.3
Ophichthidae				
Myrichthys breviceps, sharptail eel (S)			4	12.9
Congriidae				
Conger sp. or *Paraconger caudilimbatus*, conger (S)	3	6.3		
Clupeidae				
Sardinella aurita, Spanish sardine			2	4.2
Synodontidae				
Synodus foetens, inshore lizardfish (S)			6	19.4
Gadidae				
Urophycis earlli, Carolina hake (S)	9	18.8	2	6.5
Batrachoididae				
Opsanus sp., toadfish[4] (S)			1	3.2
Lophiidae				
Lophius americanus, goosefish (N)			1	2.1
Holocentridae				
Holocentrus ascensionis, longjaw squirrelfish (S)			10	32.3
Aulostomidae				
Aulostomus maculatus, trumpetfish (S)			7	22.6
Fistulariidae				
Fistularia petimba, red cornetfish (S)			2	6.5
Scorpaenidae				
Scorpaena dispar, hunchback scorpionfish (S)	1	2.1		

Serranidae				
**Centropristis striata*, black sea bass (N)	44	91.7	21	67.7
**C. ocyurus*, bank sea bass (S)	44	91.7	30	96.8
Diplectrum formosum, sand perch (S)	1	2.1	6	19.4
**Epinephelus morio*, red grouper (S)	3	6.3	10	32.3
**E. adscensionis*, rock hind (S)			13	41.9
**E. guttatus*, red hind (S)	2	6.5		
**E. cruentatus*, graysby (S)			5	16.1
Hypoplectrus unicolor, butter hamlet (S)			20	64.5
Liopropoma eukrines, wrasse bass (S)	9	18.8	20	64.5
**Mycteroperca microlepis*, gag (S)	48	100.0	30	96.8
**M. phenax*, scamp (S)	20	41.7	30	96.8
**M. interstitialis*, yellowmouth grouper (S)			8	25.8
Rypticus maculatus, whitespotted soapfish (S)	29	60.4	21	67.7
Serranus subligarius, belted sandfish (S)	41	85.4	23	74.2
S. tigrinus, harlequin bass (S)	3	6.3	17	54.8
S. phoebe, tattler (S)	3	9.7		
Priacanthidae				
Priacanthus arenatus, bigeye (S)			18	58.1
P. cruentatus, glasseye snapper (S)			3	9.7
Apogonidae				
Apogon pseudomaculatus, twospot cardinalfish (S)	4	50.0	15	48.4
Rachycentridae				
Rachycentron canadum, cobia			2	6.5
Echeneidae				
Remora remora, remora			1	3.2
Carangidae				
Caranx crysos, blue runner			4	8.3
C. ruber, bar jack	2	4.2	11	35.5
C. bartholomaei, yellow jack			5	16.1
Decapterus punctatus, round scad	26	54.2	5	16.1
**Seriola dumerili,* greater amberjack	41	85.4	28	90.3
**S. rivoliana*, almaco jack	7	14.6	11	35.5
S. zonata, banded rudderfish			4	12.9
Coryphaenidae				
Coryphaena hippurus, dolphin			2	6.5
Lutjanidae				
**Lutjanus campechanus*, red snapper (S)	17	35.4	1	3.2
**L. apodus*, schoolmaster (S)			2	6.5
**Rhomboplites aurorubens*, vermilion snapper (S)			7	14.6
Gerreidae (mojarra)			1	3.2
Haemulidae				
**Haemulon plumieri,* white grunt (S)	45	93.8	30	96.8
**H. aurolineatum,* tomtate (S)	31	64.6	26	83.9
Sparidae				
**Archosargus probatocephalus*, sheepshead (N)		2	4.2	
**Calamus leucosteus,* whitebone porgy (S)	25	52.1	18	58.1
**C. nodosus,* knobbed porgy (S)	12	25.0	30	96.8
**Diplodus holbrooki,* spottail pinfish (S)	34	70.8	14	45.2

**Pagrus pagrus,* red porgy (S)	29	60.4	14	45.2
Stenotomus caprinus, longspine porgy (S)			8	16.7
Sciaenidae				
Equetus umbrosus, cubbyu (S)	39	81.3	27	87.1
E. lanceolatus, jacknife-fish (S)	5	10.4	11	35.5
E. punctatus, spotted drum (S)			2	4.2
Mullidae				
Mulloidichthys martinicus, yellow goatfish (S)	1	2.1	9	29.0
Pseudupeneus maculatus, spotted goatfish (S)	1	2.1	17	54.8
Kyphosidae				
Kyphosus sp., chub (S)			2	4.2
Ephippidae				
Chaetodipterus faber, Atlantic spadefish	6	12.5	9	29.0
Chaetodontidae				
Chaetodon ocellatus, spotfin butterflyfish (S)	9	18.8	22	71.0
C. sedentarius, reef butterflyfish (S)	2	4.2	13	41.9
C. striatus, banded butterflyfish (S)			6	19.4
Pomacanthidae				
Holacanthus bermudensis, blue angelfish (S)	16	33.3	30	96.8
H. ciliaris, queen angelfish (S)	2	4.2	21	67.7
H. tricolor, rock beauty (S)			2	6.5
Pomacanthus paru, French angelfish (S)			4	12.9
Pomacentridae				
Abudefduf tauras, night sergeant (S)			9	29.0
Chromis multilineata, brown chromis (S)	1	2.1	1	3.2
C. insolata, sunshinefish (S)	1	2.1	14	45.2
C. scotti, purple reeffish (S)	45	93.8	29	93.5
C. cyaneus, blue chromis (S)	3	6.3	7	22.6
C. enchrysurus, yellowtail reeffish (S)	36	75.0	25	80.6
Microspathodon chrysurus, yellowtail damselfish (S)	1	2.1		
Poacentrus partitus, bicolor damselfish (S)	18	37.5	24	77.4
P. variabilis, cocoa damselfish (S)	20	41.7	27	87.1
P. fuscus, dusky damselfish (S)	3	6.3	11	35.5
Sphyraenidae				
Sphyraena barracuda, great barracuda	11	21.6	11	32.4
Labridae				
Bodianus pulchellus, spotfin hogfish (S)	8	16.7	29	93.5
B. rufus, Spanish hogfish (S)	15	31.3	26	83.9
Clepticus parrae, creole wrasse (S)			3	9.7
Halichoeres bivittatus, slippery dick (S)	39	81.3	27	87.1
H. garnoti, yellowhead wrasse (S)	10	20.8	13	41.9
**Lachnolaimus maximus,* hogfish (S)	24	77.4		
**Tautoga onitis,* tautog (N)	17	35.4	13	41.9
Thalassoma bifasciatum, bluehead (S)	9	18.8	21	67.7
Scaridae				
Scarus sp. (S)	11	35.5		
Sparisoma viride, stoplight parrotfish (S)	2	6.5		
Sparisoma sp. (S)			11	35.5
Blenniidae				

Hypleurochilus geminatus, crested blenny (S)			2	4.2
Parablennius marmoreus, seaweed blenny (S)	19	47.1	7	2.4
Gobiidae				
Coryphopterus puntipectophorus, spotted goby (S)	14	29.2	5	16.1
G. oceanops, neon goby (S)	2	4.2	2	6.5
Gobiosoma sp. (S)			2	6.5
Ioglossus calliurus, blue goby (S)	9	18.8	11	35.5
Acanthuridae				
Acanthurus bahianus, ocean surgeon (S)	4	8.3	9	29.0
A. coeruleus, blue tang (S)	2	4.2	17	54.8
A. chirurgus, doctorfish (S)			21	67.7
Scombridae				
**Euthynnus alletteratus,* little tunny			3	6.3
**Scomberomorus cavalla,* king mackerel	10	20.8	1	3.2
Balistidae				
Aluterus scriptus, scrawled filefish (S)	1	3.2		
**Balistes capriscus,* gray triggerfish (S)	18	37.5	13	41.9
Monacanthus hispidus, planehead filefish (S)	28	58.3	29	93.5
Ostraciidae,				
Lactophrys sp., boxfish (S)			1	3.2
Tetraodontidae				
Canthigaster rostrata, sharpnose puffer (S)	1	2.1	3	9.7
Diodon sp., porcupinefish (S)			1	2.1
Sphoeroides spengleri, bandtail puffer (S)	3	6.3	22	71.0
**S. maculatus,* northern puffer (N)	2	4.2	1	3.2
Molidae				
Mola mola, ocean sunfish			2	4.2
Nepheliospongiidae				
Xestospongia muta, basket sponge				X[5]
TOTAL				
SPECIES	119		85	96
FAMILIES	46		34	38

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[1] Sampling effort was extended beyond the 3-year study periods in an effort to obtain more winter data.

[2] Some totals differ from the published study because three stations were eliminated for locality comparison, and counting errors were corrected.[3] Nondesignated species were not the main concern of this study (e.g., sharks, jacks, and mackerels).

[4] *Opsanus sp*. is likely an undescribed offshore form.

[5] Although invertebrates usually were not recorded, the first observation of basket sponges was noted during our initial resurvey of the "210 Rock", and basket sponges were the subject of many underwater pictures and notations on cleaning stations throughout the second survey period.

* Target species (important in the recreational and commercial fisheries).

S Tropical species.

N Temperate species.

A total of 181 fish species has been reported from Gray's Reef National Marine Sanctuary, an inner-shelf (18-20 m) live bottom reef off Georgia (Hare et al., in prep). A study of South Atlantic Bight reef fish communities by Chester et al. (1984) confirmed that specific reef fish communities could be identified based on the type of habitat. Bottom topography and bottom water temperatures are the two most important factors which create habitats suitable for warm-temperate and tropical species.

Hardbottom habitats off mainland southeast Florida and areas off the Carolinas are often centrally placed between mid-shelf reefs to the east and estuarine habitats within inlets to the west. Therefore, they may serve as settlement habitats for immigrating larvae or as intermediate nursery habitats for juveniles emigrating out of inlets (Vare 1991; Lindeman and Snyder 1999). This cross-shelf positioning, coupled with their role as the only natural structures in these areas, suggests nearshore hardbottom may represent important Essential Fish Habitat.

Section 600.815 (a) (9) of the interim final rule on essential fish habitat determinations recognizes that subunits of EFH may be of particular concern. Such areas, termed Essential Fish Habitat-Habitat Areas of Particular Concern (EFH-HAPCs), can be identified using four criteria from the rule: a) importance of ecological functions; b) sensitivity to human degradation; c) probability and extent of effects from development activities; and d) rarity of the habitat. Applications of EFH and EFH-HAPCs in the management of the SAFMC snapper-grouper complex was examined in Lindeman et al (2000), with a focus on developmental variation and MPAs. Hardbottom habitat types which ranked high in terms of the four criteria above are summarized below.

Charleston Bump and Gyre

The topographic irregularity southeast of Charleston, South Carolina known as the Charleston Bump is an area of productive seafloor, which rising abruptly from 700 to 300 meters over 20 km. The Charleston Bump is located approximately at 32° 44' N. Latitude and 78° 06' W. Longitude and at an angle which is approximately transverse to both the general isobath pattern and the Gulf Stream currents (Figure 3.3-2). Those areas that contain the highest relief are the only known spawning locations for wreckfish. This species is fished intensively within the relatively small area of high relief, and is one of the few species within the snapper-grouper fisheries complex that has been successfully managed as a sustained fishery (Sedberry et al. 2001).

The Charleston Gyre is considered an essential nursery habitat for some offshore fish species with pelagic stages, such as reef fishes (Govoni and Hare 2001; Sedberry et al. 2001). The cyclonic Charleston Gyre is a permanent oceanographic feature of the South Atlantic Bight induced by the deflection of rapidly moving Gulf Stream waters by the Charleston Bump. The gyre produces a large area of upwelling of nutrients, which contributes significantly to primary and secondary production within the SAB region. It is also important in retention and cross-shelf transport of larvae of reef fishes that spawn at the shelf edge (Sedberry et al. 2001). The size of the deflection and physical response in terms of replacement of surface waters with nutrient rich bottom waters from depths of 450 meters to near surface (less than 50 meters) vary with seasonal position and velocity of the Gulf Stream currents (Bane et al. 2001). The nutritional contribution of the large upwelling area to productivity of the relatively nutrient poor SAB is significant. While a lot of emphasis has been placed on shallow habitats, the South Atlantic Fishery Management Council (SAFMC 1998) designated the Charleston Gyre as an essential nursery habitat for some offshore fish species with pelagic stages, such as reef fishes, because of increased productivity that is important to ichthyoplankton.

Figure 3.3-2. Southeastern U.S. continental shelf and slope, showing major topographic features (diagonal lines indicate the Charleston Bump) and boundaries of the primary commercial wreckfish grounds (heavy dots). (Source: Sedberry et. al., 1994).
TBA

The South Atlantic Bight, the Charleston Bump and Gyre are described in greater detail in several research and review papers (e.g., Bane et al. 2001; Sedberry et al. 2001; Govoni and Hare 2001 and papers cited therein). The following synopsis is based on the review by Sedberry et al. (2001) and O. Pashuk (pers. comm).

The continental shelf off the southeastern United States, commonly called the South Atlantic Bight (SAB), extends from Cape Hatteras, North Carolina, to Cape Canaveral, Florida (or according to some researchers, to West Palm Beach, Florida). The northern part of the SAB is known as the Carolina Capes Region, while the middle and southern areas are called the Georgia Embayment, or Georgia Bight. The Carolina Capes Region is characterized by complex topography, and their prominent shoals extending to the shelf break are effective in trapping Gulf Stream eddies, whereas the shelf to the south is smoother.

Shelf widths vary from just a few kilometers off West Palm Beach, FL, to a maximum of 120 km off Brunswick and Savannah, Georgia. Gently sloping shelf (about 1m/km) can be divided into the following zones: 1) **Inner shelf (0-20 m)** which is dominated by tidal currents, river runoff, local wind forcing and seasonal atmospheric changes; 2) **Midshelf zone (21-40 m)** where waters are dominated by winds but influenced by the Gulf Stream. Stratification of water column changes seasonally: mixed conditions, in general, characterize fall and winter while vertical stratification prevail during spring and summer. Strong stratification allows the upwelled waters to advect farther onshore near the bottom and, at the same time, it facilitates offshore spreading of lower salinity water in surface layer. 3) **Outer shelf (41-75 m)** is dominated by the Gulf Stream. The shelf break, generally, occurs at about 75-m depth, but is shallower southward.

Oceanographic regime on the continental shelf in the South Atlantic Bight is mainly conditioned by 1) proximity of the Gulf Stream with its frequent meanders and eddies; 2) river runoff; 3) seasonal heating and cooling; and 4) bottom topography. Winds and tides can also modify circulation patterns, especially nearshore, or where density gradients are weak. Temperature and salinity of shelf waters widely fluctuate seasonally (from 10° C to 29° C and from 33.0 ppt to 36.5 ppt), whereas warm and salty surface Gulf Stream waters have much less variable properties.

The warming influence of the Gulf Stream is especially notable in the winter near the shelf break where tropical species of fish, corals and other animals are found. A warm band of relatively constant temperature (18-22° C) and salinity (36.0 ppt - 36.2 ppt) water is observed near bottom year-round just inshore of the shelf break, bounded by seasonally variable inshore waters on one side, and by fluctuating offshore waters on the other side, which are subject to cold eddy/upwelling events and warm Gulf Stream intrusions.

Fresh water nearshore is supplied mainly by the Cape Fear, Pee Dee, Santee, Savannah, and Altamaha rivers. River runoff is the highest during late winter-early spring, with maximum in

March. The affect of runoff on coastal and shelf waters is most pronounced by April. Seasonal heating and cooling of coastal and shelf waters follow a trend in air temperature's increase and decrease, with a lag of approximately one month also.

Geostrophic southward flow develops on the continental shelf and appears to be seasonal, reflecting river runoff and heating-cooling effects. This counter-current is maximum during summer. In late fall-winter, in general, it is no longer a broad continuous flow, and is restricted to narrow patches mainly in nearshore areas in the vicinity of river mouths.

Fluctuations in the Icelandic Low, the Bermuda-Azores High, and the Ohio Valley High largely govern the mean wind patterns in the SAB. Winds, in general, are from Northeast in fall-winter, and from Southwest in spring-summer, but they can be of different directions during a passage of atmospheric fronts.

Semidiurnal (M2) tides dominate the SAB. Tidal range varies considerately in the SAB because of varying shelf widths. The maximum coastal tides of 2.2 m occur at Savannah, Georgia, where the shelf is widest, and decrease to 1.3 m at Cape Fear and 1.1 m at Cape Canaveral.

Small frontal eddies and meanders propagate northward along the western edge of the Gulf Stream every 1-2 weeks. They provide small-scale upwellings of nutrients along the shelf break in the SAB. In contrast to transit upwellings, there are two areas in the SAB where upwelling of nutrient-rich deepwater is more permanent. One such upwelling is located just to the north of Cape Canaveral which is caused by diverging isobaths. The other, much larger and stronger upwelling occurs mainly between 32° N. Latitude and 33° N. Latitude, and it results from a deflection of the Gulf Stream offshore by the topographic irregularity known as the Charleston Bump.

In general, the Gulf Stream flows along the shelf break, with very little meandering, from Florida to about 32° N latitude where it encounters the Charleston Bump and is deflected seaward forming a large offshore meander. The cyclonic Charleston Gyre is formed, with a large upwelling of nutrient-rich deepwater in its cold core. The Charleston Bump is the underwater ridge/trough feature located southeast of Charleston, South Carolina, where seafloor rises from 700 to 300 m within a relatively short distance and at a transverse angle to both the general isobaths pattern of the upper slope, and to Gulf Stream currents. Downstream of the Charleston Bump, enlarged wavelike meanders can displace the Gulf Stream front up to 150 km from the shelf break. These meanders can be easily seen in satellite images.

Although 2-3 large meanders and eddies can form downstream of the Bump, the Charleston Gyre is the largest and the most prominent feature. The consistent upwelling of nutrient-rich deepwaters from the depths over 450 m to the near-surface layer (less than 50 m) is the main steady source of nutrients near the shelf break within the entire South Atlantic Bight, and it contributes significantly to primary and secondary production in the region. The Charleston Gyre is considered an essential nursery habitat for some offshore fish species with pelagic stages. It is also implicated in retention of fish eggs and larvae and their transport onshore.

The Charleston Bump and the Gyre can also create suitable habitats for adult fish. For example, the highest relief of the Bump is the only known spawning location of the wreckfish. The Charleston Gyre may be also beneficial to other demersal species of the Snapper-Grouper complex, as well as to pelagic migratory fishes, due to food availability and unique patterns of the currents in this area.

Ten Fathom Ledge and Big Rock

The Ten Fathom Ledge and Big Rock areas are located south of Cape Lookout, North Carolina. The Ten Fathom Ledge is located at 34° 11' N. Latitude 76° 07' W. Longitude in 95 to 120 meter depth on the Continental Shelf in Onslow Bay, North Carolina, beginning along the southern edge of Cape Lookout Shoals. This area encompasses numerous patch reefs of coral-algal-sponge growth on rock outcroppings distributed over 136 square miles of ocean floor. The substrate consists of oolithic calcarenites and coquina forming a thin veneer over the underlying Yorktown formation of silty sands, clays, and calcareous quartz sandstones.

The Big Rock area encompasses 36 square miles of deep drowned reef around the 50-100 meter isobath on the outer shelf and upper slope approximately 36 miles south of Cape Lookout. Hard substrates at the Big Rock area are predominately algal limestone and calcareous sandstone. Unique bottom topography at both sites produces oases of productive bottom relief with diverse and productive epifaunal and algal communities surrounded by a generally monotonous and relatively unproductive sand bottom. Approximately 150 species of reef-associated species have been documented from the two sites (R. Parker, pers. comm.).

Shelf Break Area from Florida to North Carolina

Although the area of bottom between 100 and 300 meters depths from Cape Hatteras to Cape Canaveral is small relative to the more inshore live bottom shelf habitat as a whole, it constitutes essential fish habitat for deepwater reef fish. A series of troughs and terraces are composed of bioeroded limestone and carconate sandstone (Newton et al. 1971), and exhibit vertical relief ranging from less than half a meter to more than 10 meters. Ledge systems formed by rock outcrops and piles of irregularly sized boulders are common.

Overall, the deepwater reef fish community probably consists of fewer than 50 species. Parker and Ross (1986) observed 34 species of deepwater reef fishes representing 17 families from submersible operations off North Carolina in waters 98 to 152 meters deep. In another submersible operation in the Charleston Bump area off South Carolina, Gutherz et al. (1995) describe sightings of 27 species of deepwater reef fish in waters 185 to 220 meters in depth.

Gray's Reef National Marine Sanctuary

Gray's Reef National Marine Sanctuary (GRNMS) is located 17.5 nautical miles east of Sapelo Island, Georgia, and 35 nautical miles northeast of Brunswick, Georgia. Gray's Reef encompasses nearly 32 km^2 at a depth of about 22 meters (Parker et al. 1994). The Sanctuary contains extensive, but patchy hardbottoms of moderate relief (up to 2 meters). Rock outcrops, in the form of ledges, are often separated by wide expanses of sand, and are subject to weathering, shifting sediments, and slumping, which create a complex habitat including caves, burrows, troughs, and overhangs (Hunt 1974). Parker et al. (1994) described the habitat preference of 66 species of reef fish distributed over five different habitat types. Numbers of species and fish densities were highest on the ledge habitat, intermediate on live bottom, and lowest over sand.

Nearshore Hardbottom of Mainland East Florida

Extending semi-continuously from at least St. Augustine Cape Canaveral to the Florida Keys, nearshore hardbottom was evaluated in terms of the four HAPC criteria in Section 600.815 of the final EFH interim rule. In terms of ecological function, several lines of evidence suggest that nearshore hardbottom reefs may serve as nursery habitat. The following summary is based on the quantitative information available for the southeast Florida mainland (Lindeman 1997a and b; Lindeman and Snyder 1999; Baron et al. 2004), which also included life stage-specific abundance data. First, pooled early life stages consistently represented over 80% of the total individuals at all sites censused. Second, eight of the top ten most abundant species were consistently represented by early stages. Third, use of hardbottom habitats was recorded for newly settled stages of more than 20 species.

Although suggestive of nursery value, these lines of evidence need to be viewed in the appropriate context. The presence of more juvenile stages than adults does not guarantee a habitat is a valuable nursery. Rapid decays in the benthic or planktonic survival of early stages of marine fishes are common demographic patterns (Shulman and Ogden 1987; Richards and Lindeman 1987), ensuring that if distributions are homogeneous, all habitats will have more early stages than adults. Are early stages equally distributed among differing habitats or consistently skewed towards particular cross-shelf habitats? The high numbers of early stages on nearshore reefs appear to reflect more than just larger initial numbers of young individuals. Newly settled stages of most species of grunts and eight of nine species of snappers of the southeast mainland Florida shelf have been recorded primarily in depths less than five meters, despite substantial sampling efforts in deeper waters. Adults are infrequent or absent from the same shallow habitats. There is habitat segregation among life stages, with the earliest stages using the most shallow habitats in many species of grunts and snappers (Starck 1970; Dennis 1992; Lindeman et al. 1998). Similar ontogenetic differences in both distribution and abundance exist for many other taxa which utilize nearshore hardbottom habitats. Based on this and other evidence, Lindeman and Snyder (1999) concluded that at least 35 species utilize nearshore hardbottom as a primary or secondary nursery area. At least ten of these species are managed under the Snapper/Grouper FMP.

Because nearshore areas are relatively featureless expanses of sand in the absence of hardbottom, such structures may also have substantial value as reference points for spawning activities of inshore fishes. Many fishes require three-dimensional structure as a reference point for coarse-scale aggregation and fine-scale behavior during spawning (Thresher 1984). Using information from the literature, personal observations, and discussions with commercial fishermen, 15 species were estimated to spawn on nearshore reefs (Lindeman 1997a). An additional 20 species may also spawn on or near these reefs. Some are of substantial economic value; these include snook, pompano, and several herring species. At least 90 species known to associate with nearshore hardbottom structures are utilized in South Florida fisheries. The majority of these species are represented primarily by early life stages. Approximately 51 species are of recreational value and thirty species are of commercial value. Twenty-two species are utilized for bait and 21 species are marketed within the aquaria industry. Based on the demonstrated or potential value of these areas as nurseries and spawning sites for many economically valuable species, nearshore hardbottom habitats were estimated to support highly important ecological functions, the first HAPC criterion.

The second and third HAPC criteria, sensitivity and probability of anthropogenic stressors, are interrelated in terms of nearshore hardbottom. They are treated collectively here. Various stretches of nearshore hardbottom have been completely buried by dredging projects associated with beach management activities in this subregion (Section 7.4.2.2). They may also be subjected to indirect stressors over both short and long time scales from such projects. For example, between 1995 and 1998, up to 19 acres of nearshore hardbottom reefs were buried by beach dredging projects at two sites in Palm Beach County. Such activities occur within other counties of this subregion as well. The 50-year planning document for beach management in southeast mainland Florida (ACOE 1996), includes beach dredge-fill projects for over fifteen areas, with renourishment intervals averaging 6-8 years. Given the past and projected future, it is concluded that both the sensitivity of these habitats and the probability of anthropogenic stressors is high.

In terms of the final EFH-HAPC criterion, rarity, nearshore hardbottom also ranks high. In southeast mainland Florida, most shorelines between Dade and Broward Counties (25°30'-26°20' N) lack natural nearshore hardbottom with substantial three-dimensional structure (ACOE 1996). Although substantial stretches of nearshore hardbottom exist in portions of Palm Beach, Martin, St. Lucie, and Indian River Counties (Perkins et al. 1997) (26°20'-27°15' N) these reefs are often separated by kilometers of barren stretches of sand. Offshore, most mid-shelf areas (5-20 m) are also dominated by expanses of sand despite the variable occurrence of several mid-shelf reef lines. Therefore, there are no natural habitats in the same or adjacent nearshore areas that can support equivalent abundances of early life stages. Absences of nursery structure can logically result in increased predation and lowered growth. In newly settled and juvenile stages, such conditions could create demographic bottlenecks that ultimately result in lowered local population sizes.

Nursery usage of nearshore hardbottom reefs may be a bi-directional phenomenon. Many species utilize these habitats during both newly settled and older juvenile life stages. This suggests that nearshore hardbottom can facilitate both inshore and offshore migrations during differing ontogenetic stages of some species. Their limited availability does not necessarily decrease their value. When present, they may serve a primary nursery role as shelter for incoming early life stages which would undergo increased predation mortality without substantial habitat structure. In addition, some species use these structures as resident nurseries; settling, growing-out, and maturing sexually as permanent residents (e. g., pomacentrids, labrisomids). A secondary nursery role may result from increased growth because of higher food availabilities in structure-rich environments. Nearshore hardbottom may also serve as secondary nursery habitat for juveniles that emigrate out of inlets towards offshore reefs. This pattern is seen in gray snapper and bluestriped grunt which typically settle inside inlets and primarily use nearshore hardbottom as older juveniles (Lindeman et al. 1998).

In summary, nearshore hardbottom habitats of southeast Florida ranked high in terms of ecological function, sensitivity, probability of stressor introduction, and rarity. Based on the criteria in Section 600.815 (a) (9), it is concluded that they represent Essential Fish Habitat-Habitat Areas of Particular Concern for species managed under the Snapper/Grouper Fishery Management Plan and dozens of other species which co-occur with many species in this management unit. Many of these other species, not currently managed under the SAFMC are important prey items (Randall, 1968) for those species under management.

3.3.1.3 Deepwater coral habitat

Description and distribution

(excerpted from Chapeter 6 (Ross and Nizinski) of the 2007 Status of Deep Coral Ecosystems) The southeast U.S. slope area, including the slope off the Florida Keys, appears to have a unique assemblage of deepwater Scleractinia (Cairns and Chapman 2001). The warm temperate assemblage identified by Cairns and Chapman (2001) contained about 62 species, four endemic to the region. This group was characterized by many free living species, few species living deeper than 1000 m, and many species with amphi-Atlantic distributions. For the southeastern U.S., in areas deeper than 200 m, we report a similar assemblage, consisting of 57 species of scleractinians (including 47 solitary and ten colonial structure-forming corals), four antipatharians, one zoanthid, 44 octocorals, one pannatulid, and seven stylasterids. Thus the region contains at least 114 species of deep corals (classes Hydrozoa and Anthozoa). This list is conservative, however; we expect that more species will be discovered in the region as exploration and sampling increase. Below we discuss the major structure-forming corals that most contribute to reef-like habitats in the southeastern U.S.

Stony Corals (Class Anthozoa, Order Scleractinia)
The dominant structure-forming coral on the southeastern U.S. outer shelf (<200 m) is *Oculina varicosa* (ivory tree coral). Although it occurs from Bermuda and North Carolina south through the Gulf of Mexico and the Caribbean in 2-152 m depths, this coral only forms large reefs off east-central Florida, 27° 32’ N to 28° 59’ N, in 70-100 m (Figure 3.3-3; Reed 2002b). The shallow water form of *Oculina* may have symbiotic zooxanthellae, but the deeper form does not.

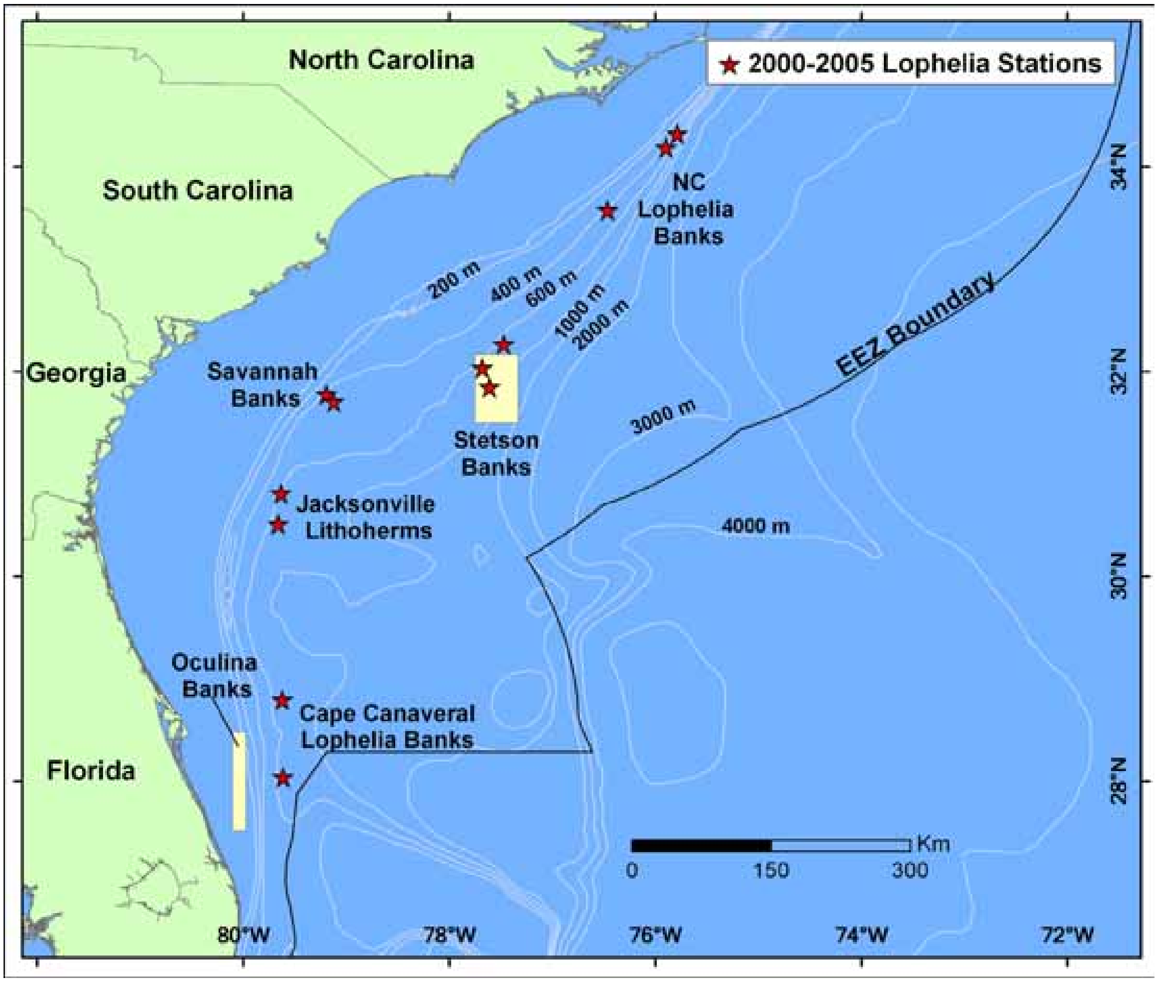


Figure 3.3-3. Southeastern United States regional report area, indicating general areas of *Oculina varicosa* reefs and the deeper coral (*Lophelia* mostly) habitats sampled by Ross et al. from 2000-2005 (red stars). The Stetson Bank (white box) is described in the text. Note that these areas do not represent all sites where deep (> 200 m) corals occur nor all sites visited by other researchers. See Reed et al. (2005, 2006) and Partyka et al. (in press) for additional deep coral sites in this region.

The deeper reefs are almost monotypic mounds and ridges which exhibit a vertical profile of 3-35 m (Avent et al. 1977; Reed 2002b). Superficially, these structures resemble the deep reefs formed by *Lophelia pertusa*. Despite cool temperatures, the shelf edge *Oculina* exhibit rapid growth, probably facilitated by regular upwellings of nutrient rich water (Reed 1983).

Lophelia pertusa, the major structure building coral in the deep sea, is the dominant scleractining off the southeastern U.S. This species has a cosmopolitan distribution, occurring on the southeastern U.S. slope, in the Gulf of Mexico, off Nova Scotia, in the northeastern Atlantic, the South Atlantic, the Mediterranean, Indian Ocean and in parts of the Pacific Ocean over a depth range of 50 to 2170 m (Cairns 1979; Rogers 1999). The 3380m depth record off New York for *L. pertusa* reported by Squires (1959) was based on a misidentified specimen (Cairns 1979). Coral habitats dominated by *Lophelia pertusa* are common throughout the southeast U.S. in depths of about 370 to at least 800 m.

Although *Lophelia* may occur in small scattered colonies attached to various hard substrata, it also forms complex, high profile features. For instance, off North Carolina, *Lophelia* forms what may be considered classic mounds that appear to be a sediment/coral rubble matrix topped with almost monotypic stands of *L. pertusa*. Along the sides and around the bases of these banks are rubble zones of dead, gray coral pieces which may extend large distances away from the mounds. To the south sediment/coral mounds vary in size, and *L. pertusa* and other hard and soft corals populate the abundant hard substrata of the Blake Plateau in great numbers

Data are lacking on how *Lophelia* coral banks in the southeastern U.S. are formed. Hypotheses for coral mound formation in the northeastern Atlantic were proposed (Hovland et al. 1998; Hovland and Risk 2003; Masson et al. 2003), but it is unclear how relevant these are off the southeastern U.S. The mounds off North Carolina and those in other locations off the southeastern U.S. (particularly east of south-central Florida) appear to be formed by successive coral growth, collapse, and sediment entrapment (Wilson 1979; Ayers and Pilkey 1981; Paull et al. 2000; Popenoe and Manheim 2001). Other coral formations in the area (especially on the Blake Plateau) seem to form by coral colonization of appropriate hard substrates, without mound formation by the corals. If bottom currents are too strong, mound formation may be prevented (Popenoe and Manheim 2001) because sediments cannot be trapped. Ayers and Pilkey (1981) suggested that Gulf Stream currents may erode coral mounds, and that present coral bank sizes may be related to historical displacements of that current. Assuming currents also carry appropriate foods, it may be that currents with variable speeds or at least currents of moderate speeds (fast enough to facilitate filter feeding but not too fast to prevent sediment entrapment) coupled with a supply of sediment are the conditions necessary to facilitate coral mound formation (Rogers 1999). Regardless of how coral formations are created, we agree with Masson et al. (2003) that elevated topography appears to be an important attribute for well developed coral communities.

Deep-coral reefs are fragile and susceptible to physical destruction (Fossa et al. 2002). It is estimated that these deep reefs may be hundreds to thousands of years old (Neumann et al. 1977; Wilson 1979; Ayers and Pilkey 1981; Mikkelsen et al. 1982; Mortensen and Rapp 1998); however, aging data are so limited (especially in the western Atlantic) that age of coral mounds in the western Atlantic is unclear. Recent drilling on coral mounds off Ireland indicated that these structures started forming over two million years ago and that formation was not related to hydrocarbon seeps (Williams T et al. 2006). While the genetic structure (gene flow, population relationships, taxonomic relationships) of *Lophelia* in the northeastern Atlantic is being described (Le Goff-Vitry et al. 2004), such studies are just beginning in the western Atlantic (C. Morrison et al. unpublished data). Preliminary genetic results from the southeast region suggest that the population structure of *L. pertusa* is more diverse than expected (C. Morrison et al. unpublished data). Understanding the population genetics and gene flow will provide insights into coral biology, dispersal and distribution of deep corals off the southeastern U.S.
Although *Lophelia* is the dominant hard coral off North Carolina, other scleractinians contribute to the overall complexity of the habitat (Table 2.18). Overall, species diversity of scleractinians increases south of Cape Fear, NC, but *L. pertusa* is still dominant. For example, the colonial corals *Madrepora oculata* and *Enallopsammia profunda*, rare off Cape Lookout, NC, are relatively common south of Cape Fear, NC. These hard corals tend not to occur singly or as

species-specific mounds, but rather live on or adjacent to the *Lophelia* mounds. A variety of solitary corals are also found off the southeastern U.S. Individuals are often attached to coral rubble or underlying hard substrata. Most species appear to be either uncommon or rare. But, in some instances, particularly in the central portion of the region, local abundance can be high. For example, aggregations of *Thecopsammia socialis* and *Bathypsammia fallosocialis* carpet the bottom adjacent to reef habitat at study sites off South Carolina and northern Florida (Ross et al., unpublished data).

Black corals (Class Anthozoa, Order Antipatharia)
Black corals (Families Leiopathidae and Schizopathidae, ca. four species) are important structure-forming corals on the southeastern U.S. slope (Table 3.3-4). These corals occur locally in moderate abundances, but their distributions seem to be limited to the region south of Cape Fear, NC. Colonies may reach heights of 1-2 m. Black coral colonies, occurring singly or in small aggregations, may be observed either in association with hard coral colonies or as separate entities. Some of these living components of the deep reefs attain ages of hundreds to thousands of years (Williams B et al. 2006; Williams et al. in press; C. Holmes and S.W. Ross, unpublished data), and thus, along with gold corals, are among the oldest known animals on Earth. Black corals form annual or regular bands, and these bands contain important chemical records on past climates, ocean physics, ocean productivity, pollution, and data relevant to global geochemical cycles. An effort to investigate these geochemical data is underway by U.S. Geological Survey (C. Holmes and S.W. Ross).

Table 3.3-4. Attributes of structure-forming deep-sea corals of the southeastern United States.

Taxa	Reef-building	Abundance	Max colony size	Morphology	Associations with other structure-forming invertebrates	Colony spatial dispersion	Overall structural importance
Lophelia pertusa	Yes	High	Large	Branching	Many	Clumped	High
Solenosmillia variabilis	No	Low	Small	Branching	Many	Clumped	Low
Enallopsammia profunda	No	Low-Medium	Small-Medium	Branching	Many	Clumped	Low-Medium
Madrepora oculata	No	Low	Small	Branching	Many	Clumped	Low
Oculina varicosa	Yes	High	Large	Branching	Many	Clumped	High
Madracis myriaster	No	Low	Small-Medium	Branching	Many	Clumped	Low
Leiopathes glaberrima	No	Medium	Medium - Large	Branching	Many	Solitary	Medium
Bathypathes alternata	No	Low	Medium - Large	Branching	Many	Solitary	Low
Keratoisis spp.	No	Medium	Medium - Large	Branching	Many	Solitary	Medium

Table Key	
Attribute	**Measure**
Reef-Building	Yes/No
Relative Abundance	Low/ Medium/ High
Size (width or height)	Small (< 30cm)/ Medium (30cm-1m)/ Large (>1m)
Morphology	Branching/ Non-branching
Associations	None/ Few (1-2)/ Many (>2)
Spatial Dispersion	Solitary/ Clumped
Overall Rating	Low/ Medium/ High

Gold corals (Class Anthozoa, Order Zoanthidae)

Gerardia spp. colonies are found most often singly away from other coral structure, but these corals are also found associated with colonies of other structure-forming corals such as *Lophelia pertusa*, *Keratoisis* spp., or antipatharians (*Leiopathes* spp.). Very little is known about this group of organisms. They apparently exhibit slow growth, reaching ages of at least 1800 years old (Griffin and Druffel 1989; Druffel et al. 1995) and may be valuable in paleoecology studies.

Gorgonians (Class Anthozoa, Order Gorgonacea)

The gorgonians are by far the most diverse taxon on the southeastern U.S. slope represented by seven families, 17 genera, and 32 species. The diversity of gorgonians increases dramatically south of Cape Fear, NC. Additional sampling is likely to increase the numbers of known species in this group for this region. To date, material we collected off Jacksonville, FL represented a newly described species (*Thourella bipinnata* Cairns 2006); the specimen of *Chrysogorgia squamata* also collected off Jacksonville represented the fifth known specimen of this species and increased our knowledge of its geographic range (previously known only from the Caribbean).

Bamboo corals (Family Isididae, four species), possibly the best known members of this group because of their larger size and distinctive morphology, are also important structure-forming corals off the southeast region (Table 3.3-4). They occur locally in moderate abundances, and their distributions also seem to be limited to the region south of Cape Fear, NC. Colonies may reach heights of 1-2 m. Bamboo coral colonies occur either singly or in small aggregations and may be observed either in association with hard coral colonies or as separate entities.

True soft corals (Class Anthozoa, Order Alcyonacea)

Three families, Alcyoniidae, Nephtheidae, and Nidaliidae, comprise the Alcyonacea off the southeastern U.S. No family is speciose; total known diversity for this group is only six species. The most abundant species observed in the region is *Anthomastus agassizi*, which is relatively abundant at sites off Florida. It is usually attached to dead *Lophelia*, but some individuals have also been observed on dermosponges and coral rubble. The majority of the alcyonacean species are smaller in size, both in vertical extent and diameter, than the gorgonians. Thus, these corals add to the overall structural complexity of the habitat by attaching to hard substrata such as dead scleractinian skeletons and coral rubble.

Stoloniferans, a suborder (Stolonifera) within the Alcyonacea, are represented by one family (Clavulariidae) off the southeast region. Six species from four genera have been reported from the region. One species, *Clavularia modesta*, is widespread throughout the western Atlantic; the other five species are known from North Carolina southward to the Caribbean.

Pennatulaceans (Class Anthozoa, Order Pennatulacea)

Little is known about pennatulids (sea pens) off the southeastern U.S. It is unlikely that this group contributes significantly to the overall complexity and diversity of the system. No sea pens have been observed during recent surveys (Ross et al., unpublished data) and based on museum records, only one species (*Kophobelemnon sertum*) is known in the region.

Stylasterids (Class Hydrozoa, Order Anthoathecatae)

Although not found in great abundances, stylasterids (lace corals) commonly occur off the southeastern U.S. Seven species representing four genera have been reported from the region. Individuals observed in situ are often attached to dead scleractinian corals or coral rubble. Abundance and diversity of stylasterids increase southward from the Carolinas.

The following detailed descriptions of deepwater coral areas included in the SAFMC's proposal for HAPC designation were extracted from reports developed by S. Ross and J. Reed for the SAFMC in 2006 and 2004, respectively.

North Carolina Deep Coral Banks (from Ross' report to the SAFMC 2006)

Off North Carolina, *Lophelia* forms what may be considered classic mounds (three areas surveyed so far) that appear to be a sediment/coral rubble matrix topped with almost monotypic stands of *L. pertusa*. Although *Lophelia* is the dominant hard coral off North Carolina, other scleractinians contribute to the overall complexity of the habitat. These include the colonial corals *Madrepora oculata* and *Enallopsammia* spp. as well as a variety of solitary corals. These hard corals tend to live on or within the *Lophelia* matrix. The three North Carolina *Lophelia* mounds are the northernmost coral banks in the southeast U.S. Because these banks seem to be a northern terminus for a significant zoogeographic region, they may be unique in biotic resources as well as habitat expression. The three NC banks are generally similar in physical attributes and faunal composition. Some observed differences, however, are being investigated, and more detailed results will be presented in several peer reviewed publications in preparation (Ross et al.). For convenience these three areas have been designated as Cape Lookout *Lophelia* Bank A, Cape Lookout *Lophelia* Bank B, and Cape Fear *Lophelia* Bank. These names are to facilitate research and may eventually be changed. General descriptions of the NC coral mounds and associated fauna follows. Since there are almost no data published for the NC deep coral banks and because they are different than those to the south, they are discussed in more detail below. Between summer 2000 and fall 2005 Ross et al. (unpubl. data) sampled these areas extensively using a variety of methods throughout the water column. Their major method for collecting bottom data on the reef proper was the *Johnson-Sea-Link* (JSL) research submersible.

Cape Lookout Lophelia Bank A

Preliminary observations suggest that this area contains the most extensive coral mounds off North Carolina; however, it must be emphasized that data are lacking to adequately judge overall sizes and areal coverage. Ross et al. JSL submersible dives in this area ranged from 370-447 m.

Mean bottom temperatures ranged from 6.3 to 10.9°C, while mean bottom salinities were always around 35 ppt. There appear to be several prominences capping a ridge system, thus, presenting a very rugged and diverse bathymetry, but there are also other mounds away from the main ridge sampled (Figure 3.3-4). The main mound system rises vertically nearly 80 m over a distance of about 1 km, and in places exhibits slopes in excess of 50-60 degrees. Sides and tops of these mounds are covered with extensive colonies of living *Lophelia pertusa*, with few other corals being observed. Dead colonies and coral rubble interspersed with sandy channels are also abundant. Extensive coral rubble zones surround the mounds for a large, but unknown, distance (exact area not yet surveyed), especially at the bases of the mounds/ridges, and in places seem to be quite thick. These mounds appear to be formed by successive coral growth, collapse, and sediment entrapment (Wilson 1979; Popenoe and Manheim 2001). These topographic highs accelerate bottom currents, which favor attached filter feeders; very strong bottom currents have also been observed.

Cape Lookout Lophelia Bank B

The least amount of data are available for this area. Mounds appear to cover a smaller area than those described above, but here again better mapping data are needed. Ross et al. JSL dives in this area ranged from 396-449 m. Mean bottom temperatures ranged from 5.8 to 10.4°C, and as above mean bottom salinities were always around 35 ppt. These mounds rise at least 53 m over a distance of about 0.4 km. There is a small mound away from the main system (Figure 3.3-5), and in general these mounds were less dramatic than those described above. They appeared to be of the same general construction as Bank A, appearing to be built of coral rubble matrix that had trapped sediments. Extensive fields of coral rubble surrounded the area. Both living and dead corals were common on this bank, with some living bushes being quite large.

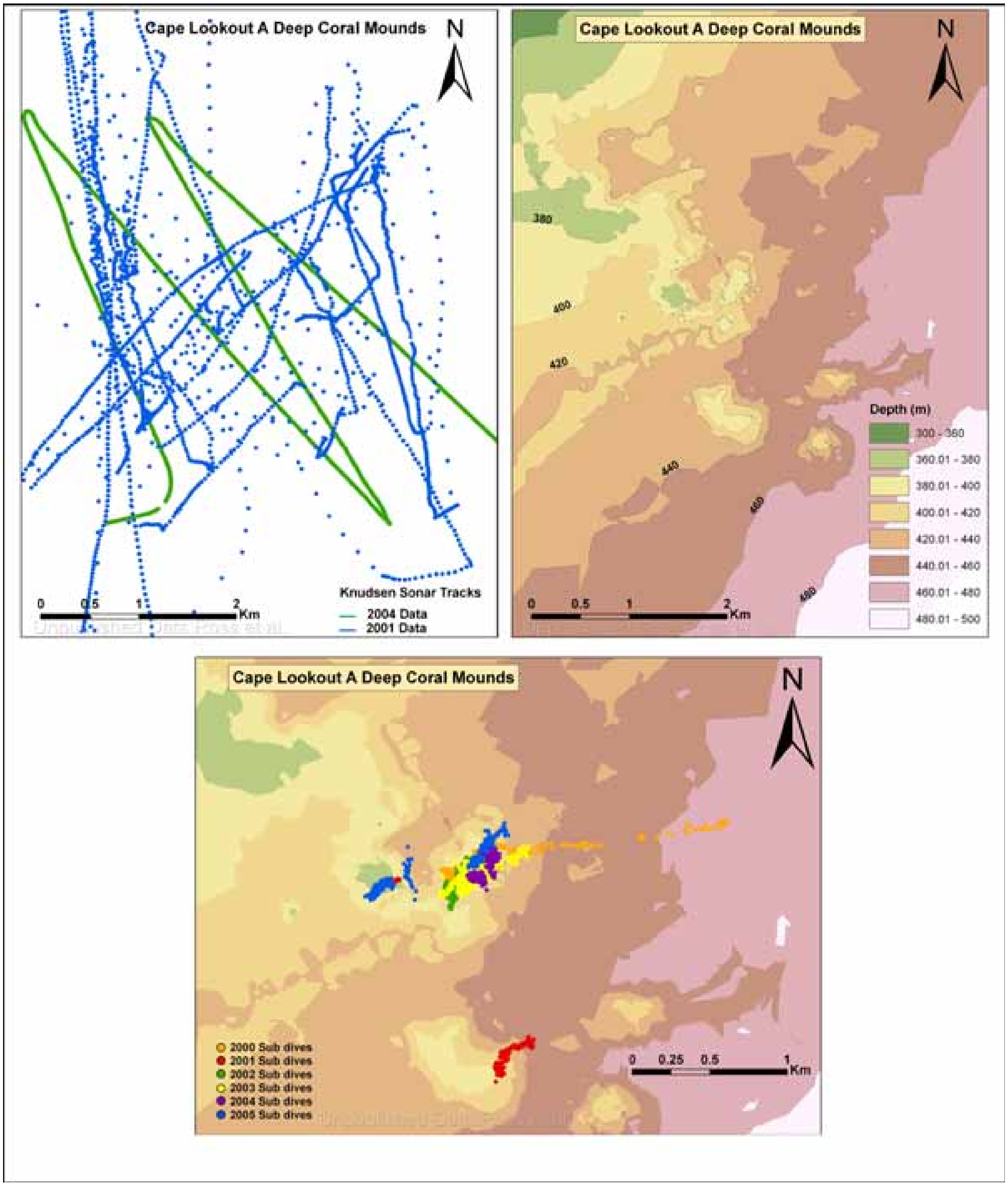


Figure 3.3-4. Ship collected sonar tracks (top left) and resulting bathymetry maps (top right) from the deep coral area off Cape Lookout, NC (A). In this area additional data from our files were added for the bathymetry map. Bottom panel shows JSL submersible dive tracks in this area from 2000- 2005. All data are from Ross et al. (unpublished). See Fig. 3.3-3 to locate this area.

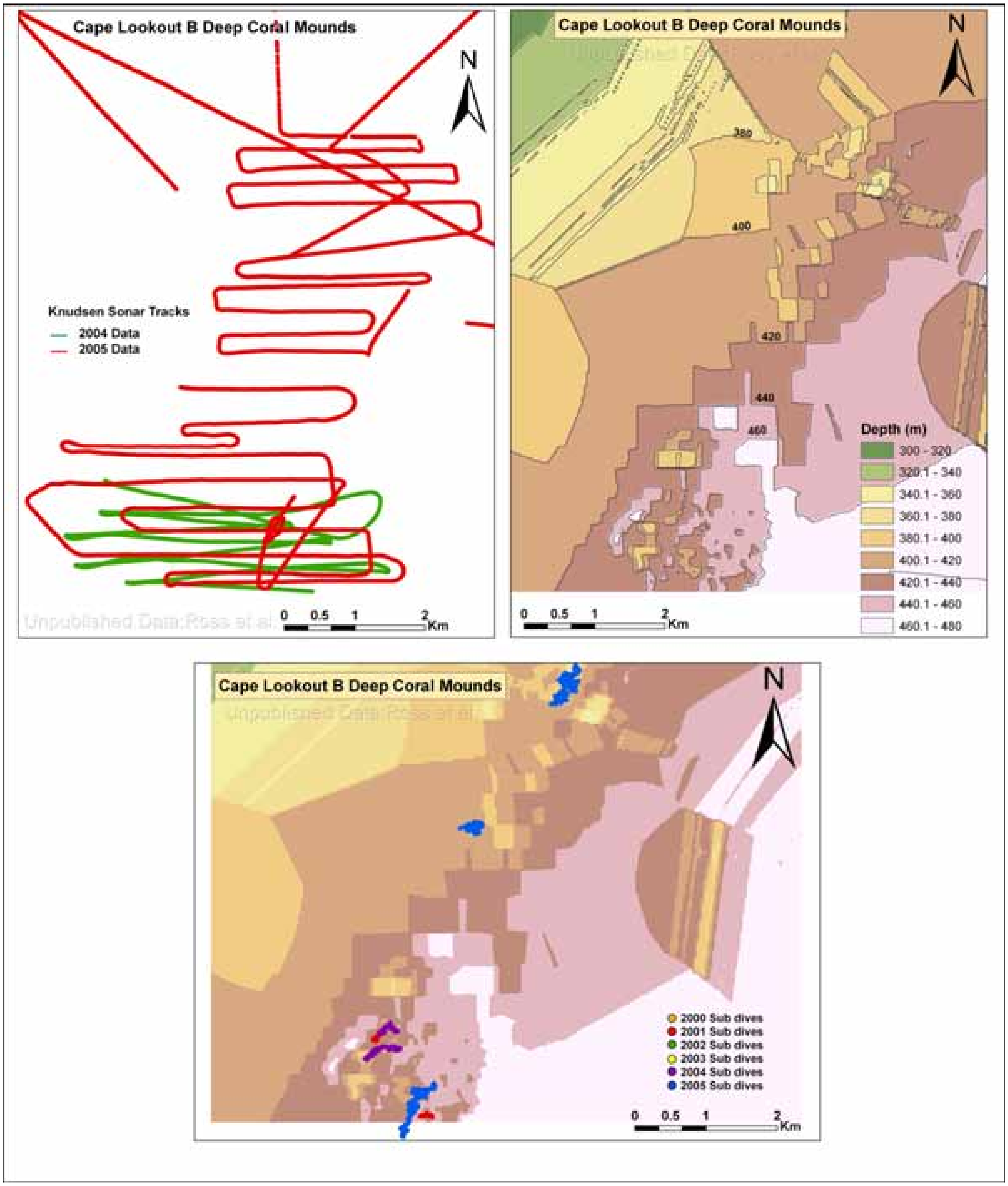


Figure 3.3-5. Ship collected sonar tracks (top left) and resulting bathymetry maps (top right) from the deep coral area off Cape Lookout, NC (B). Bottom panel shows JSL submersible dive tracks in this area from 2000-2005. All data are from Ross et al. (unpublished). See Fig. 3.3-3 to locate this area.

Cape Fear Lophelia Bank

Aside from the map in EEZ-SCAN 87 Scientific Staff (1991) there are no published data from this coral mound and no indication that it was sampled before the studies initiated by Ross et al. (unpubl. data) between summer 2002 and fall 2005. Ross et al. located this bank based on estimated coordinates from the USGS survey (EEZ-SCAN 87 Scientific Staff 1991). As above, the JSL submersible was the major method for collecting bottom data on the reef proper. Sampling in this area was focused on a relatively small area (Figure 3.3-6), but data are lacking to accurately estimate the size and area covered by coral mounds or rubble zones. Ross et al. JSL dives in this area ranged from 371-449 m. Mean bottom temperatures ranged from 8.7 to 11.7°C, and as above mean bottom salinities were always near 35 ppt. These mounds rise nearly 80 m over a distance of about 0.4 km, and exhibit some of the most rugged habitat and vertical excursion of any area sampled. This mound system also appears to be of the same general construction as Banks A and B, being built of coral rubble matrix with trapped sediments. Fields of coral rubble are common around the area. Both living and dead corals were common on this bank.

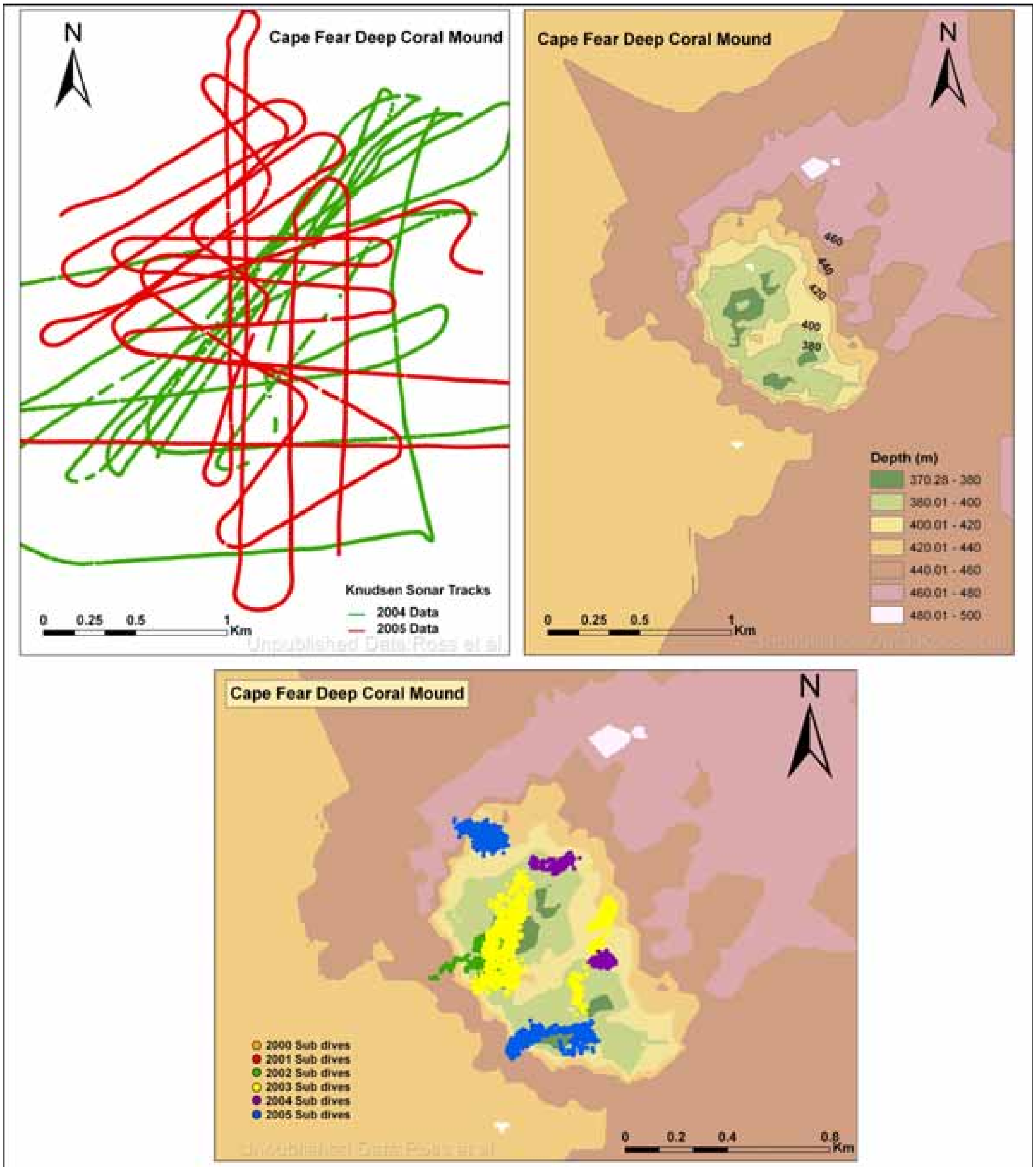


Figure 3.3-6. Ship collected sonar tracks (top left) and resulting bathymetry maps (top right) from the deep coral area off Cape Fear, NC. Bottom panel shows JSL submersible dive tracks in this area from 2000-2005. All data are from Ross et al. (unpublished). See Fig. 3.3-3 to locate this area.

Potential NC Coral Mounds

Several potential deep coral banks (Figure 3.3-3) were identified in the USGS survey of the EEZ off of North Carolina (EEZ-SCAN 87 Scientific Staff 1991). During surveys with the NR-1 submarine (Sulak and Ross unpubl. data, 1993) and again during a cruise of the R/V *Cape Hatteras* (S.W. Ross, Chief Scientist, 2001), attempts were made to locate the bank between

Cape Lookout Bank A and Bank B (Figure 3.3-3). However, no coral mounds were observed in this area. It is possible that there are coral mounds in this area but the small search pattern and potential navigation issues prevented finding them. Other banks may exist on the slope south of 33°N (Figure 3.3-3). As far as known these have not been accurately located or confirmed as coral banks, although the location referenced by George (2002) is near one of these areas. These banks would be important to confirm as they would occur in what may be a transition area between a region of coral/sediment built mounds composed almost entirely of *Lophelia pertusa* and the area to the south where coral development is generally quite different.

Coral Banks of the Blake Plateau

South of Cape Fear sediment/coral mounds are smaller and scattered; however, *L. pertusa* and other hard and soft corals populate the abundant hard substrates of the Blake Plateau in great numbers. Overall, species diversity of anthozoans and other associated sessile invertebrates (e.g., sponges, hydrozoans) increases south of Cape Fear, NC. For convenience, some deep coral study areas in this region have been named, giving the impression of isolated areas of coral habitat. It appears, however, that Blake Plateau coral habitats are larger and more continuous than these names imply. Future detailed mapping of the area combined with ground-truthing will clarify coral habitat distributions and the extent to which areas may require discrete names.

There are existing research data for this area, but historically most of it was geological. Most deepwater coral expeditions south of North Carolina concentrated around the area described by Stetson et al. (1962), referred to as “Stetson Banks” (Figure 3.3-7), an area off Georgia (“Savannah Banks”), the Charleston Bump (Sedberry 2001), a large area straddling the Georgia/Florida border (“Jacksonville Lithoherms”) and numerous coral sites along the FL East coast. General properties of these study areas were described in several papers by Reed and colleagues (Reed 2002, Reed unpubl. rept. to SAFMC 2004, Reed and Ross 2005, Reed et al. 2005, 2006). Because it is unclear that these coral study areas are physically separate, they are not discussed individually.

The Stetson Bank is a very large region of extremely diverse, rugged topography and bottom types. There is a deep canyon on the eastern side of this system with abundant corals on its western rim. While the surface waters of Stetson Bank are often outside the main Gulf Stream path, bottom currents can be quite strong. This is one of the deeper and more interesting of the Blake Plateau coral areas and warrants further exploration. The Savannah Bank system appears to have a heavier sediment load, perhaps because it is closest to the continental shelf. Deepwater corals occur there in scattered patches and are often less well developed than at other sites. Many sites in the “Jacksonville area” were composed of rocky ledges to which corals were attached, especially on the northern end. Bottom types in this area are diverse as is the fauna. Topographic highs, most having corals, are very abundant from the “Jacksonville area” to just south of Cape Canaveral (see also Reed et al. 2005, 2006). Faunal diversity is quite high in this region.

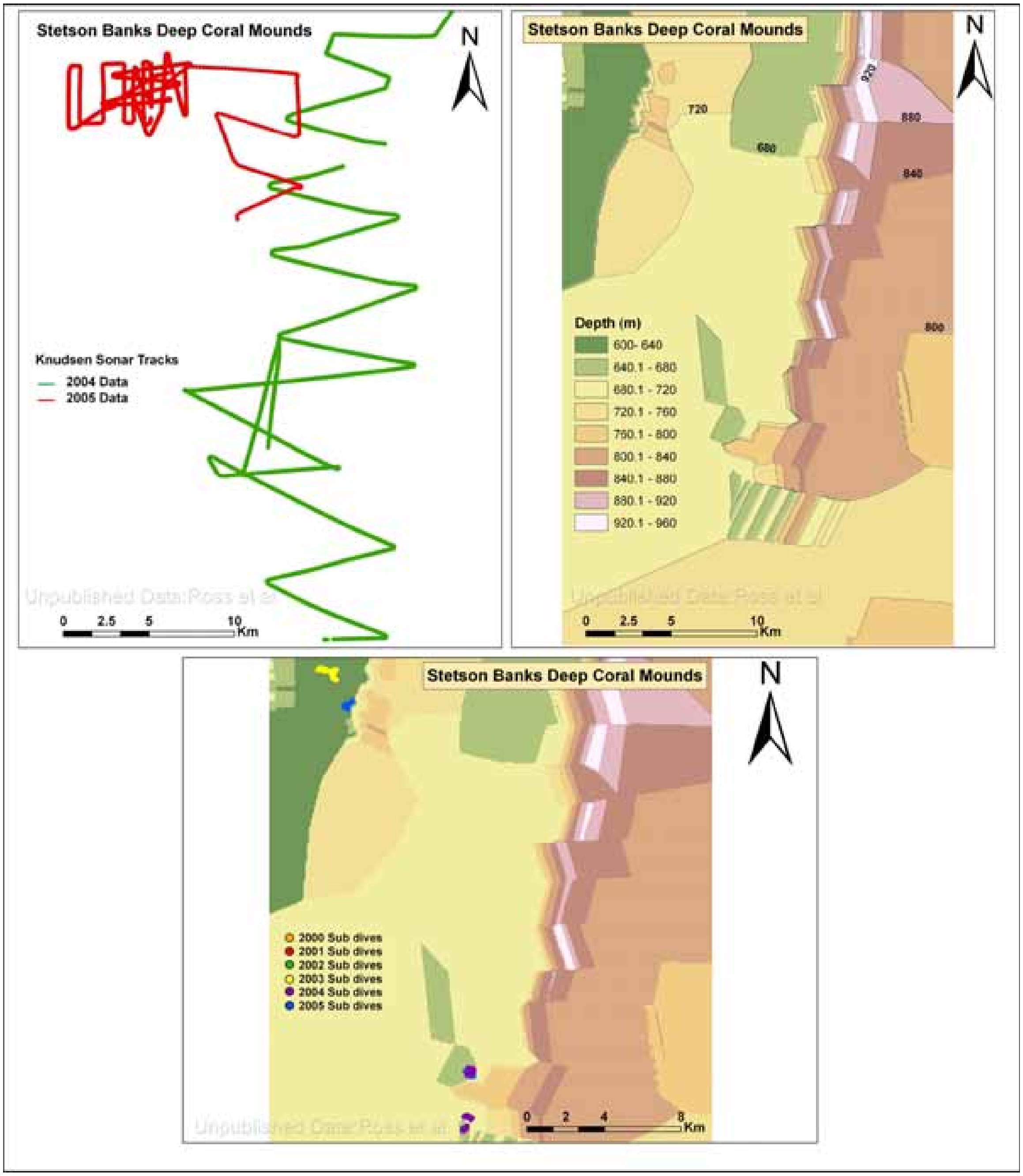


Figure 3.3-7. Ship collected sonar tracks (top left) and resulting bathymetry maps (top right) from the Stetson deep coral area off of SC. Bottom panel shows JSL submersible dive tracks in this area from 2000-2005. All data are from Ross et al. (unpublished). See Fig. 3.3-3 to locate this area.

<u>Stetson Reefs, Eastern Blake Plateau</u> (from Reed, 2002a; Reed et al., 2004b)
This site is on the outer eastern edge of the Blake Plateau, approximately 120 nm SE of Charleston, South Carolina, at depths of 640-869 m (Figures 3.3-8 and 3.3-9). Over 200 coral mounds up to 146 m in height occur over this 6174 km^2 area that was first described by Thomas

Stetson from echo soundings and bottom dredges (Stetson et al., 1962; Uchupi, 1968). These were described as steep-sloped structures with active growth on top of the banks. Live coral colonies up to 50 cm in diameter were observed with a camera sled. *Enallopsammia profunda* (=*D. profunda*) was the dominant species in all areas although *L. pertusa* was concentrated on top of the mounds. Densest coral growth occurred along an escarpment at Region D1. Stetson et al. (1962) reported an abundance of hydroids, alcyonaceans, echinoderms, actiniaria, and ophiuroids, but a rarity of large mollusks. The flabelliform gorgonians were also current-oriented. Popenoe and Manheim (2001) have made detailed geological maps of this Charleston Bump region which also indicate numerous coral mounds.

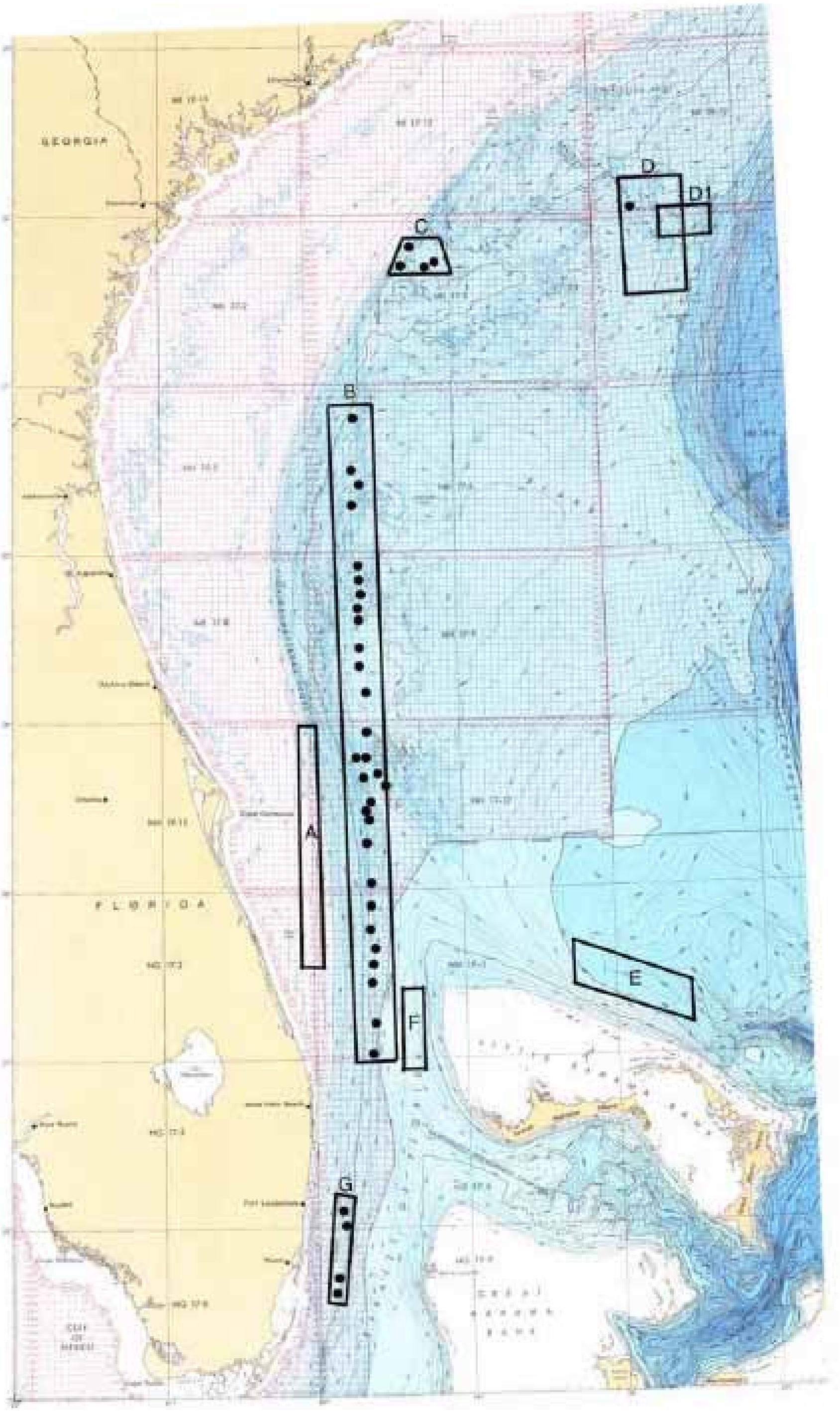


Figure 3.3-8. Deep-water coral reef regions off southeastern U.S.A. ?= *Johnson-Sea-Link* I and II submersible dive sites and echosounder sites of high-relief reefs; Regions: A=*Oculina* Coral Reefs, B= East Florida *Lophelia* Reefs, C= Savannah Lophelia Lithoherms, D= Stetson's Reefs (D1= region of dense pinnacles), E= *Enallopsammia* Reefs (Mullins et al., 1981), F= Bahama Lithoherms (Neumann et al., 1977), G= Miami Terrace Escarpment. (from Reed et al., 2004b; chart from NOAA, NOS, 1986).

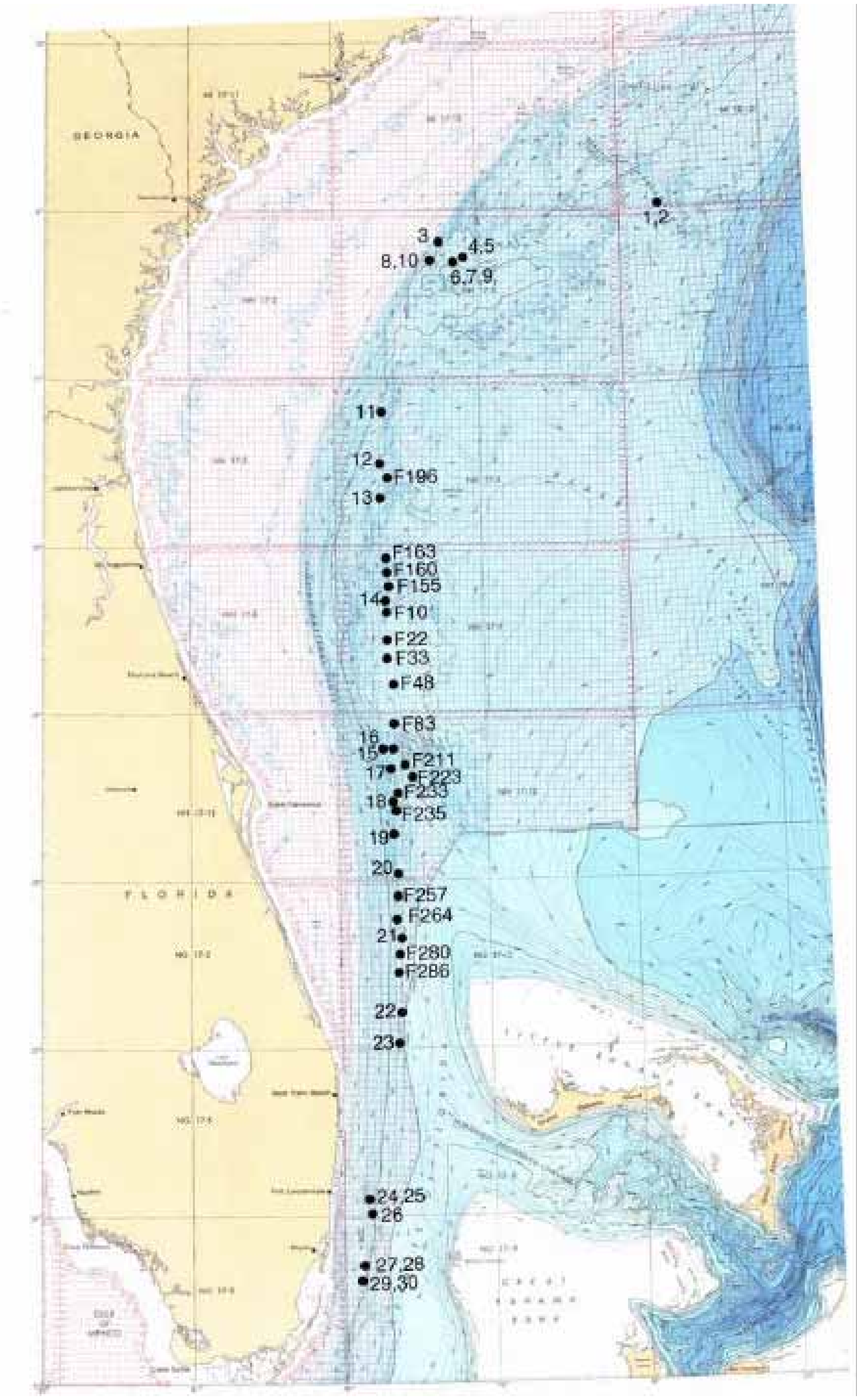


Figure 3.3-9. Bathymetry and submersible dive sites on Pourtalès Terrace at Region H. = *Johnson-Sea-Link* and *Clelia* submersible dive sites; JS= Jordan Sinkhole, MS= Marathon Sinkhole, TB1= Tennessee Humps Bioherm #1, TB2= Tennessee Humps Bioherm #2, AB3= Alligator Humps Bioherm #3, AB4= Alligator Humps Bioherm #4 (from Reed et al., 2004b; chart from Malloy and Hurley, 1970; Geol. Soc. Amer. Bull. 81: 1947-1972).

Fathometer transects by J. Reed indicated dozens and possibly hundreds of individual pinnacles and mounds within the small region that we surveyed which is only a fraction of the Stetson Bank area (Reed and Pomponi, 2002b; Reed et al., 2002; Reed et al., 2004b). Two pinnacle regions were selected from fathometer transects. Three submersible dives were made on "Pinnacle 3" and four dives on "Stetson's Peak" which is described below. A small subset of the Stetson Bank area was first mapped by six fathometer transects covering approximately 28 nm^2, in which six major peaks or pinnacles and four major scarps were plotted. The base depth of these pinnacles ranged from 689 m to 643 m, with relief of 46 to 102 m. A subset of this was further mapped with 70 fathometer transects spaced 250 m apart (recording depth, latitude and longitude ~ every 3 seconds), covering an area of 1 x 1.5 nm, resulting in a 3-D bathymetric GIS Arcview map of a major feature, which was named named Stetson's Pinnacle (Figure 3.3-10).

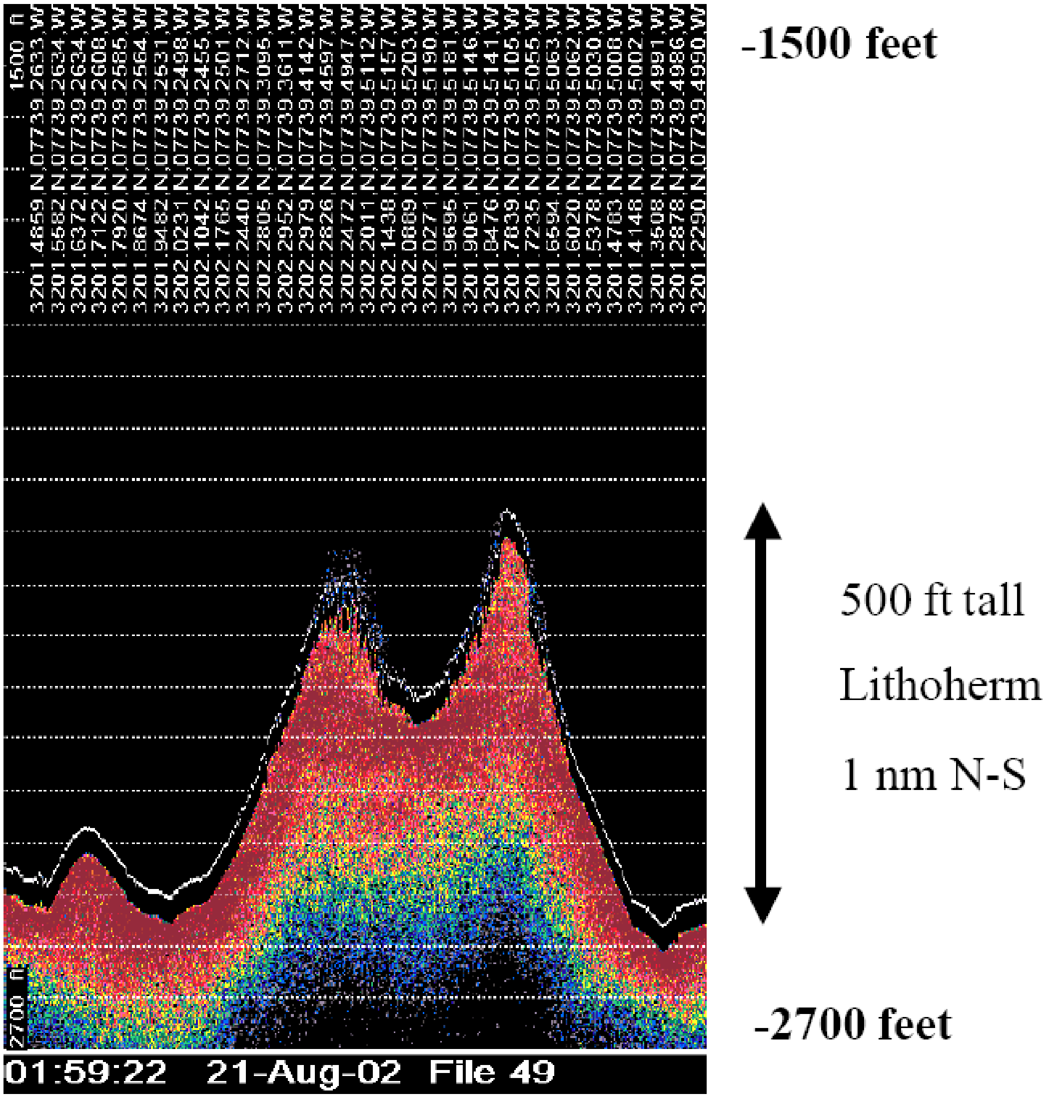


Figure 3.3-10. Echosounder profile of Stetson's Pinnacle (depth 780 m, relief 153 m) (from Reed et al., 2004b).

Stetson's Pinnacle was 780 m at the south base and the peak was 627 m. This represents one of the tallest *Lophelia* coral lithoherms known, nearly 153 m in relief. The linear distance from the south base to the peak was approximately 0.5 nm. The lower flank of the pinnacle from ~762 m to 701 m on the south face was a gentle slope of 10-30° with a series of 3-4 m high ridges and terraces that were generally aligned 60-240° across the slope face. These ridges were covered with nearly 100% *Lophelia* coral rubble, 15-30 cm colonies of live *Lophelia*, and standing dead colonies of *Lophelia*, 30-60 cm tall. Very little rock was exposed, except on the steeper exposed, eroded faces of the ridges. Some rock slabs, ~30 cm thick, have slumped from these faces. From 701 m to 677 m the slope increased from ~45° to 60 °. From 671 m to the peak, the geomorphology was very complex and rugged, consisting of 60-90° rock walls and 3-9 m tall rock outcrops. Colonies of *Lophelia*, 30-60 cm tall, were more common, and some rock ledges had nearly 100% cover of live *Lophelia* thickets. The top edge of the pinnacle was a 30 cm thick rock crust which was undercut from erosion; below this was a 90° escarpment of 3-6 m. The peak was a flat rock plateau at 625- 628 m and was approximately 0.1 nm across on a S-N submersible transect. The north face was not explored in detail but is a vertical rock wall from the peak to ~654 m then grades to a 45° slope with boulders and rock outcrops.

Dominant sessile macrofauna consisted of scleractinia, stylasterine hydrocorals, gorgonacea and sponges. The colonial scleractinia were dominated by colonies of *Lophelia pertusa* (30-60 cm tall) and *Enallopsammia profunda*, and *Solenosmilia variabilis* were present. Small stylasterine corals (15 cm tall) were common and numerous species of solitary cup corals were abundant. Dominant octocorallia consisted of colonies of Primnoidae (15-30 cm tall), paramuriceids (60-90 cm), Isididae bamboo coral (15-60 cm), stolonifera, and stalked Nephtheidae (5-10 cm). Dominant sponges consisted of Pachastrellidae (25 cm fingers and 25- 50 cm plates), Corallistidae (10 cm cups), Hexactinellida glass sponges (30 cm vase), *Geodia sp.* (15-50 cm spherical), and *Leiodermatium sp.* (50 cm frilly plates). Although motile fauna were not targeted, some dominant groups were noted. No large decapods crustaceans were common although some red portunids were observed. Two species of echinoids were common, one white urchin and one stylocidaroid. No holothurians or asteroids were noted. Dense populations of Ophiuroidea were visible in close-up video of coral clusters and sponges. No large Mollusca were noted except for some squid. Fish consisted mostly of benthic gadids and rattails. On the steeper upper flank, from 671 to 625 m the density, diversity, and size of sponges increased; 15-50 cm macro sponges were more abundant. Massive *Spongosorites sp.* were common, Pachastrellidae tube sponges were abundant, and Hexactinellida glass sponges were also common. On the peak plateau the dominant macrofauna were colonies of *Lophelia pertusa* (30-60 cm tall), coral rubble, *Phakellia sp.* fan sponges (30-50 cm), and numerous other demosponges were abundant. No large fish were seen on top.

<u>Savannah Lithoherms, Blake Plateau</u> (from Reed, 2002a; Reed et al., 2004b)
A number of high-relief lithoherms occur within this region of the Blake Plateau, approximately 90nm east of Savannah, Georgia (Figures 3.3-8 and 3.3-9). This region is at the base of the Florida-Hatteras Slope, near the western edge of the Blake Plateau, and occurs in a region of phosphoritic sand, gravel and rock pavement on the Charleston Bump (Sedberry, 2001). Wenner and Barans (2001) described 15-23 m tall coral mounds in this region that were thinly veneered with fine sediment, dead coral fragments and thickets of *Lophelia* and *Enallopsammia*. They

found that blackbellied rosefish and wreckfish were frequent associates of this habitat. In general, the high-relief *Lophelia* mounds occur in this region at depths of 490-550 m and have maximum relief of 61 m. JSL-II dives 1690, 1697 and 1698 reported a coral rubble slope with <5% cover of 30 cm, live coral colonies (Reed, 2002a). On the reef crest were 30-50 cm diameter coral colonies covering approximately 10% of the bottom.

Some areas consisted of a rock pavement with a thin veneer of sand, coral rubble, and 5-25 cm phosphoritic rocks. At *Alvin* dive sites 200 and 203, Milliman et al. (1967) reported elongate coral mounds, approximately 10 m wide and 1 km long, that were oriented NNE-SSW. The mounds had 25-37° slopes and 54 m relief. Live colonies (10-20 cm diameter) of *E. profunda* (=*D. profunda*) dominated and *L. pertusa* (=*L. prolifera*) was common. No rock outcrops were observed. These submersible dives found that these lithoherms provided habitat for large populations of massive sponges and gorgonians in addition to the smaller macroinvertebrates which have not been studied in detail. Dominant macrofauna included large plate-shaped sponges (*Pachastrella monilifera*) and stalked, fan-shaped sponges (*Phakellia ventilabrum*), up to 90 cm in diameter and height.

At certain sites (JSL-II dive 1697), these species were estimated at 1 colony/10 m^2. Densities of small stalked spherical sponges (*Stylocordyla sp*., Hadromerida) were estimated in some areas at 167 colonies/10 m^2. Hexactinellid (glass) sponges such as *Farrea*? sp. were also common. Dominant gorgonacea included *Eunicella* sp. (Plexauridae) and *Plumarella pourtalessi* (Primnoidae).

Recent fathometer transects by J. Reed at Savannah Lithoherm Site #1 (JSL II-3327) extended 2.36 nm S-N revealed a massive lithoherm feature that consisted of five major pinnacles with a base depth of 549 m, minimum depth of 465 m, and maximum relief of 83 m (Reed and Pomponi, 2002b; Reed et al., 2002; Reed et al., 2004b). The individual pinnacles ranged from 9 to 61 m in height. A single submersible transect, south to north, on Pinnacle #4 showed a minimum depth of 499 m. The south flank of the pinnacle was a gentle 10-20° slope, with ~90% cover of coarse sand, coral rubble and some 15 cm rock ledges. The peak was a sharp ridge oriented NW-SE, perpendicular to the prevailing 1 kn current. The north side face of the ridge was a 45° rock escarpment of about 3 m which dropped onto a flatter terrace. From a depth of 499 to 527 m, the north slope formed a series of terraces or shallow depressions, ~9-15 m wide, that were separated by 3 m high escarpments of 30-45°. Exposed rock surfaces showed a black phosphoritic rock pavement. The dominant sessile macrofauna occurred on the exposed pavement of the terraces and in particular at the edges of the rock outcrops and the crest of the pinnacle.

The estimated cover of sponges and gorgonians was 10% on the exposed rock areas. Colonies of *Lophelia pertusa* (15-30 cm diameter) were common but not abundant with ~1% coverage. Dominant Cnidaria included several species of gorgonacea (15-20 cm tall), Primnoidae, Plexauridae (several spp.), *Antipathes* sp. (1 m tall), and *Lophelia pertusa*. Dominant sponges included large *Phakellia ventilabrum* (fan sponges, 30-90 cm diameter), Pachastrellidae plate sponges (30 cm), *Choristida* plate sponges (30 cm), and Hexactinellid glass sponges. Motile fauna consisted of decapod crustaceans (*Chaceon fenneri*, 25 cm; and Galatheidae, 15 cm) and mollusks. Few large fish were observed but a 1.5 m swordfish, several 1 m sharks, and numerous blackbelly rosefish were noted.

A fathometer transect by J. Reed at Savannah Lithoherm Site 2 (Figure 3.3-11) extended 4.6 nm, SW to NE, mapped 8 pinnacles with maximum depth of 549 m and relief of 15-50 m.

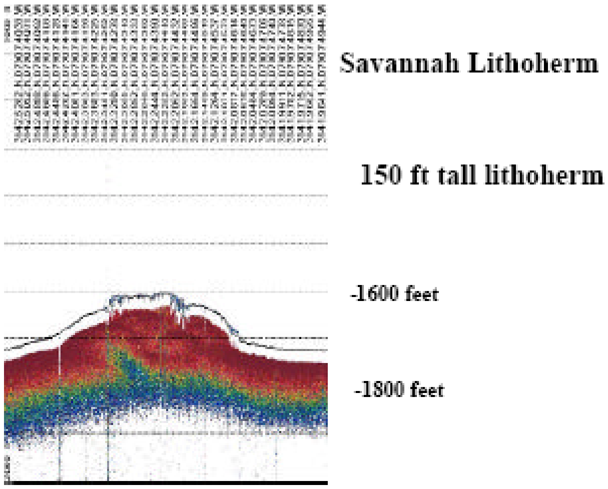


Figure 3.3-11. Echosounder profile of Savannah Lithoherm, Site 2, Pinnacle #1 (depth 537 m, relief 50 m) (from Reed et al., 2004b).

Submersible dives were made on Pinnacles 1, 5 and 6 of this group. Pinnacle 1 was the largest feature of this group; the base was 537 m and the top was 487 m. The south face, from a depth of 518 to 510 m, was a gentle 10° slope, covered with coarse brown sand and *Lophelia* coral rubble. A 3-m high ridge of phosphoritic rock, extended NE-SW, cropped out at a depth of 510 m. This was covered with nearly 100% cover of 15 cm thick standing dead *Lophelia* coral and dense live colonies of *Lophelia pertusa* (15-40 cm). From depths of 500 m to 495 m were a series of exposed rock ridges and terraces that were 3-9 m tall with 45° slopes.

Some of the terraces were ~30 m wide. Each ridge and terrace had thick layers of standing dead *Lophelia*, and dense live coral. These had nearly 100% cover of sponges (*Phakellia* sp., *Geodia* sp., Pachastrellidae, and Hexactinellida), scleractinia (*Lophelia pertusa*, *Madrepora oculata*), stylasterine hydrocorals, numerous species of gorgonacea (Ifalukellidae, Isididae, Primnoidae), and 1 m bushes of black coral (*Antipathes* sp.). Deep deposits of sand and coral rubble occurred in the depressions between the ridges. The north face, from 500 m to 524 m was a gentle slope of 10° that had deep deposits of coarse brown foraminiferal sand and coral rubble. Exposed rock pavement was sparse on the north slope, but a few low rises with live bottom habitat occurred at 524 m. Dominant mobile fauna included decapod crustaceans (*Chaceon fenneri*, 15 cm Galatheidae), rattail fish, and 60 cm sharks were common.

Florida

Deepwater coral ecosystems in U.S. EEZ waters also exist along the eastern and southwest Florida shelf slope (in addition to the Oculina HAPC and deep shelf-edge reefs with hermatypic coral). These include a variety of high-relief, hardbottom, live-bottom habitats at numerous sites along the base of the Florida-Hatteras Slope off northeastern and central eastern Florida, the Straits of Florida, the Miami Terrace and Pourtales Terrace off southeastern Florida, and the southwestern Florida shelf slope. The predominate corals on these reefs are the azooxanthellate, colonial scleractinian corals, *Lophelia pertusa*, *Madrepora oculata*, and *Enallopsammia profunda*; various species of hydrocorals of the family Stylasteridae, and species of the bamboo octocoral of the family Isididae. Various types of high- relief, live-bottom habitat have been discovered in the area: *Lophelia* mud mounds, lithoherms, sinkholes, ancient Miocene escarpments and karst topographic features (Reed 2002b; Reed et al. 2004a, b). These all provide hardbottom substrate and habitat for sessile macrofauna including deepwater corals, octocorals (gorgonians), black coral, and sponges, which in turn provide habitat and living space for a relatively unknown but biologically rich and diverse community of associated fish, crustaceans, mollusks, echinoderms, polychaete and sipunculan worms, and other macrofauna, many of which are undoubtedly undescribed species. Preliminary studies by Reed et al. (2004a, b) have found new species of octocorals and sponges from some these sites.

<u>Florida Lophelia Pinnacles</u> (from Reed, 2002a; Reed et al., 2004b)
Numerous high-relief *Lophelia* reefs and lithoherms occur in this region at the base of the Florida- Hatteras Slope and at depths of 670-866 m. The reefs in the southern portion of this region form along the western edge of the Straits of Florida and are 15-25 nm east of the *Oculina* HAPC. Along a 222-km stretch off northeastern and central Florida (from Jacksonville to Jupiter), nearly 300 mounds from 8 to 168 m in height (25- 550 ft) were recently mapped by J. Reed using a single beam echosounder (Figure 3.3-12; Reed et al. 2004b). Between 1982 and 2004, dives with the *Johnson-Sea-Link* (JSL) submersibles and ROVs by J. Reed confirmed the presence of *Lophelia* mounds and lithoherms in this region (Reed 2002a; Reed et al. 2002; Reed and Wright 2004; Reed et al. 2004b). The northern sites off Jacksonville and southern Georgia appeared to be primarily lithoherms which are pinnacles capped with exposed rock (described in part by Paull et al. 2000), whereas the features from south of St. Augustine to Jupiter were predominately *Lophelia* coral pinnacles or mud mounds capped with dense 1m-tall thickets of *Lophelia pertusa* and *Enallopsammia profunda* with varying amounts of coral debris and live coral. Dominant habitat-forming coral species were *Lophelia pertusa*, *Madrepora oculata*, *Enallopsammia profunda*, bamboo coral (Isididae), black coral (Antipatharia), and diverse populations of octocorals and sponges (Reed et al. 2004b).

Paull et al. (2000) estimated that over 40,000 coral lithoherms may be present in this region of the Straits of Florida and the Blake Plateau. Their dives with the *Johnson-Sea-Link* submersible and the U.S. Navy's submarine NR-1 described a region off northern Florida and southern Georgia of dense lithoherms forming pinnacles 5 to 150 m in height with 30-60° slopes that had thickets of live ahermatypic coral (unidentified species, but photos suggest *Lophelia* and/or *Enallopsammia*). The depths range from 440 to 900+ m but most mounds were within 500-750 m. Each lithoherm was ~100-1000 m long and the ridge crest was generally oriented perpendicular to the northerly flowing Gulf Stream current (25-50 cm/s on flat bottom, 50-100 cm/s on southern slopes and crests).

Thickets of live coral up to 1 m were mostly found on the southern facing slopes and crests whereas the northern slopes were mostly dead coral rubble. These were termed lithoherms since the mounds were partially consolidated by a carbonate crust, 20-30 cm thick, consisting of micritic wackestone with embedded planktonic foraminifera, pteropods, and coral debris (Paull et al. 2000).

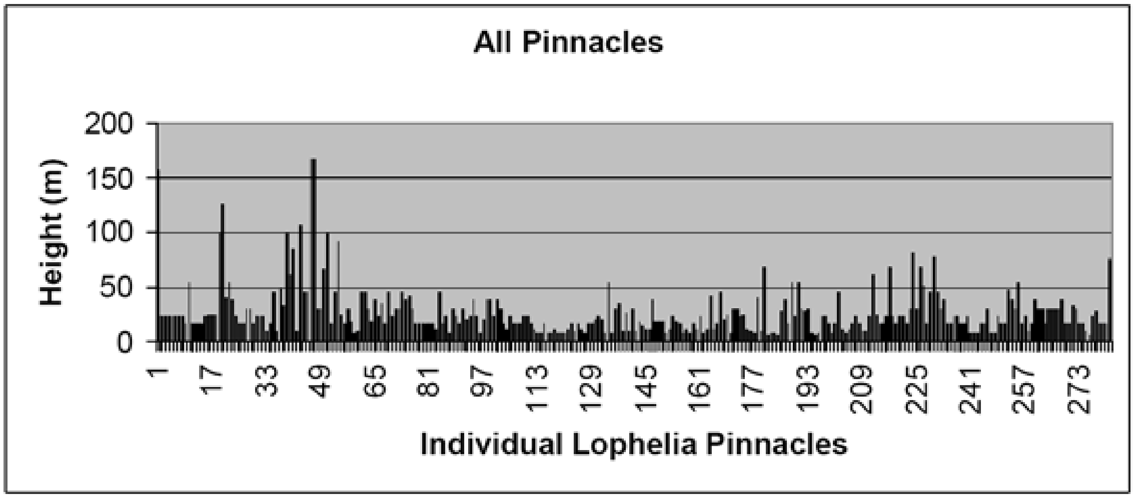


Figure 3.3-12. Height of *Lophelia* pinnacles and lithoherms on echosounder transects from Jacksonville to Jupiter, Florida at depths of 600 to 800 m. (from Reed et al. 2004b).

A recent echosounder transect by J. Reed revealed a massive lithoherm, 3.08 nm long (N-S) that consisted of at least 7 individual peaks with heights of 30-60 m (Figure 3.3-13; Reed and Wright 2004; Reed et al. 2004b). The maximum depth was 701 m with total relief of 157 m. Three submersible dives (JSL II-3333, 3334; I-4658) were made on Peak 6 of pinnacle #204B which was the tallest individual feature of the lithoherm with maximum relief of 107 m and a minimum depth at the peak of 544 m (Reed et al. 2004b). The east face was a 20-30° slope and steeper (50°) near the top. The west face was a 25-30° slope which steepened to 80° from 561 m to the top ridge. The slopes consisted of sand and mud, rock pavement and rubble. A transect up the south slope reported a 30-40° slope with a series of terraces and dense thickets of 30-60 cm tall dead and live *Lophelia* coral that were mostly found on top of mounds, ridges and terrace edges. One peak at 565 m had dense thickets of live and dead standing *Lophelia* coral (~20% live) and outcrops of thick coral rubble. Dominant sessile fauna consisted of *Lophelia pertusa*, abundant Isididae bamboo coral (30-60 cm) on the lower flanks of the mound, Antipatharia black coral, and abundant small octocorals including the gorgonacea (*Placogorgia* sp., *Chrysogorgia* sp, and Plexauridae) and Nephtheidae soft corals (*Anthomastus* sp., *Nephthya* sp.). Dominant sponges consisted of *Geodia* sp., *Phakellia* sp., *Spongosorites* sp., Petrosiidae, Pachastrellidae and Hexactinellida.

Further south off Cape Canaveral, echosounder transects by J. Reed on *Lophelia* Pinnacle #113 revealed a 61 m tall pinnacle with maximum depth of 777 m (Figure 3.3-14). The width (NW-SE) was 0.9 nm and consisted of at least 3 individual peaks or ridges on top, each with 15-19 m relief. One submersible dive (JSL II-3335) reported 30-60° slopes, with sand, coral rubble, and up to 10% cover of live coral. No exposed rock was observed. This appeared to be a classic *Lophelia* mud mound.

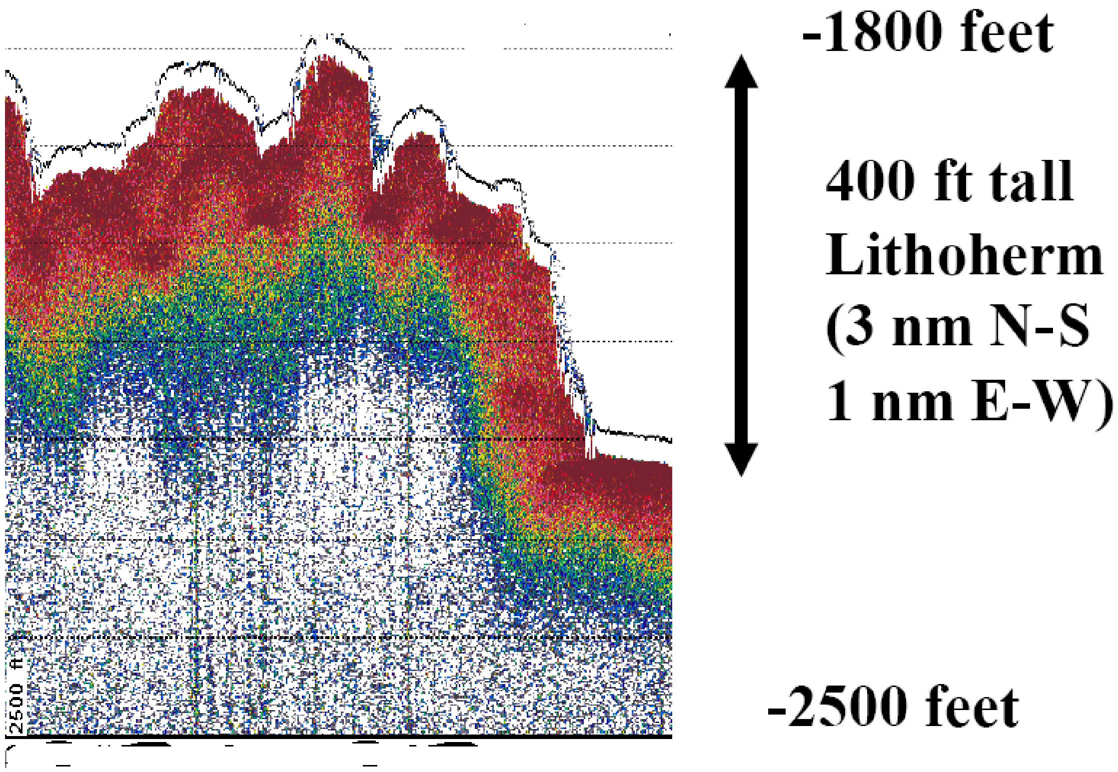


Figure 3.3-13. Echosounder profile of Jacksonville Lithoherm, Pinnacle #204B (depth 701 m, relief 157 m) (from Reed et al., 2004b).

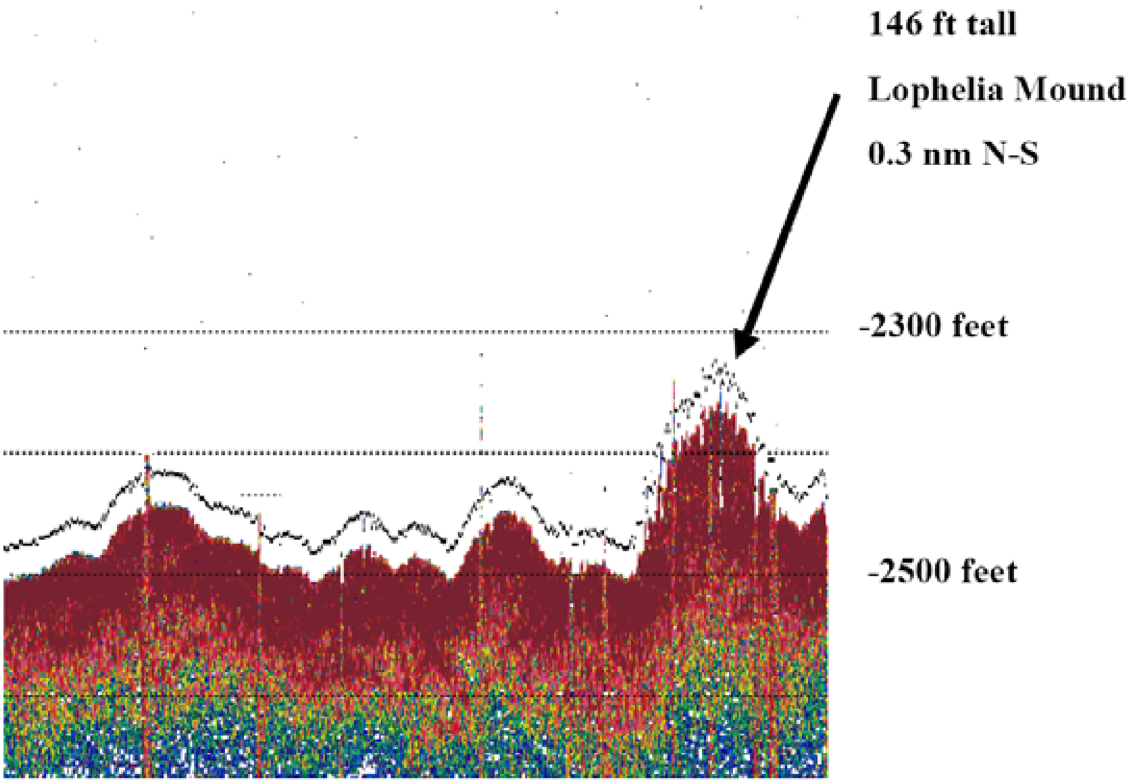


Figure 3.3-14. Echosounder profile of Cape Canaveral Lophelia Reef, Pinnacle #113 (depth 777 m, relief 61 m) (from Reed et al., 2004b).

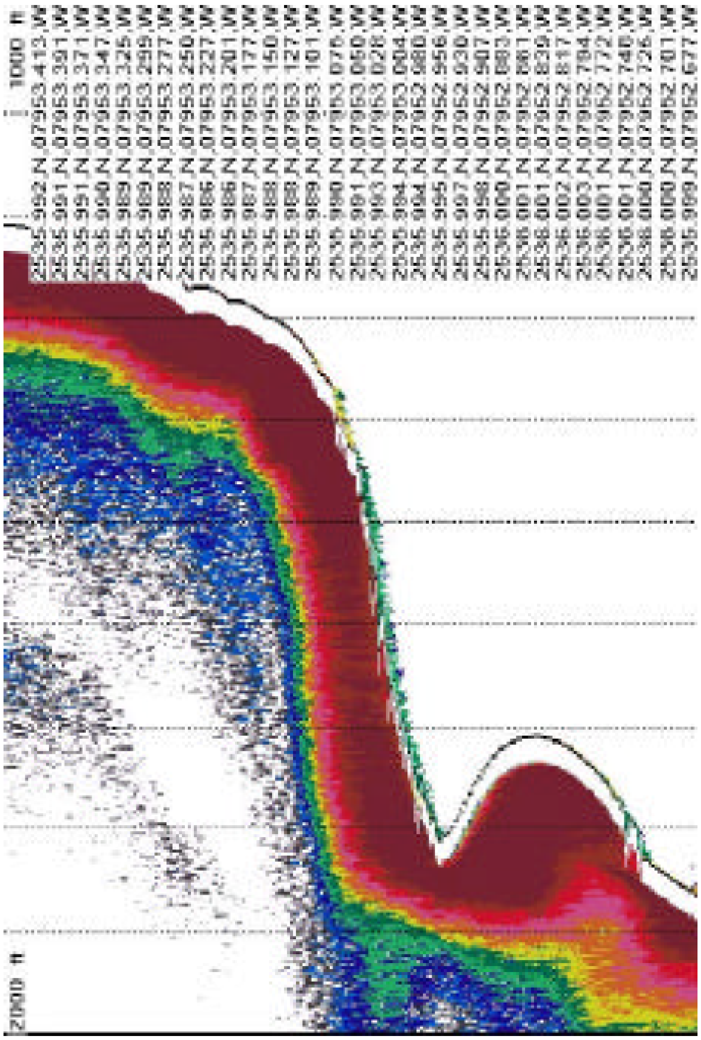
The second dive site (JSL II-3336) at Pinnacle #151 was also a deepwater *Lophelia* coral reef comprised entirely of coral and sediment. Maximum depth was 758 m, with 44 m relief, and ~0.3 nm wide (N-S). The top was a series of ridged peaks from 713 to 722 m in depth. The lower flanks of the south face was a 10-20° slope of fine light colored sand with a series of 1-3 m high sand dunes or ridges that were linear NW-SE. The ridges had ~50% cover of thickets of *Lophelia pertusa* coral. The thickets consisted of 1 m tall dead, standing and intact, *Lophelia pertusa* colonies. Approximately 1-10% was alive on the outer parts (15-30 cm) on top of the standing dead bases. There was very little broken dead coral rubble in the sand and there was no evidence of trawl or mechanical damage. Most of the coral was intact, and the dead coral was brown. The sand between the ridges was fine and light colored, with 7-15 cm sand waves. The upper slope steepened to 45° and 70-80° slope near the upper 10 m from the top. The top of the pinnacle had up to 100% cover of 1-1.5 m tall coral thickets, on a narrow ridge that was 5-10 m wide. The coral consisted of both *Lophelia pertusa* and *Enallopsammia profunda*. Approximately 10-20% cover was live coral of 30-90 cm. The north slope was nearly vertical (70-80°) for the upper 10 m then consisted of a series of coral thickets on terraces or ridges. No exposed rock was visible and the entire pinnacle appeared to be a classic *Lophelia* mud mound.

No discernable zonation of macrobenthic fauna was apparent from the base to the top. Corals consisted of *Lophelia pertusa*, *Enallopsammia profunda*, *Madrepora oculata*, and some stylasterine hydrocorals. Dominant octocoral gorgonacea included Primnoidae (2 spp.), Isididae bamboo coral (*Isidella* sp. and *Keratoisis flexibilis*), and the alcyonaceans *Anthomastus* sp. and

Nephthya sp. Dominant sponges consisted of several species of Hexactinellida glass sponges, large yellow demosponges (60-90 cm diameter), Pachastrellidae, and *Phakellia* sp. fan sponges. Echinoderms included urchins (cidaroid and *Hydrosoma*? sp.) and comatulid crinoids, but no stalked crinoids. Some large decapod crustaceans included *Chaceon fenneri* and large galatheids. No mollusks were observed but were likely within the coral habitat that was not collected. Common fish were 2 m sharks, 25 cm eels, 25 cm skates, chimaera and blackbelly rosefish.

Miami Terrace Escarpment (from Reed et al., 2004b)
The Miami Terrace is a 65-km long carbonate platform that lies between Boca Raton and South Miami at depths of 200-400 m in the northern Straits of Florida. It consists of high-relief Tertiary limestone ridges, scarps and slabs that provide extensive hardbottom habitat (Uchupi 1966, 1969; Kofoed and Malloy 1965; Uchupi and Emery 1967; Malloy and Hurley 1970; Ballard and Uchupi 1971; Neumann and Ball 1970). At the eastern edge of the Terrace, a high-relief, phosphoritic limestone escarpment of Miocene age with relief of up to 90 m at depths of 365 m is capped with *Lophelia pertusa* coral, stylasterine hydrocoral (Stylasteridae), bamboo coral (Isididae), and various sponges and octocorals (Reed et al. 2004b; Reed and Wright 2004). Dense aggregations of 50-100 wreckfish were observed here by J. Reed during JSL submersible dives in May 2004 (Reed et al. 2004b). Previous studies in this region include geological studies on the Miami Terrace (Neumann and Ball 1970; Ballard and Uchupi 1971) and dredge- and trawl-based faunal surveys in the 1970s primarily by the University of Miami (e.g., Halpern 1970; Holthuis 1971, 1974; Cairns 1979). *Lophelia* mounds are also present at the base of the escarpment (~670 m) within the axis of the Straits of Florida, but little is known of their distribution, abundance or associated fauna. Using the *Aluminaut* submersible, Neumann and Ball (1970) found thickets of *Lophelia*, *Enallopsammia* (=*Dendrophyllia*), and *Madepora* growing on elongate depressions, sand ridges and mounds. Large quantities of *L. pertusa* and *E. profunda* have also been dredged from 738-761 m at 26°22' to 24'N and 79°35' to 37'W (Cairns 1979).

Recent JSL submersible dives and fathometer transects by J. Reed at four sites (Reed Site #BU4, 6, 2, and 1b) indicated the outer rim of the Miami Terrace to consist of a double ridge with steep rocky escarpments Reed and Wright 2004; Reed et al. 2004b). At Miami Terrace Site #BU4, the narrow N-S trending east ridge was 279 m at the top and had a steep 95 m escarpment on the west face. The east and west faces of the ridges were 30-40° slopes with some near vertical sections consisting of dark brown phosphoritic rock pavement, boulders and outcrops. The crest of the east ridge was a narrow plateau approximately 10 m wide. At Site #BU6, the crest of the west ridge was 310 m and the base of the valley between the west and east ridges was 420 m. At Site #BU2, the echosounder transect showed a 13 m tall rounded mound at a depth of 636 m near the base of the terrace within the axis of the Straits of Florida. The profile indicated that it is likely a *Lophelia* mound. West of this feature the east face of the east ridge was a steep escarpment from 567 m to 412 m at the crest. The west ridge crested at 321 m. Total distance from the deep mound to the west ridge was 2.9 nm. Site #BU1b was the most southerly transect on the Miami Terrace. An E-W echosounder profile at this site indicated a double peaked east ridge cresting at 521 m, then a valley at 549 m, and the west ridge at 322 m. The east face of the west ridge consisted of a 155 m tall escarpment (Figure 3.3-15).



-1200 feet

500-ft escarpment, east slope of Miami Terrace

-1800 feet

Figure 3.3-15. Echosounder profile of Miami Terrace Escarpment, Site #BU1b, west ridge (depth 549 m at base, relief 155 m) (from Reed et al., 2004b).

There were considerable differences among the sites in habitat and fauna; however, in general, the lower slopes of the ridges and the flat pavement on top of the terrace were relatively barren. However, the steep escarpments especially near the top of the ridges were rich in corals, octocorals, and sponges. Dominant sessile fauna consisted of the following Cnidaria: small (15-30 cm) and large (60-90 cm) tall octocoral gorgonacea (*Paramuricea* spp., *Placogorgia* spp., Isididae bamboo coral); colonial scleractinia included scattered thickets of 30-60 cm tall *Lophelia pertusa* (varying from nearly 100% live to 100% dead), *Madrepora oculata* (40 cm), and *Enallopsammia profunda*; stylasterine hydrocorals (15-25 cm); and Antipatharia (30-60 cm tall). Diverse sponge populations of Hexactinellida and Demospongiae included: *Heterotella* sp., *Spongosorites* sp., *Geodia* sp., *Vetulina* sp., *Leiodermatium* sp., *Petrosia* sp., Raspailiidae, Choristida, Pachastrellidae, and Corallistidae. Other motile invertebrates included *Asteroporpa* sp. ophiuroids, *Stylocidaris* sp. urchins, Mollusca, Actiniaria, and Decapoda crustaceans (*Chaceon fenneri* and Galatheidae). Schools of ~50-100 wreckfish (*Polyprion americanus*),

~60-90 cm in length, were observed on several submersible dives along with blackbelly rosefish, skates, sharks and dense schools of jacks.

Pourtalès Terrace Lithoherms (from Reed et al., 2004a)
The Pourtalès Terrace provides extensive, high-relief, hardbottom habitat, covering 3,429 km^2 (1,000 nm^2) at depths of 200-450 m. The Terrace parallels the Florida Keys for 213 km and has a maximum width of 32 km (Jordan 1954; Jordan and Stewart 1961; Jordan et al. 1964; Gomberg 1976; Land and Paull 2000). Reed et al. (2004a) surveyed several deepwater, high-relief, hardbottom sites including the Jordan and Marathon deepwater sinkholes on the outer edge of the Terrace, and five high-relief bioherms on its central eastern portion. The JSL and *Clelia* submersibles were used to characterize coral habitat and describe the fish and associated macrobenthic communities. These submersible dives were the first to enter and explore any of these features. The upper sinkhole rims range from 175 to 461 m in depth and have a maximum relief of 180 m. The Jordan Sinkhole may be one of the deepest and largest sinkholes known.

The high-relief area of the middle and eastern portion of the Pourtalès Terrace is a 55 km-long, northeasterly trending band of what appears to be karst topography that consists of depressions flanked by well defined knolls and ridges with maximum elevation of 91 m above the terrace (Jordan et al. 1964; Land and Paull 2000). Further to the northeast of this knoll-depression zone is another zone of 40-m high topographic relief that lacks any regular pattern (Gomberg 1976). The high-relief bioherms (the proposed HAPC sites within this region) lie in 198 to 319 m, with a maximum height of 120 m. A total of 26 fish taxa were identified from the sinkhole and bioherm sites. Species of potential commercial importance included tilefish, sharks, speckled hind, yellow-edge grouper, warsaw grouper, snowy grouper, blackbelly rosefish, red porgy, drum, scorpion fish, amberjack, and phycid hakes. Many different species of Cnidaria were recorded, including Antipatharia black corals, stylasterine hydrocorals, octocorals, and one colonial scleractinian (*Solenosmilia variabilis*).

Tennessee and Alligator Humps, Bioherms #1-4- Pourtalès Terrace (from Reed et al., 2004a)
The Tennessee and Alligator Humps are among dozens of lithoherms that lie in a region called "The Humps" by local fishers, ~14 nm south of the Florida Keys and south of Tennessee and Alligator Reefs . Three dives were made by J. Reed on Bioherm #3 (Clelia 597, 598, 600; Aug. 2001), approximately 8.5 nm NE of Bioherm #2 (Figure 3.3-16). Bioherm #3 consisted of two peaks 1.05 nm apart with a maximum relief of 62 m. The North Peak's minimum depth was 155 m and was 653 m wide at the base, which was 217 m deep at the east base and 183 m at the west side. The minimum depth of South Peak was 160 m and was about 678 m in width E to W at the base. The surrounding habitat adjacent to the mounds was flat sand with about 10% cover of rock pavement. From 213 m to the top, generally on the east flank of the mound, were a series of flat rock pavement terraces at depths of 210, 203, 198, 194, 183, and 171 m and the top plateau was at 165 m. Between each terrace a 30-45° slope consisted of either rock pavement or coarse sand and rubble. Below each terrace was a vertical scarp of 1-2 m where the sediment was eroded away leaving the edge of the terrace exposed as a horizontal, thin rock crust overhang of <1 m and 15-30 cm thick. The top of the bioherm was a broad plateau of rock pavement with 50-100% exposed rock, few ledges or outcrops, and coarse brown sand. Less time was spent on the western side, which was more exposed to the strong bottom currents. The west side of South

Peak sloped more gradually than the eastern side, had more sediment, and no ledges were observed.

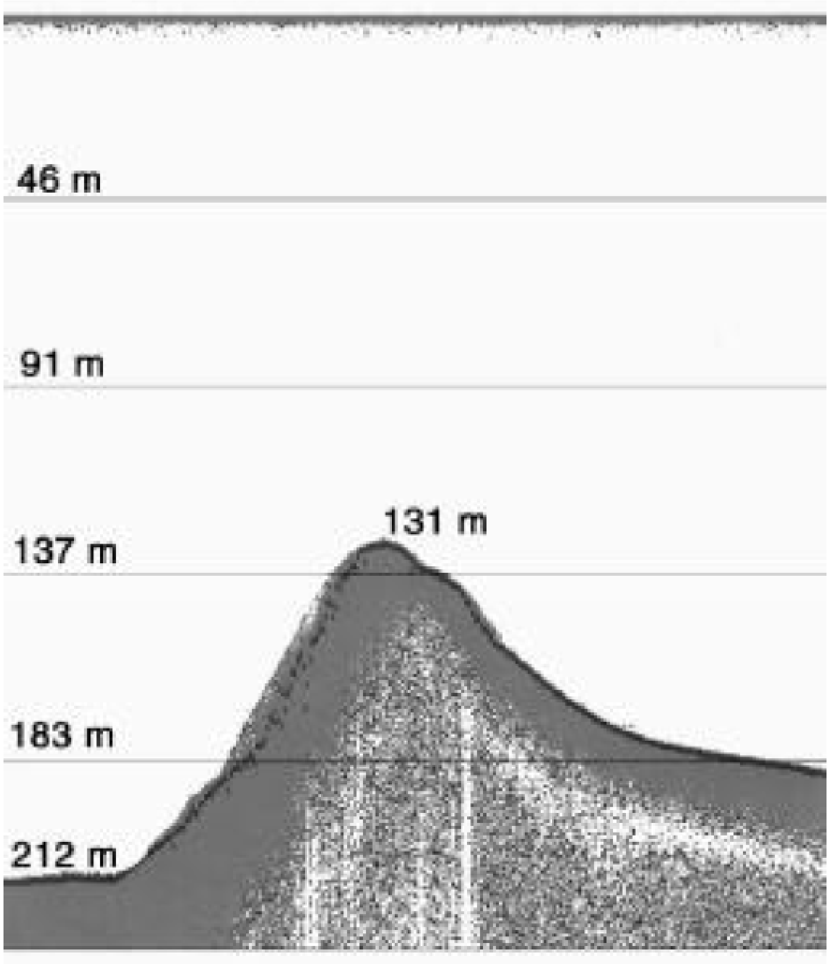


Figure 3.3-16. Echosounder profile of Pourtalès Terrace, Tennessee Bioherm #2 (depth 212 m at base, relief 85 m) (from Reed et al., 2004a)

Ecological role and function

(excerpted from Chapter 1 of the 2007 State of Deep Coral Ecosystems)
As the understanding of deep coral communities and ecosystems has increased, so has appreciation of their value. Deep coral communities can be hot-spots of biodiversity in the deeper ocean, making them of particular conservation interest. Stony coral "reefs" as well as thickets of gorgonian corals, black corals, and hydrocorals are often associated with a large number of other species. Through quantitative surveys of the macroinvertebrate fauna, Reed (2002b) found over 20,000 individual invertebrates from more than 300 species living among the branches of ivory tree coral (Oculina varicosa) off the coast of Florida. Over 1,300 species of invertebrates have been recorded in an ongoing census of numerous Lophelia reefs in the northeast Atlantic (Freiwald et al. 2004), and Mortensen and Fosså (2006) reported 361 species in 24 samples from Lophelia reefs off Norway. Gorgonian corals in the northwest Atlantic have been shown to host more than 100 species of invertebrates (Buhl-Mortensen and Mortensen

2005). An investigation by Richer de Forges et al. (2000) reported over 850 macro- and megafaunal species associated with seamounts in the Tasman and south Coral Seas with many of these species associated with the deep coral Solenosmilia variabilis (Rogers 2004). The three-dimensional structure of deep corals may function in very similar ways to their tropical counterparts, providing enhanced feeding opportunities for aggregating species, a hiding place from predators, a nursery area for juveniles, fish spawning aggregation sites, and attachment substrate for sedentary invertebrates (Fosså et al. 2002; Mortensen 2000; Reed 2002b).

The high biodiversity associated with deep coral communities is intrinsically valuable, and may provide numerous targets for chemical and biological research on marine organisms. For example, several deep-water sponges have been shown to contain bioactive compounds of pharmaceutical interest; sponges are often associated with deep coral communities. Bamboo corals (family Isididae) are being investigated for their medical potential as bone grafts and for the properties of their collagen-like gorgonin (Ehrlich et al. 2006). A number of deep corals are also of commercial importance, especially black corals (order Antipatharia) and pink and red corals (Corallium spp.), which are the basis of a large jewelry industry. Black coral is Hawaii's "State Gem."

Deep coral communities have also been identified as habitat for certain commercially-important fishes. For example, commercially valuable species of rockfish, shrimp, and crabs are known to use coral branches for suspension feeding or protection from predators in Alaskan waters (Krieger and Wing 2002). Husebø et al. (2002) documented a higher abundance and larger size of commercially valuable redfish, ling, and tusk in Norwegian waters in coral habitats compared to non-coral habitats. Costello et al. (2005), working at several sites in the Northeast Atlantic, report that 92% of fish species, and 80% of individual fish were associated with Lophelia reef habitats rather than on the surrounding seabed. Koenig (2001) found a relationship between the abundance of economically valuable fish (e.g., grouper, snapper, sea bass, and amberjack) and the condition (dead, sparse and intact) of Oculina colonies. Oculina reefs off Florida have been identified as essential fish habitat for federally-managed species, as have gorgonian-dominated deep coral communities off Alaska and the West Coast of the United States. In other cases, however, the linkages between commercial fisheries species and deep corals remain unclear (Auster 2005; Tissot et al. 2006) and may be indirect.

Due to their worldwide distribution and the fact that some gorgonian and stony coral species can live for centuries, deep corals may serve as a proxy for reconstructing past changes in global climate and oceanographic conditions (Risk et al. 2002; Williams et al. 2007). The calcium carbonate skeletons of corals incorporate trace elements and isotopes that reflect the physical and chemical conditions in which they grew. Analysis of the coral's microchemistry has allowed researchers to reconstruct past oceanic conditions.

Species composition and community structure

(Excerpted from Chapter 6 of the 2007 Status of Deep Coral Ecosystems)

***Oculina* Banks (<150 m)**

The fish community on the Florida shelf edge *Oculina* banks is typical of the southeastern U.S. shelf edge reef fauna (see review in Quattrini and Ross 2006). At least 73 species of fishes are known from the *Oculina* reefs (GOMFMC and SAFMC 1982; Koenig et al. 2005; Reed et al.

2006), and like the invertebrate community, this is a sub-tropically derived fauna. In recent years, commercial fishing on these reefs has significantly depleted members of the snapper-grouper complex and caused habitat destruction (Koenig et al. 2000, 2005). Some groupers, *Mycteroperca microlepis* (gag) and *M. phenax* (scamp), use the reefs as spawning aggregation sites (Gilmore and Jones 1992); however, these have also been negatively impacted by habitat destruction (Koenig et al. 2000).

The Florida *Oculina* reefs support a diverse invertebrate fauna with mostly sub-tropical affinities (Figure 6.2). Densities of associated invertebrates rival those of shallow coral reef systems (see review in Reed 2002b). Avent et al. (1977) presented a preliminary list of benthic invertebrates dredged from some *Oculina* mounds. Analysis of 42 small *Oculina* colonies yielded about 350 invertebrate species, including 262 mollusc species (Reed and Mikkelson 1987), 50 decapod crustacean species (Reed et al. 1982), 47 amphipod species, 21 echinoderm species, 15 pycnogoid species, and 23 families of polychaetes (Reed 2002b). The invertebrate community has been reduced by habitat destruction (Koenig et al. 2000). Although *Oculina* habitats appear to have more associated mobile macroinvertebrates than deeper coral areas, large sponges and soft/horny corals are less abundant (Reed et al. 2006).

Deep-sea slope coral areas (>150 m, but most >300 m)

Deep coral habitat may be more important to western Atlantic slope species than previously known. Some commercially valuable deep-water species congregate around deep-coral habitat (Table 2.19). Various crabs, especially galatheoids, are abundant on the deep reefs, playing a role of both predator on and food for the fishes. Other invertebrates, particularly ophiuroids, populate the coral matrix in high numbers. On the relatively barren Blake Plateau, reefs (coral and hardgrounds) and surrounding coral rubble habitat seem to offer abundant shelter and food.

There are few deep-coral ecosystem references for the southeast region related to fishes, and those are generally qualitative (fishes neither collected nor counted) or fishes were not a specific target of the research (Popenoe and Manheim 2001; Weaver and Sedberry 2001; Reed et al. 2005, 2006). In the most detailed study of fishes to date, Ross and Quattrini (2007) identified 99 benthic or benthopelagic fish species on and around southeastern U.S. deep-coral banks, 19% of which yielded new distributional data for the region. Additional publications resulting from their fish database documented the anglerfish fauna (Caruso et al. 2007), midwater fish interactions with the reefs (Gartner et al. in review), a new species of eel (McCosker and Ross in press), and a new species of hagfish (Fernholm and Quattrini in press). Although some variability in fish fauna was observed over this region, most of the deep-coral habitat was dominated by relatively few fish species (Table 3.3-5).

Table 3.3-5. Dominant benthic fish species (in phylogenetic order) observed and/or collected during submersible dives (2000-2005) on or near southeastern U.S. *Lophelia* habitat based on Ross and Quattrini (2007). Asterisk (*) indicate commercially important species.

Scientific name	Common name (if known)
Myxinidae (mixed Myxine glutinosa and Eptatretus spp.)	hagfishes
Scyliorhinus retifer	chain dogfish

Scyliorhinus meadi	
Cirrhigaleus asper	roughskin dogfish
Dysommina rugosa	
Synaphobranchus spp.	cutthroat eels
*Conger oceanicus**	conger eel
Netenchelys exoria	
Nezumia sclerorhynchus	
Laemonema barbatulum	shortbeard codling
Laemonema melanurum	reef codling
Physiculus karrerae	
Lophiodes beroe	
Hoplostethus occidentalis	western roughy
*Beryx decadactylus**	red bream
*Helicolenus dactylopterus**	blackbelly rosefish
Idiastion kyphos	
Trachyscorpia cristulata	Atlantic thornyhead
*Polyprion americanus**	wreckfish

Many of these species are cryptic, being well hidden within the corals (e.g., *Hoplostethus occidentalis*, *Netenchelys exoria*, *Conger oceanicus*). Various reef habitats were characterized by *Laemonema melanurum*, *L. barbatulum*, *Nezumia sclerorhynchus*, *Beryx decadactylus*, and *Helicolenus dactylopterus* (Ross and Quattrini 2007). Nearby off reef areas were dominated by *Fenestraja plutonia*, *Laemonema barbatulum*, *Myxine glutinosa*, and *Chlorophthalmus agassizi*. *Beryx decadactylus* usually occurs in large aggregations moving over the reef, while most other major species occur as single individuals. The morid, *Laemonema melanurum*, is one of the larger fishes abundant at most sites with corals. This fish seems to rarely leave the prime reef area, while its congener *L. barbatulum* roams over a broader range of habitats. Although *Helicolenus dactylopterus* can be common in all habitats, it occurs most often around structures. It is intimately associated with the coral substrate, and it is abundant around deep-reef habitat. Results (Ross and Quattrini 2007) suggested that some of the fishes observed around the deep-coral habitats may be primary (obligate) reef fishes.

One of the most impressive biological aspects of these coral habitats (aside from the corals themselves) is the diverse and abundant invertebrate fauna (Table 3.3-6 and Reed et al. 2006). *Eumunida picta* (galatheoid crab; squat lobster) and *Novodinia antillensis* (brisingid seastar) were particularly obvious, perched high on coral bushes to catch passing animals or filter food from the currents. One very different aspect of the North Carolina deep-coral habitat compared to the rest of the southeast region is the massive numbers of the brittle star, *Ophiacantha bidentata*, covering dead coral colonies, coral rubble, and to a lesser extent, living Lophelia colonies. It is perhaps the most abundant macroinvertebrate on these banks and may constitute a major food source for fishes (Brooks et al. 2007). In places the bottom is covered with huge numbers of several species of anemones. The hydroid fauna is also rich with many species being newly reported to the area and some species being new to science (Henry et al. in press). The abundance of filter feeders suggests a food rich habitat. Various species of sponges, echinoderms, cnidarians (Messing et al. 1990) and crustaceans (Wenner and Barans 2001) also have been reported from deep-coral reefs off Florida, the northeastern Straits of Florida and the Charleston Bump region (Reed et al. 2006). Reed et al. (2006) provided a preliminary list of invertebrates, mostly sponges and corals, from some deep-coral habitats on the Blake Plateau and Straits of Florida; however, most taxa were not identified to species. Lack of data on the invertebrate fauna associated with deep corals is a major deficiency.

Table 3.3-6. Preliminary list of dominant benthic megainvertebrates observed or collected on or near southeastern U.S. deep coral habitats. References are 1= Nizinski et al. unpublished data, 2= Reed et al. 2006, 3 = Henry et al. in review.

Dominant Non-Coralline Invertebrate Taxa	
Phylum Porifera (Sponges) Class Demospongiae multiple species[1,2] Class Hexactinellida (glass sponges) multiple species[1,2] including *Aphrocallistes beatrix*[1]	Phylum Cnidaria Class Hydrozoa (Hydroids) multiple species (≥ 37 species)[3] Class Anthozoa Order Actinaria (anemones) multiple species including *Actinaugi rugosa* (Venus flytrap anemone)[1] Order Zoanthidea (zoanthids) multiple species[1,2]
Phylum Mollusca Class Cephalopoda Squids, *Ilex* sp.[1] Octopus, multiple species[1] Class Gastropoda *Coralliophila* (?) sp.[1]	Phylum Annelida Class Polychaeta (polychaetes) multiple species including *Eunice* sp.[1]

Phylum Arthopoda Subphylum Crustacea Class Malacostraca Order Decapoda Infraorder Anomura Family Chirostylidae (squat lobster) *Eumunida picta* [1,2] *Gastroptychus salvadori*[1] *Uroptychus* spp.[1] Family Galatheidae (squat lobster) *Munida* spp.[1] *Munidopsis* spp.[1] Superfamily Paguroidea (hermit crabs and their relatives) multiple species[1] Infraorder Brachyura Family Pisidae *Rochinia crassa* (inflated spiny crab)[1] Family Geryonidae *Chaceon fenneri* (golden deepsea crab)[1,2] Family Portunidae *Bathynectes longispina* (bathyal swimming crab)[1,2] Other taxa Shrimps, multiple species[1]	Phylum Echinodermata Class Crinoidea (crinoids) multiple species[1] Class Asteroidea (sea stars) multiple species[1,2] Order Brisingida (brisingid sea star) Family Brisingidae *Novodinia antillensis*[1] Class Ophiuroidea (brittle stars) multiple species[1], including *Ophiacantha bidentata*[1] Class Echinoidea (sea urchins) Order Echinoida Family Echinidae *Echinus gracilis*[1] *E. tylodes*[1] Order Echinothurioida Family Echinothuriidae *Hygrosoma* spp.[2] Order Cidaroida Family Cidaridae *Cidaris rugosa*[1] *Stylocidaris* spp.[2]

Although the invertebrate assemblage associated with northeastern Atlantic *Lophelia* reefs has been described as being as diverse as shallow water tropical coral reefs (e.g., Jensen and Frederickson 1992), data analysis of invertebrates associated with western Atlantic deep corals is too preliminary to speculate on the degree of species richness. Preliminary data on the invertebrate fauna (Nizinski et al. unpublished data) seem to indicate a faunal and habitat transition with latitude. In addition to changes in reef structure and morphology (see above), relative abundance within a single species decreases, overall species diversity increases, and numerical dominance between species decreases with decreasing latitude. In contrast to some fishes, the reef associated invertebrate assemblage appears to use deep reefs more opportunistically.

3.3.1 Artificial reefs

Description and distribution

Artificial reefs, sometimes called man-made reefs, are broadly defined as any structure placed on the seabed, either deliberately or accidentally (i.e. shipwrecks), that acts similar to natural hardbottom or reefs. Artificial reefs may be composed of a wide variety of materials ranging from natural rock or discarded materials, such as concrete rubble, to entirely manufactured materials. Natural reefs artificially enhanced or rehabilitated by transporting and attaching living corals are usually not considered artificial reefs.

Artificial reefs are constructed for a variety of purposes, but are particularly popular sites for fishing and diving. Here we focus on the use of artificial reefs in an ecosystem approach to fisheries. The fishery focus is on fish and invertebrate fisheries, with the recognition that other biota are important ecological factors that influence fisheries as sources of food, habitat, and mortality for exploited species. Manmade reefs can be considered fishery management tools. Although manmade reefs are not identical to naturally occurring hardbottom areas or coral reefs, they share similar biota and ecological processes.

Artificial reef programs in the southeastern U.S. are overseen by individual states (Florida, Georgia, South Carolina, North Carolina) and require construction permits by the Army Corp of Engineers with review and approval by the U.S. Coast Guard and the Environmental Protection Agency.

While manmade reefs have been in use along the U.S. South Atlantic since the 1800s, their development in this region was somewhat limited through the mid-1960s. From the late 1960s to the present, reef development off the South Atlantic states (as measured by the number of permitted construction sites) has increased nearly five-fold, with approximately 250 sites now permitted in the coastal and offshore waters of these four states. Roughly half of these sites are in waters off the east coast of Florida alone. Artificial reef locations are considered live/hardbottom habitat and are available on the Council's Internet Mapping System accessible at www.safmc.net.

The total area of ocean and estuarine bottom along the South Atlantic states which has been permitted for the development of manmade reefs at present is approximately 130,000 acres (or 155 nm^2) which is a small % area of the shelf bottom and of the natural harbottom managed by the SAFMC. Due to the practical limitations of all artificial reef programs, it is very likely that only a very small percentage of any of these permitted reef sites has actually been developed through the addition of suitable hard substrate. However, since in most cases construction activities may continue indefinitely on these sites, the percentage of hardbottom habitat developed will continue to rise as new materials are added.

Recreational anglers are the chief users of manmade reefs in this region. Financial resources made available directly or indirectly through many saltwater sportfishing interests have been a prominent factor in most reef development projects. Due to favorable environmental conditions throughout most of the year along the South Atlantic states, recreational divers have also been a driving force in establishing manmade reefs in recent years. This relatively new user group will likely continue to grow as diving becomes more popular. Finally, commercial fishing interests use some manmade reefs, but are less common users compared to recreational fishing and diving users.

State marine resources management agencies in all four South Atlantic states are actively involved in various aspects of manmade reef planning, development and management in their own waters as well as contiguous federal waters. All four states have, or are in the process of developing, their own state artificial reef management plans. North Carolina, South Carolina and Georgia control all manmade reef development through programs within their respective natural resource management agencies, and hold all active permits for reef development. Florida's reef development efforts are carried out by individual county or municipal programs with a limited degree of oversight conducted by the Florida Fish and Wildlife Conservation Commission. Reef construction permits in Florida are held by state, county and municipal government agencies or programs.

North Carolina

The North Carolina Division of Marine Fisheries (DMF) has been involved in artificial reef construction since the early 1970s. Responding to interest generated by local fishing club reef projects, the DMF began a reef construction program using bundled automobile tires. Hundreds of thousands of tires were deployed on several reefs from Cape Lookout to Brunswick County.

In 1974, three 440-foot Liberty Class ships were cleaned and sunk on reef sites off Oregon Inlet, Beaufort Inlet and Masonboro Inlet. Another Liberty ship was added to the Oregon Inlet site in 1978. These surplus vessels were obtained from the federal government under Public Law 92-402, also known as the Liberty Ship Act. Artificial reef construction continued using tires and smaller surplus vessels until 1986 when the reef program was reorganized.

During 1986 and 1987, twenty-one new reef sites were permitted by the DMF and 210 train cars were deployed on these sites. Use of tires was eliminated in the early 1980s due to stability problems. Reef construction permits which were held by various counties and clubs were transferred to the DMF under a general permit issued by the U.S. Army Corps of Engineers (USACOE).

At present, the DMF maintains 47 artificial reef sites. These sites are located from one to 38 miles from shore and are strategically located near every maintained inlet and one unmaintained inlet along the coast. In recent years, most of the oceanic and some of the estuarine reefs have received new construction. Materials deployed since 1986 include 39 vessels, 10,000 pieces of large diameter concrete pipe, 210 train cars and over 40,000 tons of concrete pipe, bridge spans, railings and rubble.

In addition to USACOE construction permits, aids to navigation permits are also maintained for the buoys marking the center point of each artificial reef site requiring a buoy. The reef program uses a 130-foot landing craft for deploying and maintaining buoys, as well as for small construction projects.

Prior to 1990, emphasis was placed on artificial reef construction. With funding provided by the Federal Aid in Sportfish Restoration Program, the reef program has maintained a monitoring program to evaluate the effectiveness of reef materials, to test designed materials and to monitor fish assemblages on the reef. Past work also includes aerial surveys conducted to assess artificial reef usage along the coast and surveys of king mackerel tournament entrants are used to measure reef use, awareness and catch rates.

The DMF maintains one of the most active artificial reef programs in the nation. State and Sportfish Restoration funding, and enthusiastic support from many civic and fishing clubs along the coast continues to ensure the success of North Carolina’s artificial reef program.

South Carolina

The use of manmade structures to enhance fishing activities in South Carolina's coastal waters was first documented during the mid-1800s. During the mid-1960s the construction of offshore and coastal artificial reefs for the benefit of saltwater recreational anglers was carried out by numerous private organizations. In 1967 the state provided funding for its first manmade reef construction project, and in 1973 an on-going state-sponsored marine artificial reef program was established. This program is currently maintained by the Marine Resources Division of the South Carolina Department of Natural Resources (SCDNR) within the Division's Office of Fisheries Management. Funding for the program consists of state support through the South Carolina Marine Recreational Fisheries License, federal support through grants from the U.S. Fish and Wildlife Service-managed Sport Fish Restoration Program and donations from private fishing and diving clubs and other civic organizations.

The primary focus of the South Carolina Marine Artificial Reef Program (SCMARP) is the coordination and oversight of all activities within the state of South Carolina concerning the management of a viable system of marine artificial reefs in both state and contiguous federal waters. The primary goal of these manmade reefs is the enhancement of hardbottom marine habitats, associated fish stocks and resulting recreational fishing activities that take place on and around them. The SCMARP's responsibilities include reef planning, design, permitting, construction, monitoring, evaluation, research and marking. The program also plays a key role in interfacing with the public in areas related to general fisheries management issues as well as in providing specific reef-related information to user groups.

All manmade reef development and management in South Carolina is guided by the South Carolina Marine Artificial Reef Management Plan, adopted in 1991. As of June 2006, the state's system of marine artificial reefs consisted of 48 permitted sites (13 inside state waters) along approximately 160 miles of coastline. These sites range in location from estuarine creeks to as far as 50 miles offshore. Each manmade reef site consists of a permitted area ranging from several thousand square yards to as much as 24 square miles. Approximately 37.5 square miles of coastal and open ocean bottom has been permitted, of which only about one percent has actually been developed through the addition of manmade reef substrate.

Saltwater recreational anglers are the primary group associated with marine artificial reef utilization in South Carolina. Their annual fishing activities on manmade reef sites alone account for tens of thousands of angler-days, which result in an estimated total economic benefit to the state of over 20 million dollars each year. While some use of permitted artificial reefs by commercial fishing interests has been reported over the past three decades, this activity has been difficult to quantify since these practices do not have popular support with the majority of the fishing public, or may in some cases be illegal. Recreational divers comprise the second most common user group relying on the presence of marine artificial reefs. While sport divers have traditionally not been as large a user group as the saltwater recreational fishing community, significant expansion of the recreational diving industry in the state has resulted in a noticeable increase in this type of usage over the past two decades.

In an attempt to better manage the use of permitted manmade reefs in offshore waters and to ensure their long-term viability, the SCDNR has, through the South Atlantic Fishery Management Council, obtained Special Management Zone (SMZ) status for 29 of the 35 permitted reef sites located in federal waters. Fishing on those reef sites granted SMZ status is restricted to hand-held hook and line gear and spearfishing (without powerheads). In addition, the SCDNR has established experimental artificial reefs in order to examine the feasibility and possible benefits of establishing no-take manmade reefs in nearshore and offshore waters solely for the purpose of stock and habitat enhancement. For additional information visit: www.dnr.sc.gov/marine/pub/seascience/artreef.html.

Georgia

The continental shelf off Georgia slopes gradually eastward for over 80 miles before reaching the Gulf Stream and the continental slope. This broad, shallow shelf consists largely of dynamic sand/shell expanses that do not provide the firm foundation or structure needed for the development of reef communities, which include popular gamefish such as groupers, snappers, sea bass, and amberjack. It is estimated that only about 5% of the adjacent shelf features natural reefs or "live bottoms" anchored to rock outcrops, with most of these found well offshore. Large areas of Georgia's estuaries similarly feature broad mud and sand flats lacking the firm substrate needed for the growth of oyster reefs, which provide prey and shelter for seatrout, sheepshead, drum, and other popular sportfish in an otherwise highly energetic environment. Ditching, pollution, and coastal development have also impacted water quality and further restricted use of inshore areas by not only fish, but also fishermen, resulting in even greater demands on the remaining estuarine habitat.

Sporadic attempts to develop manmade or "artificial" reefs in Georgia were begun in earnest in the late 1950s by sport fishermen, who knew that good angling opportunities existed on scattered shipwrecks and other manmade structures found in estuarine and offshore waters. Only short-term benefits were realized through these limited initiatives when deployed materials rapidly silted in, deteriorated, or were lost. Working with coastal sport fishing clubs, the Georgia State Game and Fish Commission began experimenting with artificial reef construction in the 1960s, focusing initially on estuarine areas and expanding later to offshore waters in the 1970s. Today, the program is housed within the Coastal Resources Division of the Georgia Department of Natural Resources (GADNR) and is funded through State fishing license revenues, the Federal Aid in Sport Fish Restoration (SFR) program, and private donations, including the support of fishing and conservation organizations, tournaments, businesses, individuals, military services, and other branches of State and federal government.

Goals of Georgia's artificial reef program are to 1) create and enhance fisheries habitat and associated marine communities; 2) develop increased, more accessible recreational fishing opportunities; 3) facilitate and support fisheries management; and 4) generate economic benefits for coastal communities and the State.

To date, GADNR has initiated reef construction at 22 sites 2½ to 70 nautical miles (nm) offshore and at 15 estuarine locations along Georgia's 90-mile coast. Georgia's inshore artificial reef sites are typically small and largely inter-tidal in order to promote oyster reef development. Offshore, with the exception of three 400-yard diameter, experimental "beach reefs" sited in the State's territorial sea, the majority of the artificial reefs off Georgia are located in adjacent EEZ waters 6 to 23 nm in 30 to70 feet of water and east of coastal trawling grounds. Development of two experimental "deepwater" reefs in 120 to 160 feet of water 50 to 70 nm offshore has also been initiated to address a growing recreational component targeting tunas, wahoo, and other "bluewater" gamefish. A third, yet undeveloped deepwater reef site 65 nm east of Brunswick, Georgia, was permitted in 2005.

All artificial reefs constructed in inshore and nearshore waters within Georgia's 3-nm territorial sea require individual U.S. Army Corps of Engineers (USACOE) and State permits. In the adjacent EEZ, the State conducts artificial reef development under the authority of a USACOE Regional Permit that encompasses 20 specific reef locations. While the permitted estuarine and coastal "beach reef" sites are limited in size, the offshore EEZ sites typically average 4 nm^2. These larger areas allow for the development of multiple "patch reefs," a design that improves material performance and helps disperse fishing pressure.

Artificial reef development in Georgia has largely relied on stable and durable secondary use materials or "materials of opportunity" to create fisheries habitat. Complexity and surface area are other important factors. Similar to other early U.S. artificial reef development efforts, the Georgia program also initially utilized tires, which were bound into compressed 8-tire units using rebar and anchored with concrete. While many tire units remain intact at Georgia's offshore reefs, several have also deteriorated; however, due to early concerns expressed by the trawler fleet in coastal waters, most units were also placed well offshore and many have sunken into the soft sand bottoms at the reef sites closest to shore.

Perhaps the best known and most popular materials of opportunity used for artificial reef development are metal vessels, which have been employed as materials off Georgia for over fifty years or more. Prior to sinking, all vessels are cleaned, cut down to satisfy required water depth clearances, and modified to promote sunlight and water flow. As vessels age and collapse, they often become more complex, improving the overall growth and development of associated reef communities. Ranging from 34 to 447 feet in length, almost 70 vessels are found on Georgia's offshore reefs, including tugs, barges, landing craft, sailboats, steel trawlers, a dredge, a USCG buoy tender, a former Japanese research vessel, and two Liberty ships -- the *Edwin S. Nettleton* and the *Addie Bagley Daniels*.

Emulating the rock outcroppings underlying temperate natural reef communities, marine grade concrete is another preferred material of opportunity used for reef development in Georgia's estuarine and adjacent offshore waters. To date, almost 200,000 tons of concrete pipe, pilings, and bridge/wharf rubble generated through coastal construction projects have been deployed on Georgia's artificial reefs. Other notable materials of opportunity also utilized for offshore artificial reef development in Georgia include 55 U.S. Army battle tanks and 50 New York City Transit System subway cars.

Designed for stability, complexity, and long-term service, several thousand concrete fisheries enhancement units have been deployed by the program since the mid-1990s on Georgia's inshore and offshore artificial reefs. Commercially available, the final unit design selected is dictated by project goals, site characteristics, cost per-unit-deployed, and the availability of comparable reef materials.

Normally occurring during the warmer months, SCUBA diving at Georgia's artificial reefs primarily takes place on the reef sites 15 nm and further offshore due to poor water visibilities and strong tidal influences found closer to shore. The larger wrecks popular with divers are also found on the artificial reefs located further offshore deeper water depths. However, Georgia's artificial reefs are constructed to first provide fisheries habitat and angling opportunities and are not designed for diving. Entanglement and entrapment are diving hazards unavoidably associated with artificial reef structures, especially as the materials age, deteriorate, and collapse.

The artificial reefs located in Georgia's adjacent EEZ waters have been established as Special Management Zones (SMZs) under the SAFMC's Snapper-Grouper Fishery Management Plan. In conjunction with this designation, allowable gears the reefs are restricted to handheld hook-and-line and spearfishing gear, including powerheads or "bangsticks." Powerheads may only be used to harvest a recreational bag limit and any powerheaded catches in excess of the bag limits aboard a vessel at a SMZ is considered *prima facie* evidence of a violation.

Further information on Georgia's marine artificial reefs may be obtained through Coastal Resources Division, One Conservation Way, Suite 300, Brunswick, GA 31520; phone # (912) 264-7218, or by going to http://crd.dnr.state.ga.us.

Florida (East Coast)

Encompassing 34 of 35 different coastal counties spread along 2,184 kilometers (1,357 miles) of ocean fronting coastline (1,362 kilometers fronting the Gulf of Mexico and 822 kilometers fronting the Atlantic Ocean), Florida manages one of the most diverse, and most active artificial reef programs in the United States. Florida leads the nation in the number of public manmade fishing reefs developed. The first permitted artificial reef off Florida was constructed in 1918. Manmade reefs are found in waters ranging from eight feet to over 400 feet with an average depth of 65 feet. As of September 2006, no fewer than 790 deployments of manmade reef materials off the Florida East Coast are on record with the Florida Fish and Wildlife Conservation Commission (FWC). Over the last 40 years the state artificial reef program has experienced a gradual transition in construction materials use, funding sources, and recognition of the importance of measuring effectiveness.

The State's involvement in funding manmade reef construction began in the mid-1960s when the Florida Board of Conservation awarded a limited number of grants to local governments to fund reef development projects. In 1971 a Florida Recreational Development Assistance Program grant was awarded to a local government by the DNR Division of Recreation and Parks for reef construction. Between 1976 and 1980 the DNR Division of Marine Resources received, and oversaw the preparation and placement of five Liberty ships, secured as a result of passage of the Liberty Ship Act, which facilitated the release of obsolete troop and cargo ships for use as artificial reefs.

In 1978 a systematic state artificial reef program was begun. The Division of Marine Resources received a large grant from the Coastal Plains Regional Commission for artificial reef development. Rules for disbursing these funds were developed, defining a grants-in-aid program with projects selected through a competitive evaluation of local government proposals. In 1979 the State Legislature appropriated general revenue funds for reef construction which continued on an annual basis, with the exception of one year, through 1990. In 1982, in addition to receiving general revenue funds, the program was officially established as a grants-in-aid program by law (s. 370.25, Florida Statutes). One staff position was assigned responsibility for program administration.

The rapid proliferation of publicly funded artificial reefs in Florida beginning in the mid- 1980s is the result of increased levels of federal, state and local government funding for artificial reef development. Prior to that, other state funding sources intermittently provided reef development assistance. In 1966 there were seven permitted artificial reef sites off Florida in the Atlantic Ocean. By 1987, this number had grown to 112. Consistent federal funding for Florida's reef program became available in 1986 as a result of the Wallop-Breaux amendment to the 1950 Federal Aid in Sport Fish Restoration Act (Dingle-Johnson). During the decade of reef-building activity from 1986 to 1996, Sport Fish Restoration Funds provided almost three million dollars to complete 164 Florida reef projects.

In January 1990, Florida instituted a saltwater fishing license program. About 5% of the revenue from the sale of over 850,000 fishing licenses annually became available for additional artificial reef projects. Two additional personnel were hired into the state artificial reef program to assist with coordination, information sharing, grant monitoring/compliance and diving assessment of artificial reefs. Funding in Florida was steady from 1996 through 2005, with $300,000 coming from the Federal Aid to Sport Fish Restoration Program matched with $100,000 in state saltwater license funds and another $200,000 state saltwater license funds for a total of $600,000 annual appropriation. In 2006 the total annual appropriation was increased to $700,000 with $400,000 coming from the Federal Aid in Sport Fish Restoration Program and $300,000 from state saltwater license funds.

Florida is the only southeastern Atlantic coastal state active in artificial reef development which does not have a direct state-managed artificial reef program. For the last 20 years, Florida's artificial reef program has been a cooperative local and state government effort, with additional input provided by non-governmental fishing and diving interests. The state program's primary objective has been to provide grants-in-aid to local coastal governments for the purpose of developing artificial fishing reefs in state and adjacent federal waters off both coasts in order to locally increase sport fishing resources and enhance sport fishing opportunities. All but three active permitted reef sites are held by individual coastal counties or cities.

Reef management expertise at the local government level is variable. Reef programs are found in solid waste management, public works, natural resources, recreation and parks, administrative, and planning departments. Local government reef coordinators range from biologists and marine engineers to city clerks, grants coordinators, planners, and even unpaid volunteers. Reef management and coordination are generally collateral duties for most local government reef coordinators.

In response to long-range planning initiatives, in 2003 the FWC completed a long-range Artificial Reef Strategic Plan (Florida Fish and Wildlife Commission, 2003) to serve as a blueprint for both the FWC and the local coastal government reef programs. Representing the broad range of public interests in artificial reefs throughout Florida, the plan is comprised of guiding principles, goals, and objectives that optimize biological and economic benefits, provide policy guidance, support research and data collection, pursue additional funding opportunities, provide a framework for public education and outreach, and provide guidance for operational planning at the state, regional, and local levels of artificial reef construction and monitoring. The Strategic Plan is available at http://myfwc.com/marine/ar/FLARStrategicPlan2.pdf

Due to its long coastline, ideal conditions, and large number of academic and research-oriented institutions, a significant quantity of the existing body of field research dealing with manmade reefs has been conducted in waters off Florida. Artificial reef research projects undertaken with over $3.6 million dollars in state funding since 1990 have included studies on reef spacing and design, material stability and storm impact studies, long term studies of reef community succession, residency of gag grouper on patch reefs through tagging and radio telemetry, juvenile recruitment to reefs, impacts of directed fishing, remote biological monitoring techniques, and the effects of unpublished manmade reefs.

As with most other artificial reef programs in the U.S., there has been a shift in the types of materials used in the construction of manmade reefs in Florida waters over the past 40 years. Through experience, reef builders have learned which materials work best in providing effective long-lived manmade reefs. Modern construction practices have evolved to a point where reef programs are much more selective in the types of materials they use.

Concrete materials, chiefly culverts and other prefabricated steel reinforced concrete, were the primary reef material in nearly 67% of the 2,349 public reef deployments in waters off Florida as of September 2006. Engineered artificial reef units have been a growing component of the state's manmade reef development efforts since the early 1990s and now represent 24% of the manmade reefs off Florida. Most, but not all, units designed specifically for use as artificial reefs have proven to be durable and stable in major storm events. Prefabricated units designed specifically for use as manmade reefs have focused on improving upon habitat complexity, stability and durability, as well as providing a standard design for research and monitoring projects.

Secondary use materials such as obsolete oil platforms and steel vessels have also been used off Florida in the development of manmade reefs. Twenty-eight percent of Florida's manmade reef structures are metal structures, including 460 sunken vessels and barges. These vessel reefs have catered to fishermen fishing for pelagic species, and a rapidly expanding resident and tourist diving population. The majority of vessels sunk as manmade reefs are concentrated off Miami-Dade, Palm Beach, and Broward Counties. On May 18, 2006, in partnership with the U.S. Navy, Florida's artificial reef program and Escambia County successfully deployed the *Oriskany*, an 888 foot-long aircraft carrier, 23 miles southeast of Pensacola, FL. The *Oriskany* is presently the largest vessel in the world intentionally deployed as a manmade reef.

Ecological role and function

Manmade reefs have the effect of changing habitats from a soft substrate to a hard substrate system or to add vertical profile to low profile (< 1m) hard substrate systems. When manmade reefs are constructed, they provide new primary hard substrate similar in function to newly exposed hardbottom (Goren 1985). Aside from the often obvious differences in the physical characteristics and nature of the materials involved in creating a manmade reef, the ecological succession and processes involved in the establishment of the epibenthic assemblages occur in a similar fashion on natural hard substrates and man-placed hard substrates (Wendt et al. 1989). Demersal reef-dwelling finfish, pelagic planktivores and pelagic predators use natural and manmade hard substrates in very similar ways and often interchangeably (Sedberry 1988). The changes in species composition and local abundance of important species in a specific area are often seen as the primary benefits of reef deployment activities.

Hardbottom habitats can be formed when overlying soft sediments are transported away from an area by storms, currents or other forces. The underlying rock or hard-packed sediment which is exposed provides new primary hard substrate for the attachment and development of epibenthic assemblages (Sheer 1945; Goldberg 1973a; Jackson 1976; Osmand 1977). This substrate is colonized when marine algae and larvae of epibenthic animals successfully settle and thrive. Species composition and abundance of individuals increase quickly until all suitable primary space is used by the epibenthos. At some point, a dynamic equilibrium may be reached with the number of species and number of new recruits leveling off. Competition for space and grazing pressure become significant ecological processes in determining which epibenthic species may persist (Kirby-Smith and Ustach 1986; Paine 1974; Sutherland and Karlson 1977). The reef community itself should remain intact as long as the supporting hard substrate remains and is not buried under too great an overburden of sediment.

Concurrent with the development of the epibenthic assemblage, demersal reef-dwelling finfish recruit to the new hardbottom habitat. Juvenile life stages will use this habitat for protection from predators, orientation in the water column or on the reef itself and as a feeding area. Adult life stages of demersal reef-dwelling finfish can use the habitat for protection from predation, feeding opportunities, orientation in the water column and on the reef and as spawning sites.

Pelagic planktivores can occur on hardbottom habitats in high densities and use these habitats for orientation in the water column and feeding opportunities. These species provide important food resources to demersal reef-dwelling and pelagic piscivores. The pelagic piscivores use the hardbottom habitats for feeding opportunistically. Most of these species do not take up residence on individual hardbottom outcrops, but will transit through hardbottom areas and feed for varying periods of time (Sedberry and Van Dolah 1984).

As noted by researchers the physical characteristics of manmade reef habitat may result in differences in the observed behavior of fish species on or around such structures in contrast to behavior observed on equivalent areas of natural hardbottoms (Bohnsack 1989). Some reef structures, particularly those of higher profile, seem to yield generally higher densities of managed and non-managed pelagic and demersal species than a more widely spread lower profile, natural hardbottom or reef (Rountree 1989). The fishery management implications of these differences must be recognized and taken into consideration when planning, developing, and managing manmade reefs as essential fish habitat.

Other manmade hard substrates in marine and estuarine systems provide habitat of varying value to fisheries resources. Coastal engineering structures such as bridges, jetties, breakwaters and shipwrecks provide significant hard substrate for epibenthic colonization and development of an associated finfish assemblage (Van Dolah 1987). Some of these structures also provide habitat in the water column and intertidal zone which differs significantly from typical benthic reefs.

The result of the different ecotones provided by these coastal structures is often higher species diversity than was present before the structure was placed on site. These structures also may provide refuge from predation as well as feeding opportunities and orientation points for juvenile and adult life stages of important finfish species in the South Atlantic region. They differ from manmade reefs as defined above, in that there is generally no direct intention in their design or placement to achieve specific fishery management objectives. However, their impacts should be considered just as any other activity which modifies habitats in the marine environment.

Fisheries Enhancement

The proper placement of manmade materials in the marine environment can provide for the development of a healthy reef ecosystem, including intensive invertebrate communities and fish assemblages of value to both recreational and commercial fishermen. The effectiveness of a manmade reef in the enhancement of fishing varies and is dictated by geographical location, species targeted, stock health, and design and construction of the reef (Bohnsack 1989). An examination of both the historical and present use of manmade reefs along each of the South Atlantic states reveals that fisheries enhancement was the primary reason for establishing these sites. Manmade reefs have developed an impressive track-record of providing beneficial results, as measured by fishing success for a wide range of finfish species. To date, manmade reefs have been chiefly employed to create specific, reliable and more accessible opportunities for recreational anglers. They have been used to a lesser extent to enhance commercial fishing probably because manmade reef total area is small compared to much larger, traditionally relied-upon, natural commercial fishing grounds.

In their present scale and typical design, most manmade reefs, while well-suited for use by recreational anglers, would be unable to withstand intensive commercial fishing pressure, especially for many of the popularly sought-after demersal finfish species, for more than a short period of time. Currently, most manmade reef programs receive the majority of their funding through sources tied directly to recreational fishing interests.

Special Management Zones

Conceptualized by the South Atlantic Fishery Management Council within the Snapper/Grouper Management Plan, several “Special Management Zones” or “SMZs” have been established in the South Atlantic off South Carolina, Georgia, and Florida to provide gear and harvest regulations for defined locations. The basic premise of this concept is to reduce user conflicts through gear and landings regulations at locations that feature limited resources, managed for specific user groups. Generally, manmade reefs have been developed for recreational use utilizing recreational resources. The ability to regulate gear types utilized over the relatively limited area of a manmade reef enables fisheries managers to prevent rapid depletion of these sites and promote a more even allocation of reef resources and opportunities.

Present SMZ regulations apply to about 30 manmade reef sites off South Atlantic States, with several more proposed. Since regulations concerning the management of SMZs are tied to specific gear restrictions, it is possible that the use of SMZs in the future could be expanded to a point where any possible type of fishing gear could be restricted for a set period of time or indefinitely. This could provide fishery managers with the ability to turn individual manmade reef sites “on or off” as the specific needs of the fishery in question dictate. The ability to have some degree of control over fishing activities on these sites would give managers more power to use artificial reefs as a true fishery management tool.

Hardbottom Habitat Enhancement

Habitat enhancement through the construction of manmade reefs can be achieved by converting some other type bottom habitat into a hardbottom community. Mud, sand, shell or other relatively soft bottom habitat can be altered by the addition of hard structure with low to high profile to add to the total amount of hardbottom reef environment in a given area. While it would be difficult and particularly costly to construct manmade reefs with an equivalent area of most typical hardbottom found off the southeastern U.S., substantial areas of ocean bottom can be effectively converted to hardbottom over time given sufficient planning, proper design and adequate resources.

In areas where existing hardbottom habitat is limited spatially, temporally, or structurally, manmade structures may be used to augment what is already in place. Hardbottom with or without a thin veneer of sediment constitutes a preferred substrate for this type of manmade reef development, as opposed to sand and mud bottoms; however, deployment of structures in already productive areas carries a certain degree of risk. Existing hardbottom may be directly damaged or impacted by modified current regimes, movement of materials and potentially increased user pressure. Although sparse, the hardbottom may constitute valuable juvenile habitat and refugia that may be severely compromised by creating additional habitat conducive to predators. On the other hand, a properly planned manmade reef could be constructed without impact to existing resources by utilizing stable materials that are designed to enhance juvenile habitat and survival.

In cases where critical hardbottom habitat is damaged or lost due to natural forces such as severe storms or burial, the addition of manmade reef material could be used to compensate for this loss on site or in adjacent areas. Manmade reef structures can also be used to repair damaged habitat or mitigate for its loss in cases where stable, hard substrate placed on the bottom would provide the closest in-kind replacement as possible, or at least provide the long-term base for the eventual re-establishment of the hardbottom reef community that was originally impacted.

Manmade Marine Reserves

Marine reserves and sanctuaries are a proven management technique that has been implemented successfully worldwide to protect essential fisheries habitat and sustain fisheries stocks and genetic variability. Although the concept of marine reserves has gained some support in the southeastern United States, the actual application of this management measure has generated resistance among user groups who feel that the establishment of such reserves will adversely impact fishing opportunities by limiting access to existing habitat. For areas with little fisheries habitat, these impacts are viewed as significant.

The potential role that manmade reefs could play in implementing marine reserves and similar management measures remains largely unexplored at present. It is conceivable that effective marine reserves consisting of manmade structures could be developed in habitat-limited areas to assist specifically in such roles as habitat and stock enhancement. Detailed research needed to measure their effectiveness in these roles is needed. Substantial resources and funds would also be required to develop the large reserve areas proposed, although smaller sanctuaries are entirely feasible. Manmade structures could be utilized to enhance existing marine reserve areas by improving existing habitat or providing additional hardbottom substrate. Manmade reef reserves could also be used as test platforms to demonstrate to the public the potential effectiveness of such areas, without impacting existing fisheries practices on sites in a given area.

At this time, perhaps the most important contribution that manmade reef technology can provide for fisheries management efforts employing marine reserves would be to create additional habitat and fisheries to "compensate" user groups for perceived "losses." Coupled with positive effects of adjacent marine reserves, properly sited, more accessible artificial reefs would increase benefits to user groups. Another potential function could be to enhance areas that are not being fished and create reserves; that way, fishers would not be giving up "fishable" area and could benefit from spillover.

Enhancement of Eco-Tourism Activities

Along with other eco-tourism activities, recreational diving is one of the fastest growing sports in the United States. Properly planned, manmade reefs can be designed to encourage diving and to reduce spatial conflicts with other user groups, including fishermen. Specific SMZ or other regulations established for a manmade reef could conceivably allow non-extractive uses only, including diving, underwater photography, snorkeling, and other eco-tourism activities. Materials selected could be designed and deployed to create specific fisheries habitat for tropical, cryptic, and other species valued by tourists, conservationists, naturalists, photographers and other non-extractive users.

The establishment of additional hardbottom reef communities in areas with thriving dive-related industries could be used to reduce diving-related pressures on existing natural reefs, especially in the case of sensitive coral reefs in the Florida Keys (Leeworthy et al., 2006). Finally, a non-extractive, conservation reef would essentially constitute a sanctuary, providing fisheries and the associated habitat with *de facto* protection.

Manmade reef construction practices

Manmade reefs have been built from a wide variety of materials over the years. Throughout the present century, most construction materials relied upon in the South Atlantic states have been forms of scrap or surplus; some more suitable for this purpose than others. In an effort to decrease dependency of successful reef development on the availability of scrap or surplus materials, and to improve the overall effectiveness and safety of manmade reefs, most artificial reef programs have, in recent years, designed, manufactured and/or evaluated a number of specifically engineered reef habitat structures which may become a more viable option for future reef development projects. Due primarily to improved financial support for most artificial reef programs in the South Atlantic states and a willingness within private industry to develop new and affordable designed reef structures, the use of such reef construction material is now much more feasible.

Whether specifically designed or secondary-use materials are utilized to construct manmade reefs, individual state resource management agencies should be able to define particular materials that are deemed acceptable for use as reef structures in their coastal and adjacent offshore waters. The decision to allow or disallow the use of certain materials should be based on existing state and federal regulations and guidelines, as well as any soundly based policies established by a particular state. Materials should only be considered for use if they possess characteristics which allow them to safely meet the established objectives for the manmade reef project under consideration, and present no real risk to the environment in which they are being placed. The document entitled *Guidelines for Marine Artificial Reef Materials* (Gulf States Marine Fisheries Commission, 1997) provides detailed information of the experiences, benefits, and drawbacks of past uses of a variety of materials by state resource management agencies. This, as well as other related documents (e.g National Artificial Reef Plan), and the collective experiences of individual artificial reef programs, may be relied upon as the best available data in making decisions regarding the use of certain types of materials in manmade reef development.

Secondary Use Materials

Although past artificial reef development in most states has been directly tied to the availability of surplus or "secondary use" materials due to budgetary constraints, this may not be the most desirable situation for continued planning and development of reef construction efforts in the future. While a total dependency on scrap and surplus materials is not the most effective means of managing reef development activities, some secondary use materials, when available in the proper condition, are very desirable in carrying out manmade reef construction projects and should continue to be utilized to enhance fisheries habitat.

In some cases naturally occurring materials such as quarry rock, limestone, or even shell have been utilized to construct manmade reefs. While these are not by definition scrap materials, their availability is sometimes dictated by a desire to move them from an existing site where for some reason they may no longer be desired. In these cases, they could be classified as a "material of opportunity." In other cases, as in the intent to build a reef to provide a rocky bottom substrate, material such as quarry rock or limestone may be the most suitable material available to create the intended habitat, and may be specifically sought after.

In the South Atlantic states individual state artificial reef programs, resource management agencies, or other approved reef programs serve as the central contact and coordination point for evaluating, approving, distributing and deploying secondary use materials on a given state's system of artificial reefs. Before agreeing to approve any materials for use in reef construction, the managing or oversight agency must carefully inspect the items and ensure that they are environmentally safe, structurally and physically stable, needed, practical, and can be deployed in a cost-effective and safe manner. A detailed discussion of the benefits, limitations and problems encountered in using the almost limitless list of secondary use materials that have been employed over the years in the construction of manmade reefs is well beyond the scope of this document. However, the Atlantic and Gulf State Marine Fisheries Commission's, as well as other individual artificial reef programs have produced publications which cover in great detail, many of the strengths and weaknesses of secondary use materials which have been employed in reef development.

Designed Habitat Structures

If an artificial reef program is to function in a manner that is conducive to effective long-term planning and the pursuit of realistic (fishery management driven) reef development goals, it can not continue to base reef construction solely on the unpredictable availability and diminished quantity of acceptable scrap or surplus materials. The only practical solution is to consider the incorporation of manufactured reef structures into planned reef development activities.

Manufactured manmade reef structures can be developed which possess the characteristics desired of a reef substrate for a specific environment, application, or end result. Although the initial costs in procuring these reef materials may be higher than those involved in obtaining many secondary use materials, the transportation, handling and deployment costs are typically about the same, and the lack of expense in having to clean or otherwise prepare these structures can often balance out this difference. Being able to engineer into a reef material design specific qualities of stability, durability, structural integrity, transportability and biological effectiveness also gives manufactured reef structures a great advantage over most secondary use materials which are often severely limited in how they can be modified or deployed.

Manufactured reef units can be deployed in any quantity, profile and pattern required, allowing them to provide for maximum efficiency of the materials used in achieving the desired results. Secondary use materials such as ships must be deployed in a single unit, often with a great deal of the total material volume being taken up in vertical profile. The same volume of designed reef materials that would be found in a vessel can be spread over a much larger area of ocean bottom with much less relief, allowing for better access to a larger number of reef users and a “more natural” appearance in the layout of the reef.

One of the most significant advantages offered by the use of designed reef structures is the ability to procure them in any quantity any time they are needed. This allows reef managers to plan ahead and make the best possible use of available funding, as well as predict exact costs needed to accomplish specific reef construction objectives from month to month or year to year. When depending on secondary use materials for reef development, this type of short and long-term planning is rarely available.

Standards for Manmade Reef Construction

The National Fishing Enhancement Act of 1984 (Title II of P.L.98-623) provides broad standards for the development of manmade reefs in the United States. The purpose of the Act was to “promote and facilitate responsible and effective efforts to establish artificial reefs in the navigable waters of the US and waters superjacent to the outer continental shelf (as defined in 43 USC, Section 1331) to the extent such waters exist in or are adjacent to any State.” In Section 203, the Act establishes the following standards for artificial reef development. “Based on the best scientific information available, artificial reefs in waters covered under the Act...shall be sited and constructed, and subsequently monitored and managed in a manner which will:

(1) enhance fishery resources to the maximum extent practicable;
(2) facilitate access and utilization by U.S. recreational and commercial fishermen;
(3) minimize conflicts among competing uses of waters covered under this title and the resources in such waters;
(4) minimize environmental risks and risks to personal health and property; and
(5) be consistent with generally accepted principles of international law (e.g MARPOL) and shall not create any unreasonable obstruction to navigation.”

Section 204 of the Act also calls for the development of a National Artificial Reef Plan consistent with these standards. This plan was first published by the National Marine Fisheries Service in 1985 and includes discussions of criteria for siting and constructing manmade reefs, as well as mechanisms and methodologies for monitoring and managing such reefs. While the Plan itself lacked any degree of regulatory authority, adopted regulations subsequently developed by the U.S. Army Corps of Engineers for dealing with the issuance of artificial reef construction permits were based on the standards set forth in the Act as well as wording taken from the Plan. The plan, National Artificial Reef Plan (as Amended): Guidelines for Siting, Construction, Development, and Assessment of Artificial Reefs (NOAA, 2007) was approved in 2007 and is available at http://www.nmfs.noaa.gov/sfa/PartnershipsCommunications/NARPwCover3.pdf

Each state artificial reef program has its own set of standards for the development and management of artificial reefs. In most cases these state standards were developed with the federal standards from the National Fisheries Enhancement Act and the National Artificial Reef Plan in mind. While specific state programs may differ in matters involving technical operation or specific management issues, they are all very similar in their adoption of the national standards that exist.

Human use and environmental concerns

Different artificial reef uses can potentially conflict. Fishing, for example, may conflict with research, education, non-extractive diving, or conservation. Conflicts can occur between commercial and recreational fishing and between spearfishers and hook-and-line anglers. Large ships used as artificial reefs can entrap divers who get disoriented or lost or acts as an attractive nuisance by luring divers to attempt diving at unsafe depths or under other unsafe conditions. With some exceptions (i.e. Johns et al. 2001), the costs and benefits of artificial reef construction from social and economic perspectives have rarely been evaluated. Illegally constructed artificial reefs, such as casitas used to attract spiny lobster, for example, are a public concern in terms of causing environmental damage and social and economic imbalance in terms of resource allocation.

Poorly designed or positioned manmade reefs can damage or alter natural habitat, create hazards to navigation, disrupt some fishing operations (e.g. shrimp trawling), become sources of pollution or contamination, and can contribute to overfishing or aesthetic pollution. Because the southeastern U.S. is vulnerable to storm, wave, and hurricane damage, durability and stability become especially important design considerations to avoid damaging surrounding habitat from structural failures and reef movement.

Cumulative impacts of artificial reefs are poorly understood. Despite the existence of extensive construction programs, it remains unclear whether artificial reefs provide significant long-term biological benefits to primary or secondary productivity, in part because all artificial reefs usually are only a small portion of existing natural hardbottom. Replacing natural habitats with artificial reefs may lead to environmental concerns about altering food webs, behavior, and settlement patterns, as well as possible detrimental impacts to adjacent habitats.

Public pressure to build artificial reefs often develops in response to signs of fishery depletion. In these cases other management actions may be needed in addition to or instead of constructing artifical reefs for rebuilding stocks. In these cases enthusiasm for building artificial reefs may divert limited resources away from more effective measures, such as improving habitat protection or strengthening fishing effort controls. Aggregation of fish by artificial reefs may increase fishing success at least in the short-term, but over the long-term, aggregation or increased total fishing activity at artificial reefs may overwhelm production and aggravate overfising problems.

Artificial reefs as Essential Fish Habitat

Earlier sections have discussed the ways in which manmade reefs are specifically used by both invertebrate and finfish species. Since manmade reefs are established by marine resource managers throughout the entire South Atlantic Bight, the diversity of species present on and around such structures is extremely wide. Manmade reefs are used in almost every possible marine environment, from shallow-water estuarine creeks to offshore sites up to several hundred feet in depth. Due to the broad distribution of reef sites along the South Atlantic states, many different species may interact with manmade reefs at different life-stages and at different times. For species which may be to some degree habitat-limited, the establishment of additional suitable habitat targeted to specific life-history stages may improve survival (Herrnkind et al., 1997). Additional manmade habitat designed specifically to promote survival of targeted species in "protected" areas could potentially enhance existing ecosystems or create new ones to fill in gaps where essential fish habitat had been damaged, lost, or severely overfished. Man-made structures also may provide essential habitat while simultaneously acting as a deterrent to illegal fishing practices in specially managed areas (e.g. Oculina HAPC).

Since the majority of the manmade reefs constructed along the southeastern U.S. are in coastal and offshore waters, the species most often present on these sites are predominantly the adult and/or sub-adult stages of virtually all species within the South Atlantic Snapper Grouper Complex, as well as all species managed within the Coastal Migratory Pelagics Fishery Management Plan. Depending on environmental conditions on a specific reef site, and the behavior patterns of certain fish, species within the Snapper Grouper Complex tend to be long to short-term reef residents, while those among the Coastal Pelagics tend to be more transient visitors to the reefs as they migrate up and down the coast. Red drum and spiny lobster, as well as some of the managed shrimp species, may be found on and around specific reef sites at different times of the year, depending on the exact location and design of the reef. While some species of managed corals may occur on reef structures as far north as the Carolinas, the waters off South Florida are the predominant site where such species are found attached to manmade substrate.

Artificial reefs are constructed from a wide range of materials, and used for a variety of purposes. They function by altering natural habitat and are especially popular sites for fishing and diving. Considerable evidence exists that artificial reefs attract and concentrate certain exploited species and can lead to short-term increases in catch rates. Artificial reefs constitute a habitat-based tool that ideally should be incorporated into an integrated holistic approach to fishery management.

3.3.2 Sargassum Habitat

Description and distribution

(from Dolphin Wahoo FMP)

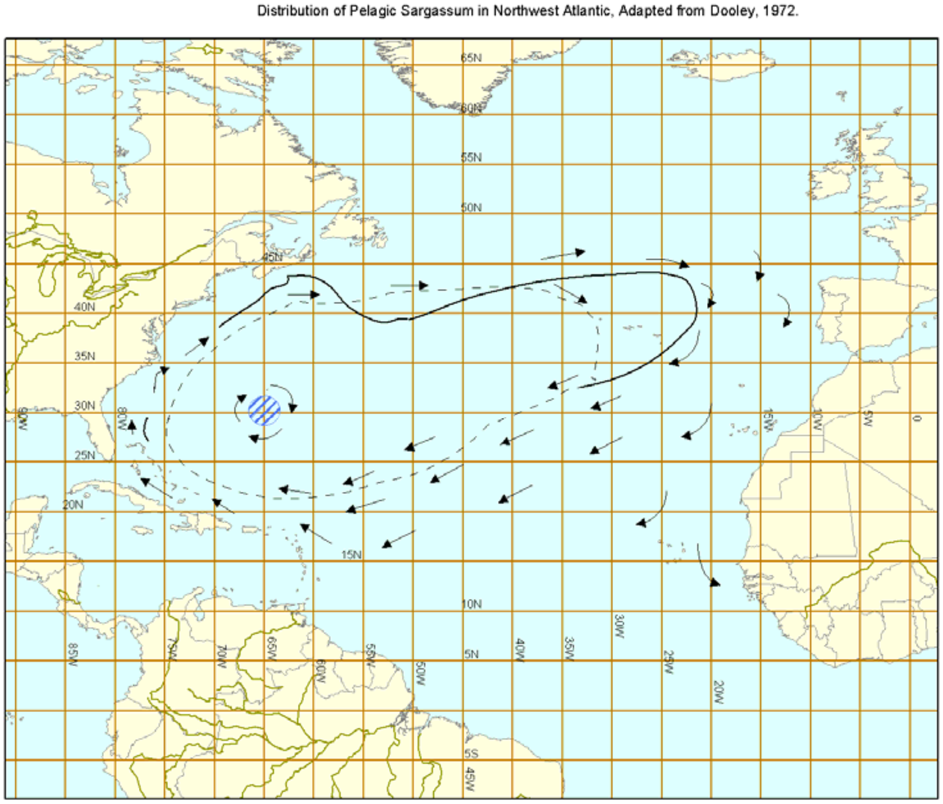
Within warm waters of the western North Atlantic, pelagic brown algae *Sargassum natans* and *S. fluitans* (Phaeophyta: Phaeophyceae: Fucales: Sargassaceae) form a dynamic structural habitat. These holopelagic species are believed to have evolved from benthic ancestors at least 40 million years ago. Evidence supporting this contention include: 1) lack of sexual reproduction characteristic of benthic species, 2) absence of a basal holdfast, 3) endemic faunal elements (10 invertebrates and 2 vertebrates), 4) greater buoyancy than benthic forms, and 5) late Eocene to early Miocene fossil remains from the Carpathian basin of the Tethys Sea (Winge 1923; Parr 1939; Friedrich 1969; Butler et al. 1983; Stoner and Greening 1984, Luning 1990). *Sargassum natans* is much more abundant than *S. fluitans*, comprising up to 90% of the total drift macroalgae in the Sargasso Sea. Limited quantities of several benthic species, including *S. filipendula*, *S. hystrix*, *S. polycertium*, *S. platycarpum* and *S. pteropleuron*, detached from coastal areas during storms, are also frequently encountered adrift. However, the drifting fragments of these benthic species soon perish (Hoyt 1918; Winge 1923; Parr 1939; Butler et al. 1983).

The pelagic species are golden to brownish in color and typically 20 to 80 cm in diameter. Both species are sterile and propagation is by vegetative fragmentation. The plants exhibit complex branching of the thallus, lush foliage of lancolate to linear serrate phylloids and numerous berry-like pneumatocysts. Perhaps the most conspicuous features are the pneumatocysts. These small vesicles function as floats and keep the plants positively buoyant. Gas within these bladders is predominately oxygen with limited amounts of nitrogen and carbon dioxide. The volume of oxygen within the pneumatocysts fluctuates diurnally in response, not to diurnal cycles of photosynthesis, but to changes in the partial pressure of oxygen in the surrounding medium (Woodcock 1950; Hurka 1971). There are generally a large number of pneumatocysts on a healthy plant: up to 80% of the bladders can be removed and the plants will remain positively buoyant (Zaitsev 1971). Under calm sea states the algae are at the surface with less than 0.3% of their total mass exposed above the air-water interface. Experiments indicate that an exposure to dry air of 7 to 10 minutes will kill phylloids, whereas pneumatocysts and thallomes can tolerate exposures of 20 to 30 minutes and 40 minutes, respectively. Wetting of exposed parts with seawater at 1 minute intervals, however, is enough to prevent tissue damage (Zaitsev 1971). In nature, such stress is likely encountered only during the calmest seas or when the alga is cast ashore. Illustrations and descriptions of *S. natans* and *S. fluitans* are given in Hoyt (1918), Winge (1923), Parr (1939), Taylor (1960), Prescott (1968), Humm (1979), Littler et al. (1989) and Schneider and Searles (1991).

Most pelagic *Sargassum* circulates between 20°N and 40°N latitudes and 30°W longitude and the western edge of the Florida Current/Gulf Stream (Figure 3.3-17). The greatest concentrations are found within the North Atlantic Central Gyre in the Sargasso Sea (Winge 1923; Parr 1939; Ryther 1956; Dooley 1972; Butler et al. 1983; Butler and Stoner 1984; Nierman et al. 1986). Total biomass is unknown, but, estimates obtained from net tows range from 800 to 2000 kg wet weight/km^2. Within the Sargasso Sea, this translates into a standing crop of 4 to 11 million metric tons (Parr 1939; Zaitzev 1971; Peres 1982; Butler et al. 1983; Butler and Stoner 1984; Nierman et al. 1986; Luning 1990). Stoner (1983) suggested that there had been a significant decline in biomass this century, but later recanted (Butler and Stoner 1984). Nierman et al. (1986) also calculated that no apparent decline had occurred.

Pelagic *Sargassum* contributes a small fraction to total primary production in the North Atlantic. However, within the oligotrophic waters of the Sargasso Sea it may constitute as much as 60% of total production in the upper meter of the water column (Howard and Menzies 1969; Carpenter and Cox 1974; Hanson 1977; Peres 1982). Estimates of production are typically around 1 mg C/m^2/d with slightly higher values reported from more nutrient rich shelf waters. Production has been shown to double under conditions of nitrogen and phosphorus enrichment (LaPointe 1986, 1995). Hanisak and Samuel (1984) found *Sargassum* to have low nitrogen and phosphorus requirements, and optimal growth at water temperatures of 24 to 30°C and salinity of 36 ppt. Nitrogen fixation by epiphytic cyanobacteria of the genera *Dichothrix*, *Trichodesmium*, and *Synechococcus* may enhance production (Carpenter 1972; Carpenter and Cox 1974; Phlips and Zeman 1990; Spiller and Shanmugam 1987). Photosynthesis in both *Sargassum* and the blue-green epiphytes is not inhibited at high light intensities (Hanisak and Samuel 1984; Phlips et al. 1986): not surprising in view of the neustonic niche they occupy.

Large quantities of *Sargassum* frequently occur on the continental shelf off the southeastern United States. Depending on prevailing surface currents, this material may remain on the shelf for extended periods, be entrained into the Gulf Stream, or be cast ashore (Hoyt 1918; Humm 1951; Howard and Menzies 1969; Carr and Meylen 1980; Winston 1982; Haney 1986; Baugh 1991). During calm conditions *Sargassum* may form large irregular mats or simply be scattered in small clumps. Langmuir circulations, internal waves, and convergence zones along fronts aggregate the algae along with other flotsam into long linear or meandering rows collectively termed “windrows” (Winge 1923; Langmuir 1938; Ewing 1950; Faller and Woodcock 1964; Stommel 1965; Barstow, 1983; Shanks 1988; Kingsford 1990). The algae sink in these convergence zones when downwelling velocities exceed 4.5 cm/sec. Buoyancy is not lost unless the algae sink below about 100 m or are held under at lesser depths for extended periods (Woodcock 1950). A time-at-depth relationship exists which affects the critical depth at which bladder failure ensues (Johnson and Richardson 1977). If buoyancy is lost, plants slowly sink to the sea floor. Schoener and Rowe (1970) indicate that sinking algae can reach 5000 m in about 2 days. Such sinking events contribute to the flux of carbon and other nutrients from the surface to the benthos (Schoener and Rowe 1970; Pestana 1985; Fabry and Deuser 1991). However, the flux of *Sargassum* to the sea floor has not been quantified and there is no information on the fate of this surface export.



Solid line refers to the outer boundary of regular occurrence; dashed line refers to the area in which there is a> 5% probability of encounter within 1° square; hatched circle represents possible center of distribution.

Figure 3.3-17. Distribution of pelagic Sargassum in the Northwest Atlantic (Source: Dolphin Wahoo FMP, Adapted from Dooley 1972).

Current understanding of the seasonal distribution and areal abundance (i.e., biomass per unit area) of pelagic *Sargassum* within the EEZ is poor. Gross estimates of the standing stock for the North Atlantic obtained from towed net samples are highly variable and range between 4 and 11 million metric tons. There is a clear need to improve the understanding of the distribution and abundance of this important habitat. Remote technology could aid to that end. Satellite-based Synthetic Aperture Radar (SAR) offers potential for assessing the distribution of large aggregations over broad swaths of the ocean surface. Coincident ship-based ground-truthing would permit an evaluation of the applicability of routine remote measurements of *Sargassum* distribution and abundance.

Ecological role and function

(from DW FMP)

Pelagic *Sargassum* supports a diverse assemblage of marine organisms including fungi (Winge 1923; Kohlmeyer 1971), micro-and macro-epiphytes (Carpenter 1970; Carpenter and Cox 1974; Mogelberg et al. 1983), at least 145 species of invertebrates (Winge 1923; Parr 1939; Adams 1960; Yeatman 1962; Weis 1968; Friedrich 1969; Fine 1970; Dooley 1972; Morris and Mogelberg 1973; Ryland 1974; Teal and Teal 1975; Peres 1982; Butler et al. 1983; Deason

1983; Andres and John 1984; Stoner and Greening 1984; Morgan et al. 1985; Nierman 1986; see Table 1 in Coston-Clements et al. 1991), over 100 species of fishes (Adams 1960; Parin 1970; Zaitzev 1971; Dooley 1972; Bortone et al. 1977; Fedoryako 1980, 1989; Gorelova and Fedoryako 1986; Settle 1993; Moser et al., in press), four species of sea turtles (Smith 1968; Fletemeyer 1978; Carr and Meylan 1980; Redfoot et al. 1985; Ross 1989; Carr 1986, 1987a, 1987b; Schwartz 1988; 1989; Witham, 1988; Manzella and Williams, 1991; Richardson and McGillivary, 1991), and numerous marine birds (Haney 1986). Many of the organisms most closely associated with *Sargassum* have evolved adaptive coloration or mimic the algae in appearance (Crawford and Powers 1953; Adams 1960; Teal and Teal 1975; Gorelova and Fedoryako 1986; Hacker and Madin 1991).

The following points noted in Manooch et al. (1984) and Table 3.3-7 developed from information presented in Manooch et al. (1984), further emphasizes the complexity of the *Sargassum* community and the importance of pelagic *Sargassum* habitat to pelagic fishes especially dolphin (*Coryphaena hippurus*).

"One major contribution of this paper is that we have documented the importance of the Sargassum community to dolphin, and therefore to anglers that fish for the species. Traditionally, fishermen seek weed-lines to land dolphin and other pelagic fishes. Seasonal angling success has been associated with the distribution of Sargassum along the southeastern United States. For instance, Rose and Hassler (1974) suggested that diminished landings of dolphin off North Carolina were probably caused by lack of tide-lines (usually caused by floating rows of Sargassum) rather than overfishing in previous years as some believed."

"Much of the material indicated that dolphin frequently feed at the surface and ingest fishes, crustaceans, insects, plants, and inorganic items that are associated with floating Sargassum."

"Sargassum which occurred in 48.6% of the stomachs was considered to be consumed incidental to normal foods."

Table 3.3-7. Percentages occurrence of *Sargassum* in the stomachs of dolphin, *Coryphaena hippurus* and yellowfin tuna (Data Source: Manooch et al. 1984; Rose and Hassler 1974; and Manooch and Mason 1983).

	Species	Number	Season or Size (FL) stomach	% Occurrence of Sargassum in
Rose and Hassler (1974)	Dolphin	396	All	28%
Manooch et al. (1984)	Dolphin	2,219	All	48.6%
Manooch et al. (1984)	Dolphin	158	Spring	55.1%
Manooch et al. (1984)	Dolphin	845	Summer	50.9%
Manooch et al. (1984)	Dolphin	61	Fall	29.5%
Manooch et al. (1984)	Dolphin	14	Winter	41.2%
Manooch et al. (1984)	Dolphin	13	≥300 mm	23%
Manooch et al. (1984)	Dolphin	987	≥300-500 mm	49%
Manooch et al. (1984)	Dolphin	686	≥500-700 mm	55%
Manooch et al. (1984)	Dolphin	192	≥700-900 mm	43.8%
Manooch et al. (1984)	Dolphin	189	≥900-1,100 mm	43%

Manooch et al. (1984)	Dolphin	71	≥1,100 mm	38%
Manooch and Mason (1983)	Yellowfin tuna			26.5%
Manooch and Mason (1983)	Blackfin tuna			12.4%

"The relative contribution of the Sargassum community to the diet may be indicative of physiological constraints on the foraging behavior of these pelagic predators. The pursuit and capture of free-swimming prey in the open ocean is energetically expensive, while grazing on relatively sessile animals associated with Sargassum can be accomplished without great energy expenditure. The tunas consume a greater proportion of pelagic, adult fishes and take less prey from the Sargassum community than do dolphin. Although both tunas and dolphin are capable of high speed pursuit, tunas have highly vascularized locomotion muscles enabling sustained aerobic metabolism. Dolphin, with a much smaller portion of red muscle, must rely primarily on anaerobic metabolic pathways (mainly glycolosis), and therefore are limited to short bursts of acceleration. Thus, the energetic strategy for dolphin seems to be forage primarily on smaller prey from the Sargassum community, but also to capture larger prey with short bursts of high speed pursuit if the opportunity arises."

Species composition and community structure

Fishes

The fishes associated with pelagic *Sargassum* in the western North Atlantic have been studied by a number of investigators (Adams 1960; Parin 1970; Zaitzev 1971; Dooley 1972; Bortone et al. 1977; Fedoryako 1980, 1989; Gorelova and Fedoryako 1986; Settle 1993; Moser et al., in press). Similar research has also addressed the ichthyofauna of drift algae in the Pacific (Uchida and Shojima 1958; Besednov 1960; Hirosaki 1960b; Shojima and Ueki 1964; Anraku and Azeta 1965; Kingsford and Choat 1985; Kingsford and Milicich 1987; Nakata et al. 1988). In all cases, juvenile fishes were numerically dominant. Sampling designs and gear avoidance have no doubt contributed to the poorly described adult fish fauna. However, studies by Gibbs and Collette (1959), Beardsley (1967), Parin (1970), Manooch and Hogarth (1983), Manooch and Mason (1983), Manooch et al. (1984, 1985), and Fedoryako (1989) clearly indicate that large, pelagic, adult fishes utilize *Sargassum* resources. This becomes even more evident when one observes the efforts of fishermen targeting "weedlines."

Many of the fishes found in association with *Sargassum* are not restricted to that habitat and are known to frequent various types of drift material and fish aggregating devices (Besednov 1960; Mansueti 1963; Hunter and Mitchell 1967; Kojima 1966; Kulczycki et al. 1981; Lenanton et al. 1982; Robertson 1982; Nakata et al. 1988; Fedoryako 1989; Rountree 1989, 1990). Protection, feeding opportunity, cleaning, shade, structural affinity, visual reference, tactile stimulation, historical accident, passive drift, and use as a spawning substrate have all been postulated as reasons for such associations (Hirosaki 1960a; Hunter and Mitchell 1968; Senta 1966a, 1966b, 1966c; Dooley 1972; Helfman 1981).

Species composition and abundance of fishes associated with *Sargassum* are affected by surface residence time, season, and geographic location. Most of the young fishes that associate with the algae are surface forms (Fahay 1975; Powles and Stender 1976) and it is not known if they remain near the *Sargassum* when it is submerged. Recruitment of fishes to drift algae and flotsam is initially rapid and continues to increase over time (Senta 1966a; Hunter and Mitchell

1968; Kingsford and Choat 1985; Kingsford 1992). The abundance of larval and juvenile fishes varies seasonally and regionally, both in terms of numbers of fish and fish biomass (Dooley 1972; Settle 1993).

Regional trends in the mean abundance and biomass of young fish show a decrease in abundance across the continental shelf and into the Gulf Stream and Sargasso Sea, and a decrease from spring through winter (Settle 1993). Species richness is generally highest on the outer shelf during spring and summer and further offshore during the fall and winter (Settle, 1993). Overall, diversity is greatest in offshore waters (Bortone et al. 1977; Fedoryako 1980, 1989; Settle 1993).

Fish abundance has been found to be positively correlated with *Sargassum* biomass. Correlations were significant over the middle shelf throughout the year. Fish biomass was also positively correlated over the outer shelf during the fall (Settle, 1993). No correlation was observed in the Gulf Stream or Sargasso Sea (Dooley, 1972; Fedoryako, 1980; Settle, 1993).

The types of *Sargassum* habitats (e.g., individual clumps, small patches, large rafts, and weedlines) and the "age" (i.e., growth stage and degree of epibiont colonization) also affect the distribution and abundance of associated fishes. Ida et al. (1967a, b), Fedoryako (1980), Gorelova and Fedoryako (1986) and Moser et al. (in press) described the spatial distribution of fishes in and around clumps and rafts of *Sargassum*. Juvenile *Diodon*, *Coryphaena*, *Lobotes*, and the exocoetids occupy the outer periphery, whereas *Canthidermis*, *Balistes*, *Kyphosus*, *Abudefduf*, *Caranx*, and *Seriola* are distributed below the algae. Other genera such as *Histrio* and *Syngnathus* are typically hidden within the foliage. Larger juveniles and adults occupy nearby waters out to several tens of meters from the patches. With regard to algal age, Conover and Sieburth (1964) and Sieburth and Conover (1965) suggest that the community could be significantly controlled by the effects of exogenous metabolites on algal epibionts. These substances, which are released during periods of new algal growth, inhibit epibiotic colonization, and could alter the trophic resources available to associated macrofauna, including fish (Gorelova and Fedoryako 1986). Stoner and Greening (1984) concluded that algal age did affect the macrofaunal composition, but the abundance of carnivores remained stable. However, since their study dealt primarily with the invertebrate fauna, the effects of these substances on other trophic links remains unknown although similar compounds are known to deter some herbivores (Paul 1987; Hay and Fenical 1988; Hay et al. 1988; Steinberg 1988).

There have been well over 100 species of fishes collected or observed associated with the *Sargassum* habitat (Table 3.3-8). The carangids and balistids are the most conspicuous, being represented by 21 and 15 species respectively. The planehead filefish, *Monacanthus hispidus*, is clearly the most abundant species in shelf waters off the southeastern U.S. and in the Gulf of Mexico (Dooley 1972; Bortone et al. 1977; Settle 1993; Moser et al., in press).

A number of species have direct fisheries value although not all of them are common. However, the seasonal abundances of *Caranx* spp., *Elagatis bipinnulata*, *Seriola* spp., *Coryphaena hippurus*, *Pagrus pagrus*, *Mugil* spp., *Peprilus triacanthus*, and *Balistes capriscus* illustrate the importance of the habitat to the early life stages of these species.

Table 3.3-8. List of fishes collected or observed in association with pelagic *Sargassum* in the North Atlantic Ocean including the Gulf of Mexico and Caribbean Sea. Life-stages are E=egg, L=larva, J=juvenile, and A=adult. Nomenclature follows Robins et al. (1991) (Source: Larry Settle NMFS SEFSC pers. comm. 1997).

Family Genus and species	Common name	Life-stage(s)
Carcharhinidae	requiem sharks	
Carcharhinus falciformis	silky shark	A
C. limbatus	blacktip shark	A
C. longimanus	oceanic whitetip shark	A
Muraenidae	morays	
Unidentified	moray	L
Clupeidae	herrings	
Sardinella aurita	Spanish sardine	J
Gonostomatidae	lightfishes	
Unidentified	lightfish	L
Myctophidae	lanternfishes	
Unidentified	lanternfish	L
Gadidae	cods	
Urophycis chuss	red hake	L, J
U. earlli	Carolina hake	L, J
U. floridana	southern hake	L, J
U. regia	spotted hake	L, J
Antennariidae	frogfishes	
Histrio histrio	*Sargassum*fish	L, J, A
Exocoetidae	flyingfishes	
Cypselurus furcatus	spotfin flyingfish	E, L, J, A
C. melanurus	Atlantic flyingfish	E, L, J, A
Exocoetus obtusirostris	oceanic two-wing flyingfish	J
Hemirhamphus balao	balao	J
H. brasiliensis	ballyhoo	J
Hirundichthys affinis	fourwing flyingfish	E, L, J, A
Hyporhamphus unifasciatus	silverstripe halfbeak	L, J
Paraexocoetus brachypterus	sailfin flyingfish	E, L, J, A
Prognichthys gibbifrons	bluntnose flyingfish	E, L, J, A
Belonidae	needlefishes	
Tylosurus acus	agujon	L, J
Fistulariidae	cornetfishes	
Fistularia tabacaria	bluespotted cornetfish	J
Centriscidae	snipefishes	
Macroramphosus scolopax	longspine snipefish	J
Syngnathidae	pipefishes	
Hippocampus erectus	lined seahorse	J
H. reidi	longsnout seahorse	J
Microphis brachurus	opossum pipefish	J
Syngnathus caribbaeus	Caribbean pipefish	J
S. floridae	dusky pipefish	J
S. fuscus	northern pipefish	J
S. louisianae	chain pipefish	J
S. pelagicus	*Sargassum* pipefish	E, L, J, A
S. scovelli	gulf pipefish	J
S. springeri	bull pipefish	J
Dactylopteridae	flying gurnards	

Dactylopterus volitans	flying gurnard	L, J
Scorpaenidae	scorpionfishes	
Unidentified	scorpionfish	L
Serranidae	sea basses	
Epinephelus inermis	marbled grouper	J
Priacanthidae	bigeyes	
Priacanthus arenatus	bigeye	J
Pristigenys alta	short bigeye	L, J
Apogonidae	cardinalfishes	
Apogon maculatus	flamefish	L
Pomatomidae	bluefish	
Pomatomus saltatrix	bluefish	L
Rachycentridae	cobias	
Rachycentron canadum	cobia	E, L, J, A
Echeneidae	remoras	
Phtheirichthys lineatus	slender suckerfish	J
Carangidae	jacks	
Caranx bartholomaei	yellow jack	L, J
C. crysos	blue runner	L, J
C. dentex	white trevally	J
C. hippos	crevalle jack	J
C. latus	horse-eye jack	J
C. ruber	bar jack	L, J
Chloroscombrus chrysurus	Atlantic bumper	L, J
Decapterus macerellus	mackerel scad	J
D. punctatus	round scad	J
D. tabl	redtail scad	J
Elagatis bipinnulata	rainbow runner	L, J, A
Naucrates ductor	pilotfish	J
Selar crumenophthalmus	bigeye scad	L, J
Selene vomer	lookdown	J
Seriola dumerili	greater amberjack	L, J
S. fasciata	lesser amberjack	J
S. rivoliana	almaco jack	L, J, A
S. zonata	banded rudderfish	J
Trachinotus falcatus	permit	L, J
T. goodei	palometa	J
Trachurus lathami	rough scad	L, J
Coryphaenidae	dolphins	
Coryphaena equisetis	pompano dolphin	L, J, A
C. hippurus	dolphin	L, J, A
Lutjanidae	snappers	
Lutjanus sp.	snapper	L
Rhomboplites aurorubens	vermilion snapper	L, J
Lobotidae	tripletails	
Lobotes surinamensis	tripletail	L, J, A
Gerreidae	mojarras	
Eucinostomus sp.	mojarra	L
Sparidae	porgies	
Pagrus pagrus	red porgy	L, J
Mullidae	goatfishes	
Mullus auratus	red goatfish	L, J
Unidentified	goatfish	L
Kyphosidae	sea chubs	

Kyphosus incisor	yellow chub	L, J
K. sectatrix	Bermuda chub	L, J
Chaetodontidae	butterflyfishes	
Chaetodon ocellatus	spotfin butterflyfish	J
C. striatus	banded butterflyfish	J
Pomacentridae	damselfishes	
Abudefduf saxatilis	sergeant major	L, J
Mugilidae	mullets	
Mugil cephalus	striped mullet	L
M. curema	white mullet	L
Sphyraenidae	barracudas	
Sphyraena barracuda	great barracuda	A
S. borealis	northern sennet	L, J
Polynemidae	threadfins	
Polydactylus virginicus	barbu	J
Labridae	wrasses	
Bodianus pulchellus	spotfin hogfish	J
Thalassoma bifasciatum	bluehead	J
Scaridae	parrotfishes	
Unidentified	parrotfish	L
Uranoscopidae	stargazers	
Unidentified	stargazer	L
Blenniidae	combtooth blennies	
Hypsoblennius hentzi	feather blenny	L
Parablennius marmoreus	seaweed blenny	L
Gobiidae	gobies	
Microgobius sp.	goby	L
Acanthuridae	surgeonfishes	
Acanthurus randalli	gulf surgeonfish	J
Acanthurus sp.	surgeonfish	L
Trichiuridae	snake mackerels	
Unidentified	snake mackerel	L
Scombridae	mackerels	
Acanthocybium solandri	wahoo	J, A
Auxis thazard	frigate mackerel	J, A
Euthynnus alletteratus	little tunny	A
Katsuwonus pelamis	skipjack tuna	A
Scomber japonicus	chub mackerel	J
Scomberomorus cavalla	king mackerel	A
Thunnus albacares	yellowfin tuna	J, A
T. atlanticus	blackfin tuna	A
Xiphiidae	swordfishes	
Xiphius gladius	swordfish	L, J
Istiophorus platypterus	sailfish	L, J
Makaira nigricans	blue marlin	L, J, A
Tetrapturus albidus	white marlin	L, J, A
Stromateidae	butterfishes	
Ariomma sp.	driftfish	L
Centrolophus sp.	ruff	J
Cubiceps pauciradiatus	bigeye cigarfish	J
Hyperoglyphe bythites	black driftfish	J
H. perciformis	barrelfish	J
Peprilus triacanthus	butterfish	L, J
Psenes cyanophrys	freckled driftfish	J

Bothidae	lefteye flounders	
Bothus sp.	flounder	L
Cyclopsetta fimbriata	spotfin flounder	L
Balistidae	leatherjackets	
Aluterus heudeloti	dotterel filefish	L, J
A. monoceros	unicorn filefish	L, J
A. schoepfi	orange filefish	L, J
A. scriptus	scrawled filefish	L, J
Balistes capriscus	gray triggerfish	J, A
B. vetula	queen triggerfish	J
Cantherhines macrocerus	whitespotted filefish	J
C. pullus	orangespotted filefish	J, A
Canthidermis maculata	rough triggerfish	J
C. sufflamen	ocean triggerfish	J
Monacanthus ciliatus	fringed filefish	J
M. hispidus	planehead filefish	J
M. setifer	pygmy filefish	J
M. tuckeri	slender filefish	J
Xanthichthys ringens	*Sargassum* triggerfish	J
Ostraciidae	boxfishes	
Lactophrys sp.	cowfish	L
Tetraodontidae	puffers	
Chilomycterus antennatus	bridled burrfish	J
C. schoepfi	striped burrfish	J
Diodon holocanthus	ballonfish	J
D. hystrix	porcupinefish	J
Sphoeroides maculatus	northern puffer	L
S. spengleri	bandtail puffer	L
Unidentified	puffer	L
Molidae	molas	
Mola sp.	mola	J

Turtles

There are five species of sea turtles that associate with *Sargassum* and all are highly migratory. The offshore waters of the Western Atlantic may be used by these species as post-hatchling developmental habitat, foraging habitat, or migratory pathways. No individual members of any of the species are likely to be year-round residents of *Sargassum*. Individual animals will make migrations into nearshore waters as well as other areas of the North Atlantic Ocean, Caribbean Sea, and the Gulf of Mexico.

Sargassum as Essential Fish Habitat

The SAFMC has designated *Sargassum* as EFH for species in the snapper grouper complex and for species under the Coastal Migratory Pelagics Fishery Management Plan, including dolphin.

3.3.3 Marine Water Column

Description and distribution

Specific habitats in the water column can best be defined in terms of gradients and discontinuities physical and biological characteristics, such as temperature, salinity, density, nutrients, light and depth. These “structural” components of the water column environment (sensu Peters and Cross 1992) are not static but change both in time and space. Therefore, there are numerous potentially distinct water column habitats for a broad array of species and life-stages within species.

Winds are important in all layers of the marine water column. Wind stress can alter or reverse the generally southern pattern of flow in the coastal frontal zone, CFZ (Blanton et al. 1999). Winds can also mix and move water masses inshore. In the mid-Atlantic, waters from Gulf Stream intrusions move across the shelf at a rate of approximately 2-3 mi/day (3-5 km/day), and parallel to the coast at a rate of approximately 3-9 mi/day (5-15 km/day) (Hare et al. 1999). Georgian shelf waters flow into the North Carolina Capes region during periods of persistent southwesterly winds, while Virginian coastal waters flow south across Diamond, and occasionally Lookout, shoals during periods of persistent northerly winds (Pietrafesa 1989). Current and wind patterns will have a strong effect on the recruitment and retention of various fish larvae from different offshore areas.

The continental shelf off the southeastern U.S., extending from the Dry Tortugas to Cape Hatteras, encompasses an area in excess of 100,000 km^2 (Menzel 1993). Based on physical oceanography and geomorphology, this environment can be divided into two regions: Dry Tortugas to Cape Canaveral and Cape Canaveral to Cape Hatteras. The break between these two regions is not precise and ranges from West Palm Beach to the Florida-Georgia border depending on the specific data considered. The shelf from the Dry Tortugas to Miami is ~25 km wide and narrows to approximately 5 km off Palm Beach. The shelf then broadens to approximately 120 km off of Georgia and South Carolina before narrowing to 30 km off Cape Hatteras. The Florida Current/Gulf Stream flows along the shelf edge throughout the region. In the southern region, this boundary current dominates the physics of the entire shelf (Lee et al. 1992, 1994). In the northern region, additional physical processes are important and the shelf environment can be subdivided into three oceanographic zones (Atkinson et al. 1985; Menzel 1993). The outer shelf (40-75 m) is influenced primarily by the Gulf Stream and secondarily by winds and tides. On the mid-shelf (20-40 m), the Gulf Stream, winds, and tides almost equally affect the water column. Freshwater runoff, winds, tides and bottom friction influence inner shelf waters (0-20 m).

Several water masses are present in the region. From the Dry Tortugas to Cape Canaveral, the three water types are: Florida Current Water (FCW), waters originating in Florida Bay, and shelf water. Shelf waters off the Florida Keys are an admixture of FCW and waters from Florida Bay (Lee et al. 1992, 1994). From Cape Canaveral to Cape Hatteras, four water masses are found: Gulf Stream Water (GSW), Carolina Capes Water (CCW), Georgia Water (GW) and Virginia Coastal Water (VCW). Virginia Coastal Water enters the region from north of Cape Hatteras. Carolina Capes Water and GW are admixtures of freshwater runoff and GSW (Pietrafesa et al. 1985, 1994).

Spatial and temporal variation in the position of the western boundary current has dramatic affects on water column habitats. Variation in the path of the Florida Current near the Dry Tortugas induces formation of the Tortugas Gyre (Lee et al. 1992, 1994). This cyclonic eddy has horizontal dimensions on the order of 100 km and may persist in the vicinity of the Florida Keys for several months. The Pourtales Gyre, which has been found to the east, is formed when the

Tortugas Gyres moves eastward along the shelf. Upwelling occurs in the center of these gyres, thereby adding nutrients to the near surface (<100 m) water column. Wind and input of Florida Bay water also influence the water column structure on the shelf off the Florida Keys (Smith 1994; Wang et al. 1994).

Similarly, further downstream, the Gulf Stream encounters the Charleston Bump, a topographic rise on the upper Blake Ridge. Here the current is often deflected offshore, again resulting in the formation a cold, quasi-permanent cyclonic gyre, and associated upwelling (Brooks and Bane 1978). Along the entire length of the Florida Current and Gulf Stream, cold cyclonic eddies are imbedded in meanders along the western front. Three areas of eddy amplification are known: Downstream of Dry Tortugas, downstream of Jupiter Inlet (27°N to 30°N latitude) ("The Point" or "Amberjack Hole"), and downstream of the Charleston Bump (32°N to 34°N latitude) ("The Charleston Gyre"). Meanders propagate northward (i.e., downstream) as waves. The crests and troughs represent the onshore and offshore positions of the Gulf Stream front. Cross-shelf amplitudes of these waves are on the order 10 to 100 km. Upwelling within meander troughs is the dominant source of "new" nutrients to the southeastern U.S. shelf and supports primary, secondary, and ultimately fisheries production (Yoder 1985; Menzel 1993). Off Cape Hatteras the Gulf Stream turns offshore to the northeast. Here, the confluence of the Gulf Stream, the Western Boundary Under-Current (WBUC), Mid-Atlantic Shelf Water (MASW), Slope Sea Water (SSW), CCW, and VCW create a dynamic and highly productive environment, known as the "Hatteras Corner" or "The Point" (Figure 3.3-18).

On the continental shelf, offshore projecting shoals at Cape Fear, Cape Lookout and Cape Hatteras affect longshore coastal currents and interact with Gulf Stream intrusions to produce local upwelling (Blanton et al. 1981; Janowitz and Pietrafesa 1982). Shoreward of the Gulf Stream, seasonal horizontal temperature and salinity gradients define the mid-shelf and inner-shelf fronts. In coastal waters, river discharge and estuarine tidal plumes contribute to the water column structure.

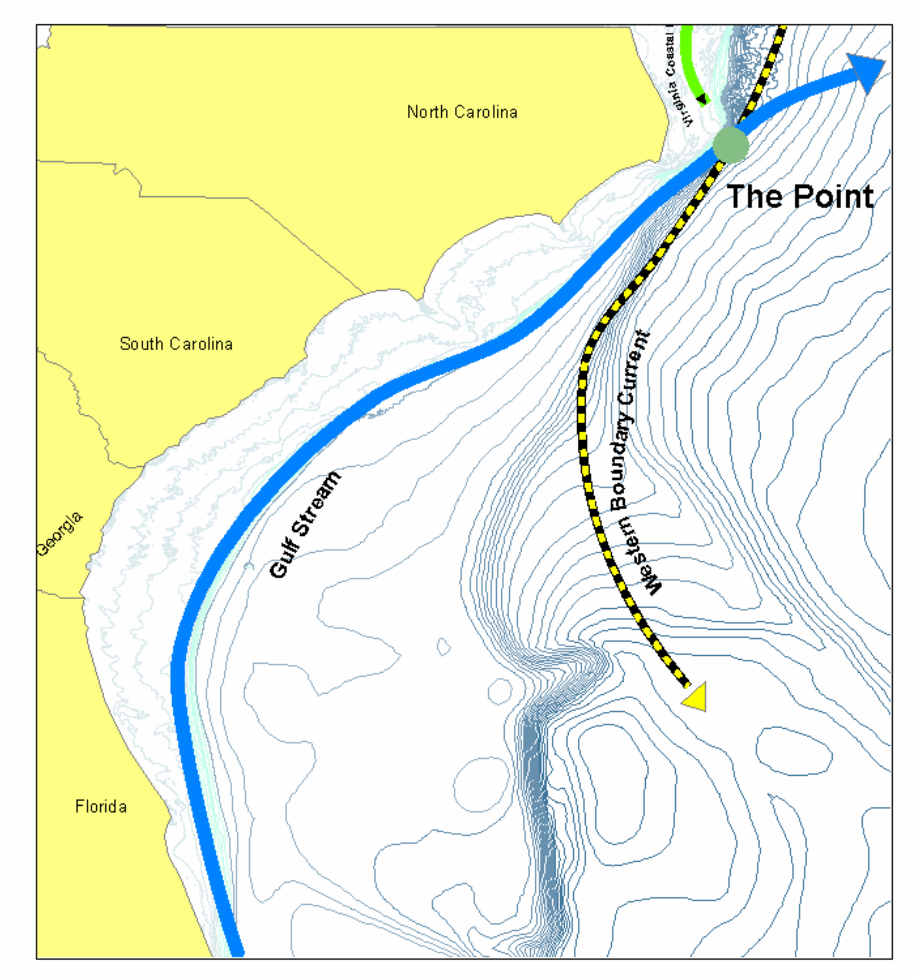


Figure 3.3-18. Water Masses off North Carolina (Source: Dolphin Wahoo FMP, Adapted from Shepard and Hulbert 1994).

Ecological role and function

(from DW FMP)
Coastal waters off the southeastern U.S. are split into two zoogeographic provinces based on shore fishes and continental shelf invertebrate species. The Caribbean Province includes the Florida Keys and extends northward to approximately the Florida-Georgia border, but its northern boundary is not sharp. The Carolinian Province extends from this border, northwards to Cape Hatteras (Briggs 1974). A similar faunal break is evident in mesopelagic fish fauna. The boundary between the North Sargasso Sea Province and the South Sargasso Sea Province occurs approximately parallel with Jupiter Inlet, Florida (Backus et al. 1977).

The water column from Dry Tortugas to Cape Hatteras serves as habitat for a variety of marine fish and shellfish. Most marine fish and shellfish broadcast spawn pelagic eggs and thus, most fishery-targeted species utilize the water column during some portion of their early life history (e.g., egg, larvae, and juvenile stages). Larvae of shrimp, lobsters, crabs, and larvae of reef, demersal and pelagic fishes are found in the water column (e.g., Fahay 1975; Powels and Stender 1976; Leis 1991; Yeung and McGowan 1991; Criales and McGowan 1994). Challenges with species-level identifications impede an exact accounting of the number of fishes whose larvae inhabit the water column, but the number of families represented in ichthyoplankton collections ranges from 40 to 91 depending on location, season, and sampling method.

In nearshore ocean waters, the depth that light penetrates to allow photosynthesis (euphotic zone) may be quite shallow because of high turbidity and wind mixing. Proceeding offshore there is generally a sharp decrease in chlorophyll a where the water column becomes more stratified. Menzel (1993) reported that primary production rates decreased significantly from the inner shelf to the outer shelf of the South Atlantic Bight. Production levels may increase by a factor of three to ten with warm core intrusions from the Gulf Stream. Because these intrusions occur irregularly on the inner shelf zone, this nearshore area depends more on nutrients recycled or resuspended by wind or tidal forces (Menzel 1993). Zooplankton distribution is directly related to location of phytoplankton blooms. Cahoon et al. (1990) found that on the inner shelf in Onslow Bay, NC, 80% of the chlorophyll a was associated with the sediment. Benthic microalgal biomass (average density =36.4 mg chlorophyll a/m^2) always exceeded phytoplankton biomass (average density =8.2 mg chlorophyll a/m^2) (Cahoon and Cooke 1992). Hackney et al. (1996) reported that, because of circulation patterns, inorganic nutrients could be resuspended and retained in sufficient amounts to allow localized phytoplankton blooms within the surf zone. Primary production within the water column can also come from macroalgae detached from hard substrate (e.g., *Enteromorpha*) or floating on the surface (e.g., *Sargassum*).

The surf zone and shallow intertidal waters are important corridors for seasonal fish migrations and for larval transport in and out of estuarine waters. Several studies have focused on surf zone fishes in North Carolina (Francesconi 1994; Hackney et al. 1996; Ross and Lancaster 1996). These studies reported 47 species in North Carolina's surf zone. About 130 species of fishes have been reported from North Carolina through Georgia (Tagatz and Dudley 1961).

The surf zone is an important migratory path for larval and juvenile fish moving toward the estuaries in the winter and spring. Adult fish are thought to migrate close to shore in the surf zone during the fall migration offshore (Hackney et al. 1996). Adult fish abundance in the surf zone is highly seasonal with lowest abundance and diversity in the winter and maximum abundance and diversity in the late summer (Hackney et al. 1996). When including all life stages, maximum biomass occurs in the fall when juveniles are at peak sizes, and large schools of fish migrate from the estuaries along the beaches.

Larval fish are an important component of zooplankton in the coastal ocean water column. In Onslow Bay, NC, Powell and Robbins (1998) documented a total of 110 families from ichthyoplankton samples. Estuarine-dependent species such as menhaden, spot, and Atlantic croaker are an important component of the ichthyoplankton during late fall and winter. These species spawn offshore and must be transported into estuaries through the water column. Ichthyoplankton from estuarine-dependent species that spawn in the sounds, inlets, and nearshore ocean waters during spring and early summer (e.g., pigfish, silver perch, weakfish) were also found in the ocean water column shortly afterward. Reef fish larvae were most abundant during spring, summer, and early fall. The frequent occurrence of larvae from deepwater oceanic species indicates that Gulf Stream waters transported those larvae to shelf waters off North Carolina.

Inlets are important corridors (or bottlenecks) through which many fish must successfully pass to complete their life cycles. Larval fish diversity in North Carolina's inlets is very high. Sixty-one larval species have been found in Oregon Inlet; Atlantic croaker and summer flounder were particularly abundant (Hettler and Barker 1993). Some of the other species included bluefish, black sea bass, gray snapper, several flounder species, pigfish, pinfish, spotted seatrout, weakfish, spot, kingfish, red drum, mullet, and butterfish. In North Carolina, Beaufort, Ocracoke, and Oregon inlets also support significant larval fish passage, although Oregon Inlet may be especially important due to the great distance between it and adjacent inlets, its orientation along the shoreline, and the direction of prevailing winds. Oregon Inlet provides the only opening into Pamlico Sound north of Cape Hatteras for larvae spawned and transported from the Mid-Atlantic Bight.

Research projects conducted under the South Atlantic Bight Recruitment Experiment (SABRE) studied transport of winter-spawned fish larvae into the estuaries. Larvae concentrate on the shelf in a narrow "withdrawal zone" upwind of an inlet within the 23-foot (7 m) deep isobath. Upon the appropriate conditions of ocean currents, the larvae pass through the inlets. Even during best wind and tidal conditions, only about 10% of the available larvae are successfully drawn into the inlet (Blanton et al. 1999). Larvae passing downwind and outside the narrow withdrawal zone pass seaward of the inlet shoals and, given the right conditions, will be transported into the next available inlet downstream. Churchill et al. (1999) noted that transport dynamics in the immediate vicinity of inlets are complex, and that larvae may also remain near an inlet or move in and out repeatedly before actually immigrating. However, since the along-shore flow component of the coast is four to five times greater than the cross-shelf component, larvae are highly dependent on being transported along the shore in a narrow zone and then injected through the inlet (Hare et al. 1999). Offshore-spawning, estuarine-dependent species include many of the region's most important commercial and recreational fish species, such as menhaden, spot, Atlantic croaker, pinfish, flounders, shrimp, black sea bass, and gag. Red drum and blue crabs, which spawn in and near the inlets, also require transport of larvae through inlet systems. Consequently, successful movement of larvae through the inlets is of great importance to regional fisheries, particularly where inlets are limited.

The marine spawning species generally spawn in locations where prevailing currents will carry their eggs and larvae to nursery areas within estuaries and nearshore ocean waters. Spot, Atlantic croaker, southern flounder, Atlantic menhaden, and striped mullet spawn offshore where they produce planktonic eggs and larvae from fall to late winter (Anderson 1958; Epperly and Ross 1986). Their larvae are transported into the estuaries where they settle in nursery areas with low to moderate-salinity. The spawning function of pelagic waters for demersal species is therefore limited to egg dispersal. The specific time of spawning is determined by coincidence of environmental conditions in the water column. The other group of marine spawners reproduces at various times, but their nursery habitat consists of higher salinity areas.

Bluefish, Florida pompano and Gulf kingfish use the surf zone and nearshore ocean waters as a nursery (Hackney et al. 1996). Juveniles of these species tend to stay in one area and use the surf zone for an extended time (>25 days during the summer months) (Ross and Lancaster 1996). Some fish, such as anchovies and king mackerel, rely on the nearshore boundaries of ocean water masses as nursery habitats (SAFMC 1998a). Juveniles of other estuarine species, such as red drum, Spanish mackerel, bluefish, and black sea bass, use the surf zone and nearshore waters seasonally while migrating between estuarine and ocean waters (Godcharles and Murphy 1986; DMF 2000a). Pelagic species that use nearshore ocean waters as a nursery to some extent include butterfish, pinfish, striped anchovy, striped mullet, and Atlantic thread herring (F. Rohde, DMF, pers. com. 2001). The major recruitment period for juvenile fish to surf zone nurseries is late spring through early summer.

A large number of fish inhabits the marine water column as adults. Coastal pelagics, highly migratory species, and anadromous fish species are dependent on the water column for adequate foraging (Manooch and Hogarth 1983). The boundaries of water masses (coastal fronts) in the nearshore ocean are favorite foraging areas for mackerel and dolphin (SAFMC 1998a). King and Spanish mackerel feed on baitfish that congregate seasonally on shoals and natural and artificial reefs. The SAFMC (1998a) has designated the cape shoals of North Carolina as Habitat Areas of Particular Concern (HAPC) for both mackerels. Anadromous species such as shad, river herring, and striped bass utilize the cape shoals as a staging area for migration along the coast. Large aggregations of striped bass have been documented, in the northern, nearshore coastal area of the state during winter months, feeding and resting prior to initiation of an extensive northward spawning migration (Holland and Yelverton 1973; Laney et al. 1999). This wintering ground is shared by the Chesapeake, Hudson, and Roanoke/Albemarle striped bass stocks, and is therefore important to the entire Atlantic coast population (Benton 1992). The water column off the Outer Banks during winter supports an abundance of anchovies and menhaden, weakfish and other sciaenids, on which the striped bass feed. Laney et al. (1999) considered the existence of an area with such abundant food sources to be critical for building energy reserves for successful migration and reproduction of striped bass.

The value of floating plants has been evaluated in marine systems, where *Sargassum* floating in the water column supports a diverse assemblage of marine organisms, including at least 145 species of invertebrates, 100 species of fish, four species of marine turtles, and numerous marine birds (see section 3.3.2). *Sargassum* is concentrated as small patches, large rafts, or weedlines at the convergence of water masses in the coastal ocean, such as those found along “tide lines” near coastal inlets. The greatest concentrations of *Sargassum* patches are found in the Sargasso Sea and on the outer continental shelf of the South Atlantic, although they can be pushed into nearshore waters by winds and currents. Large pelagic adult fish such as dolphin and sailfish feed on the small prey in and around *Sargassum*. This behavior prompts sport fishermen to target *Sargassum* patches.

Species composition and community structure

Temperature varies least in the marine system (Peterson and Peterson 1979; Nybakken 1993) and marine species tend to be less tolerant of temperature extremes and rapid changes in temperature. Water temperature is one of the most important factors in determining use of coastal ocean habitat by warm temperate and tropical species (SAFMC 1998a). Tropical species occur off the North Carolina coast where offshore bottom water temperatures range from approximately 52-81°F (11–27°C) (SAFMC 1998a). Temperatures less than 54°F (12°C) may result in the death of some tropical fish and invertebrates (Wenner et al. 1984; SAFMC 1998a). Estuarine-dependent species in the nearshore ocean, such as black sea bass and southern flounder, have a broader temperature tolerance (Reagan and Wingo 1985; Steimle et al. 1999). Research in North Carolina marine waters has found that fish species composition over hardbottom shifted during a 15-year period, with an increase in tropical species and decrease in temperate species (Parker and Dixon 1998). The change in species composition was associated with global warming trends.

Species- and life-stage-specific patterns of water column habitat utilization are not well known for most fishes. Some utilize nearshore fronts as feeding or nursery habitats (e.g., *Anchoa*, *Scomberomorus*); others utilize offshore fronts (e.g., *Coryphaena*, *Xiphius*). Important spawning locations include estuarine fronts (e.g., *Cynoscion*, *Sciaenops*), the mid-shelf front (e.g., *Micropogonias*, *Leiostomus*, *Paralichthys*), and the Gulf Stream front (e.g., *Coryphaena*, *Xiphius*). Studies have shown an accumulation of fish larvae in these shelf fronts (Govoni 1993). Movement of the Gulf Stream front also affects the distribution of adult fishes (Magnuson et al. 1981) and hook and line fishermen and longliners target much of their effort for pelagic species in these frontal zones. In addition, the quasi-permanent gyres which impinge upon the shelf near the Florida Keys and downstream from the Charleston Bump probably serve as important spawning/larval retention habitat for a variety of fishes including (Collins and Stender 1987; Lee et al.1994). The region known as "The Point" off Cape Hatteras supports an unusually high biomass of dolphin and wahoo and other upper trophic level predators, including many important pelagic fishes. It has been suggested that the area is the most productive sport fishery on the east coast targeting dolphin, wahoo, and other pelagic species including billfish (Ross 1989).

Common, year-round residents of the nearshore marine zone include bottom fish such as black sea bass, gag, kingfishes, dogfish sharks, and summer flounder, along with more pelagic species like Spanish mackerel, king mackerel, cobia, silversides, and bluefish. Juveniles and adults of these species are also common in the high-salinity estuarine zone (NOAA 2001). Many high-salinity estuarine species are also found in the nearshore ocean (e.g., red drum, spotted seatrout, weakfish, black drum). During late fall and winter, the nearshore marine zone is flooded with adult offshore spawning estuarine species like southern flounder, Atlantic croaker, spot, shrimp, striped mullet, and Atlantic menhaden. Florida pompano and Gulf kingfish are common species in the nearshore marine zone (primarily during the summer).

Marine water column as Essential Fish Habitat

Due to their important ecological function, areas of the offshore pelagic environments discussed above and the associated benthic habitats have been designated essential fish habitat-habitat areas of particular concern (EFH-HAPC) (SAFMC 1998b). These include The Point, The Ten-Fathom Ledge, and Big Rock (North Carolina); The Charleston Bump and the Georgetown Hole (South Carolina); for species in the Snapper Grouper complex, Coastal Migratory Pelagic species including dolphin and Coral and Live/Hardbottom Habitat. Additional EFH-HAPCs were designated for Coastal Migratory Pelagics including: Amberjack Hole (The Point) off Jupiter Inlet (Florida); The Hump off Islamorada, Florida; The Marathon Hump off Marathon, Florida; and The "Wall" off of the Florida Keys. These areas are productive and highly dynamic oceanic areas. A quasi-permanent cyclonic eddy with, attendant upwelling of nutrient-rich deepwater, sets up in the wake of the Charleston Bump. Upwelling results in persistent primary and secondary production that may well result in an important, if not essential feeding environment for the larvae of fishes that congregate to spawn there. The hydrodynamics of the eddy may serve in the retention of fish propagules that are lost from local populations elsewhere through entrainment into the Gulf Stream. “The Point” off Cape Hatteras is also highly productive due to the confluence of as many as four water masses. Adults of highly migratory species congregate in this area, while the diversity of larval fishes found there is truly astounding (SAFMC, 1998b). Other water column habitats with high production or dynamic bottom habitats include “Big Rock” and “The Ten Fathon Ledge.” Other areas where water flow is affected by bottom habitat concentrating bait and increasing availability of pelagic habitat like *Sargassum*, include “The Georgetown Hole” off South Carolina.

3.3.4 Marine Soft Bottom

Description and distribution

(from NC CHPP)

Ocean intertidal beaches and subtidal bottom

The seafloor off the North Carolina coast is part of the Atlantic continental shelf, which slopes gradually from the coastline before dropping off steeply at approximately the 160–250 ft (50–75 m) isobath where the continental slope begins. In North Carolina, the continental shelf is relatively narrow, approximately 16 mi (30 km) off Cape Hatteras, 32 mi (60 km) off Cape Lookout, and about 49 mi (90 km) off Cape Fear. Water depth at the seaward limit of state territorial waters ranges from 50–70 ft (15–21 m). Because North Carolina is located at a transition between two major physiographic and zoogeographic zones, the marine subtidal bottom supports a high diversity of invertebrates.

North of Cape Hatteras, the shoreline and adjacent shoals tend to be linear, the shelf is relatively steep, and the bottom consists of a regional depositional basin known as the Albemarle Embayment, resulting in few exposed rock outcrops. Several prominent shoals, such as Wimble, Kinnekeet, and Platt shoals, also occur in this region, as well as a series of prominent ridges and swales that are spaced about 1,300–2,000 ft (400–600 m) apart, with mean relief of 3–23 ft (1–7 m), averaging 6–10 ft (2–3 m) in height (Inman and Dolan 1989; Rice et al. 1998). Shoals closest to shore, such as Wimble and Kinnekeet shoals, tend to be oriented at a 20–30 degree angle from the coastline, while those farther offshore run more parallel to the coast (MMS 1993).

The coastline south of Cape Hatteras consists of a series of arcs, dominated by three major capes (Hatteras, Lookout, and Fear) and three associated bays (Raleigh, Onslow, and Long). Long Bay continues into South Carolina to Cape Romain. Large shoals extend across the shelf from each cape (Diamond, Lookout, and Frying Pan shoals) for more than 11 mi (20 km). South of Cape Hatteras, the continental shelf has a greater amount of exposed rock outcroppings and is intersected with younger sediments originating from filled ancient river valleys (Riggs et al. 1995).

The continental shelf off North Carolina has a relatively low supply of incoming sand, due to low direct river input, entrapment of most river-borne sediment in the upper estuaries and sounds, and minimal sediment exchange between adjacent shelf embayments (Riggs et al. 1998). The shoreface is the generally concave, upward surface extending from the surf zone to the point where the slope matches that of the continental shelf (Thieler et al. 1995). The base of the shoreface off North Carolina occurs at approximately 33–40 ft (10–12 m) water depth. The shoreface represents the area of active beach sand movement. Six classes of shoreface systems were recognized by Riggs et al. (1995) based on differences in the underlying geology. The nature of these shorefaces affects the geologic composition of the surface and underlying substrate of the subtidal bottom and shoreline and partially explains the patterns of localized erosion or deposition.

The intertidal zone of oceanfront barrier island beaches is the area periodically exposed and submerged by waves, varying with frequency and with lunar tide cycles. In this high energy area, waves continually rework and sort sediment by grain size. The uprush of water carries sediment onto the beach, with larger sediments deposited first and finer-grained sediment carried farther landward. The backwash carries some sediment back into the water. Because of this regular high wave energy, as well as occasional storm events associated with extreme wave action, the intertidal beach and surf zone typically have rapid scour and fill events. The sediments are generally much coarser, more highly sorted, and contain less organic matter than in protected estuarine intertidal flats (Donoghue 1999).

The surf zone is the shallow subtidal area of breaking waves seaward of the intertidal beach. Within the surf zone, longshore sandbars frequently develop and shift seasonally in response to wave energy. Seaward of the surf zone, the subtidal bottom consists of a series of minor ridges and swales. Ripple scour depressions, ranging from 130–330 ft (40–100 m) in width and up to 3 ft (1 m) in depth, occur along the southern portion of the coast and are perpendicularly oriented to the beach, extending to the base of the shoreface (Thieler et al. 1995; Reed and Wells 2000). These features are located adjacent to areas experiencing chronic severe beach erosion, and may be indicative of rapid offshore transport of sand during storms (Thieler et al. 1995).

Three major shoals extend perpendicular to Cape Hatteras, Cape Lookout, and Cape Fear: Diamond Shoals, Cape Lookout Shoals, and Frying Pan Shoals, respectively. Water depth on the shoals ranges from 2–18 ft (0.6–5.5 m), in contrast to adjacent waters that are 20–40 ft (6–12 m) deep. Due to an interest in beach nourishment projects for Dare County, Boss and Hoffman (2000) collected detailed information on the sand resources of North Carolina's Outer Banks, including specific data about Diamond Shoals. Diamond Shoals extend approximately 11 nautical miles (nm) (20 km) and are about 5.5 nm (11 km) wide. The estimated total volume of sand on the shoal was at least 1.66 billion cubic yards, with approximately 256 million cubic yards within state waters (Boss and Hoffman 2000). As such, cape shoals are major sand resources for coastal processes. Detailed mapping of the bottom has been done in other areas of the coast to varying extent with different techniques. The results of these studies need to be compiled in a comprehensive and comparable manner to evaluate changes and trends in substrate character, as well as the feasibility of beach nourishment projects.

Ecological role and function

(from CHPP)

Several species of sharks pup in North Carolina's nearshore ocean waters. North of Cape Hatteras, pupping of spiny dogfish over subtidal bottom has been documented in winter months (W. Laney, USFWS, pers. com. 2003). Subtidal bottom in the southern portion of North Carolina state waters serves as pupping grounds for the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), bonnethead shark (*Sphyrna tiburo*), blacknose shark (*Carcharhinus acronotus*), spinner shark (*C. brevipinna*), dusky shark (*C. obscurus*), and, to a lesser extent, blacktip shark (*C. limbatus*), sandbar shark (*C. plumbeus*), and scalloped hammerhead shark (*S. lewini*). Most neonate (newborn) sharks were found in June and July (Beresoff and Thorpe 1997; Thorpe et al. 2003).

Most ocean spawning activity by estuarine dependent species occurs beyond state waters during the winter months. However, eggs and larvae are carried in the water column by currents through nearshore state waters and inlets to estuarine nursery areas. Important spawning aggregations of summer flounder occur on Wimble, Platt, and Kinnekeet shoals off the Outer Banks, in state and federal waters from November to March, peaking near January in North Carolina (MAFMC 1998). Locations of summer flounder spawning aggregations are linked to environmental conditions, such as water temperature and wind direction, and are generally concentrated north of Cape Hatteras, but extend to Cape Lookout.

Nearshore ocean subtidal bottom is also a nursery area for summer flounder and shark species. The primary nursery grounds for coastal shark species is in the vicinity of where pupping occurs. Small coastal sharks that use this habitat for a nursery area include spinner (*C. brevipinna*), blacknose (*C. acronotus*), and dusky (*C. obscurus*) sharks (Beresoff and Thorpe 1997; Thorpe et al. 2003). Juvenile Atlantic sturgeon and spiny dogfish, both demersal feeders with overfished fishery status, have been documented over nearshore subtidal bottom between Oregon Inlet and Kitty Hawk during winter months (Cooperative Striped Bass Tagging Program, unpub. data). Subtidal bottom, particularly the surf zone, is also a nursery area for Florida pompano, southern and gulf kingfish (Hackney et al. 1996).

Species composition and community structure

On oceanfront beaches, most benthic animals in the intertidal zone consist of infaunal burrowing forms. A diverse assemblage of meiofauna (0.06 – 0.4 mm in size) occurs in the lower beach community and acts as an important food source for many juvenile fish (Levinton 1982; Hackney et al. 1996). A relatively low diversity of macrofauna (>0.5 mm in size) (~ 20 – 50 species) exists in the intertidal beach compared to estuarine intertidal flats (~ 300 – 400 species) (Hackney et al. 1996). The dominant macrofauna by biomass in North Carolina's oceanfront intertidal beaches are mole crabs (*Emerita talpoida*) and coquina clams (*Donax variablis*, *D. parvula*) (Hackney et al. 1996; Donoghue 1999). Several species of amphipods and the spionid polychaete (*Scolelepis squamata*) have been reported as highly abundant on some beaches as well (Lindquist and Manning 2001).

Polychaete worms, isopods, mollusks, echinoderms, amphipods, and other crustaceans occur in sediments in the oceanfront intertidal beaches, cape and ebb tide shoals, surf zone and other subtidal bottom (Jutte 1999; Peterson et al. 1999). Three general groups of polychaetes occur in intertidal beaches (Hackney et al. 1996): 1) burrowing deposit feeders, including thread worms (*Lumbrineris* sp., *Scolelepsis* sp.), and red-lined worms (*Nepthys* sp.); 2) suspension feeders; and 3) tube building burrow dwellers, such as plumed worms (*Diopatra* sp.) and lugworms (*Arenicola* sp.). Offshore sand bottom communities along the North Carolina coast are relatively diverse habitats containing over a hundred polychaete taxa (Lindquist et al. 1994; Posey and Ambrose 1994). Tube dwellers and permanent burrow dwellers are important benthic prey for fish and epibenthic invertebrates. These species are also most susceptible to sediment deposition, turbidity, erosion, or changes in sediment structure associated with sand mining activities, compared to other more mobile polychaetes (Hackney et al. 1996). In South Carolina, 243 species of benthic invertebrates were documented in the nearshore subtidal bottom (Van Dolah et al. 1994). Polychaetes and amphipods were the most abundant, although oligochaetes, bivalves, and crabs were also highly represented (Van Dolah et al. 1994). On ebb tide deltas, polychaetes, crustaceans (primarily amphipods), and mollusks (primarily bivalves) were the most abundant infauna, while decapod crustaceans and echinoderms (sand dollars) dominated the epifauna. Because periodic storms can affect benthic communities along the Atlantic coast to a depth of about 115 ft (35 m), the soft bottom community tends to be dominated by opportunistic taxa that are adapted to recover relatively quickly from disturbance (Posey and Alphin 2001). Many faunal species documented on the ebb tide delta are important food sources for demersal predatory fishes and mobile crustaceans, including spot, croaker, weakfish, red drum, and penaeid shrimp. These fish species congregate in and around inlets during various times of the year (Peterson and Peterson 1979), presumably to enhance successful prey acquisition and reproduction.

Ocean subtidal bottom serves as important foraging grounds for numerous fish species, particularly for Florida pompano, red drum, kingfish, spot, and Atlantic croaker, weakfish, and striped bass. Many commercially or recreationally important fish and invertebrate species, such as red drum, striped bass, shrimp, and summer flounder, are caught while they aggregate and feed over subtidal bottom in nearshore ocean waters. These species appear to be strongly associated with distinct topographic features of the subtidal bottom, such as the cape shoals, channel bottoms, sandbars, and sloughs. The natural processes that create these features need to be maintained.

The food resources present in and on soft bottom are needed to support hardbottom fish species. Demersal zooplankton and infaunal macroinvertebrates from sand substrate have been found to be a quantitatively important component of many species' diets and an important link to reef fish production (Cahoon and Cooke 1992; Thomas and Cahoon 1993; Lindquist et al. 1994). Reef species documented foraging over sand bottom away from the reef include tomtate (*Haemulon aurolineatum*), whitebone porgy (*Calamus leucosteus*), cubbyu (*Equetus umbrosus*), black sea bass (*Centropristis striata*), and scup (*Stenotomus chrysops*) (Lindquist et al. 1994). Therefore, benthic microalgal production on the subtidal bottom of Onslow Bay, as well as other similar shelf habitats, is an important component to the continental shelf productivity and is an important link to the ecology of hardbottom habitats.

4.0 Species' Biology, Distribution and Status

4.1 Species under management by the South Atlantic Council

4.1.1 Penaeid and Deepwater Shrimp

4.1.1.1 Penaeid Shrimp

Description and distribution

The shrimp fishery management unit in the South Atlantic includes six species: brown shrimp (*Farfantepeneaus aztecus*), pink shrimp (*Farfantepenaeus duorarum*), white shrimp (*Litopenaeus setiferus*), seabob shrimp (*Xiphopenaeus kroyeri*), rock shrimp (*Sicyonia brevirostris*), and royal red shrimp (*Pleoticus robustus*). The shrimp species of the southeastern U.S. occupy similar habitats with the greatest differences being in optimal substrate and salinity.

White shrimp

Common names for the white shrimp (Figure 4.1-1) include gray shrimp, lake shrimp, green shrimp, green-tailed shrimp, blue tailed shrimp, rainbow shrimp, Daytona shrimp, common shrimp, and southern shrimp.

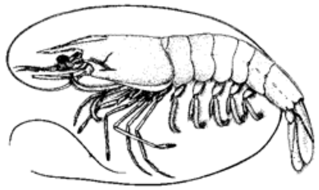


Figure 4.1-1. White shrimp, *Litopenaeus setiferus* (Williams 1984).

White shrimp range from Fire Island, New York to St. Lucie Inlet on the Atlantic Coast of Florida. Along the Atlantic Coast of the U.S., the white shrimp has centers of abundance in South Carolina, Georgia, and northeast Florida. White shrimp are generally concentrated in waters of 27 m (89 ft) or less, although occasionally found much deeper (up to 270 ft).

Brown shrimp

The **brown shrimp** (Figure 4.1-2) is also known as brownie, green lake shrimp, red shrimp, redtail shrimp, golden shrimp, native shrimp, and also the summer shrimp in North Carolina.

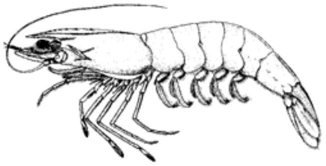


Figure 4.1-2. Brown shrimp, *Farfantepenaeus aztecus* (Williams 1984).

On the Atlantic Coast, brown shrimp occur from Martha's Vineyard, Massachusetts to the Florida Keys. While it may occur seasonally along the Mid-Atlantic states, breeding populations apparently do not range north of North Carolina. The species may occur in commercial quantities in waters as deep as 110 m (361 ft), but they are most abundant in water less than 55 m (180 ft).

Pink shrimp

Other names for the **pink shrimp** (Figure 4.1-3) include spotted shrimp, hopper, pink spotted shrimp, brown spotted shrimp, grooved shrimp, green shrimp, pink night shrimp, red shrimp, skipper, and pushed shrimp.

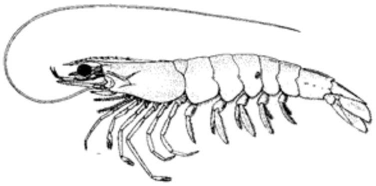


Figure 4.1-3. Pink shrimp, *Farfantepenaeus duorarum* (Williams 1984).

Along the Atlantic, pink shrimp occur from southern Chesapeake Bay to the Florida Keys. Maximum abundance is reached off southwestern Florida. Pink shrimp are most abundant in waters of 11-37 m (36-121 ft) although in some areas they may be abundant as deep as 65 m (213 ft). Pink shrimp are common in the estuaries and shallow marine waters surrounding southern Florida and into deepwater (approximately 100 meters) southeast of the Keys, and are the dominant species within the Dry Tortugas shrimping grounds and Florida Bay (Solamon 1968).

Seabob shrimp

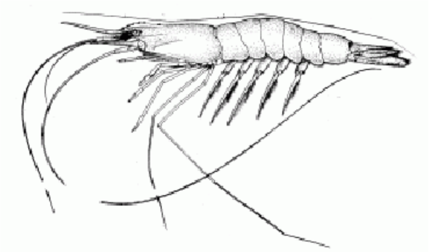


Figure 4.1-4. Seabob shrimp, *Xiphopenaeus kroyeri* (FAO FIGIS Species Factsheet 2007. Available online at http://www.fao.org/fi/website/FIRetrieveAction.do?dom=species&fid=2600)

Seabob shrimp (Figure 4.1-4) range from North Carolina to Estado de Santa Catarina (Brazil). Seabobs inhabit waters from 1 to 70 m, usually less than 27 m over mud or sand bottom. They are found in marine, brackish and exceptionally fresh waters and are most plentiful in areas near river estuaries. This species is of limited commercial importance off the southeast Atlantic coast (see William, 1984 for review). Burkenroad (1949) found ripe or nearly ripe females off North Carolina in May. Information on the biology of seabob shrimp is scant so the discussion in following sections pertains only to the other three penaeid species in the management unit.

Reproduction

White Shrimp

White shrimp attain sexual maturity at about 35-140 mm (5.3-5.5 in) total length (TL). Fecundity for all penaeid species ranges from 500,000 to 1,000,000 ova. Eggs are demersal (sink to the bottom) and measure 0.28 mm in diameter (SAFMC 1996b).

Off Georgia and northern Florida, some white shrimp spawning may occur inshore, although most spawning occurs more than 1.2 miles from the coastline. Off Florida, spawning occasionally takes place inshore, at or near inlets, but most occurs offshore in depths of 6.1 to 24.4 m (20-80 ft). In South Carolina, most spawning occurs within about four miles of the coast. Spawning is correlated with bottom water temperatures of 17° to 29°C (62.6 to 84.2° F) although spawning generally occurs between 22° and 29°C (71.6 and 84.2° F). White shrimp begin spawning during April off Florida and Georgia, and late April or May off South Carolina (Lindner and Anderson 1956). Spawning may continue into September or October (SAFMC 1996b).

Brown shrimp

Similar to white shrimp, brown shrimp reach sexual maturity at about 140 mm TL (5.5 in). Eggs are demersal and measure 0.26 mm in diameter (SAFMC 1996b).

Brown shrimp spawn in relatively deep water. In the Gulf of Mexico, it was concluded that brown shrimp did not spawn in water less than 13.7 m (45 ft) deep and the greatest percentage of ripe females were at 45.7 m (150 ft) (Renfro and Brusher 1982). Spawning season for brown shrimp is uncertain, although there is an influx of postlarvae into the estuaries during February and March (Bearden 1961; DeLancey et al. 1994). Mature males and females have been found off South Carolina during October and November (SAFMC 1996b).

Pink Shrimp

Pink shrimp reach sexual maturity at about 85 mm TL (3.3 in). Eggs are demersal measuring 0.31-0.33 mm in diameter (SAFMC 1996b).

Pink shrimp apparently spawn at depths of 3.7 to 15.8 m (12 to 52 ft). Off eastern Florida, peak spawning activity probably occurs during the summer. In North Carolina, roe-bearing females are found as early as May, and by June, most pink shrimp are sexually mature (Williams 1955).

Development, growth and movement patterns

All three penaeid species have 11 larval stages before developing into postlarvae. Duration of the larval period is dependent on temperature, food and habitat. Records suggest larval periods of 10 to12 days for white shrimp, 11 to 17 days for brown shrimp and 15 to 25 days for pink shrimp. Brown shrimp postlarvae appear to overwinter in offshore bottom sediments. Postlarval sizes are similar for white and pink shrimp ranging from approximately 2.9 to 12 mm TL (0.1-0.5 in); brown shrimp are usually larger (SAFMC 1996b).

The mechanisms that transport penaeid shrimp postlarvae from distant spawning areas to inside estuaries are not well known. Shoreward countercurrents north of Cape Canaveral have been suggested as a mechanism for transport of pink shrimp postlarvae from spawning areas to nursery areas along the northeast Florida coast (Kennedy and Barber 1981). Favorable winds may enhance movement of postlarvae toward oceanic inlets (Wenner et al. 1998).

White shrimp

Movement of white shrimp postlarvae into the estuary is most likely a result of nearshore tidal currents as white shrimp spawn relatively close to shore. In the South Atlantic, white shrimp enter the estuaries at about the same time as pink shrimp, usually beginning in April and early May in the southern part of their range and in June and July in North Carolina sounds where white shrimp are relatively less abundant than in more southern states.

Smaller (juvenile and subadult) individuals may overwinter inside estuaries forming part of the overwintering stock (SAFMC 1996b). Harsh winter conditions such as cold water temperatures and rainfall can affect the survival of overwintering stocks and subsequent year-class strength.

Large white shrimp begin emigrating out of the estuary to the commercial fishing areas in mid-summer. In North Carolina, white shrimp begin entering the commercial fishery in July and continue to be caught through December (Williams 1955). In Florida, white shrimp leave inshore waters at about 120 mm TL (4.7 in). This movement to offshore waters may be caused by cold weather, storms, high tides and/or large influxes of fresh water, but size is the principal determinant (SAFMC, 1996b). The migrating white shrimp, called roe shrimp, make up the spring fishery and also produce the summer and fall crops of shrimp. When a majority of white shrimp do not survive the winter, the North Carolina and South Carolina fisheries are believed to be dependent on a northward spring migration of white shrimp from more southerly areas to form the spawning stock. However, tagging data are inconclusive on the extent of this northward movement, and recruitment of postlarvae from southern spawning stocks may account for much of the replenishment of the populations.

White shrimp grow from 1.0 to 2.3 mm (0.04 to 0.09 in) per day (SAFMC 1993). Salinity is a factor determining growth rate in white shrimp. Although field studies indicate that juvenile white shrimp prefer low salinities, laboratory studies have revealed that they tolerate a wide range of salinities; they have been successfully reared at salinities of 18 to 34 ppt (Perez-Farfante 1969). Nevertheless, McKenzie and Whitaker (1981) cited several studies in which fast growth was reported for white shrimp at lower salinities of 7 to 15 ppt. The lowest salinity in which white shrimp were recorded in the northern Gulf of Mexico was 0.42 ppt (Perez-Farfante 1969). High salinities appear to inhibit growth in white shrimp, but for brown shrimp, salinities in excess of 10 ppt seem to enhance growth rate. Relatedly, during years of low densities, the average size of white shrimp is generally larger.

Water temperature directly or indirectly influences white shrimp spawning, growth, habitat selection, osmoregulation, movement, migration and mortality (Muncy 1984). Spring water temperature increases trigger spawning, and rapid water temperature declines in fall portend the end of spawning (Lindner and Anderson 1956). Ingress of white shrimp postlarvae has also been linked to temperature (Wenner et al. 2002). Growth is fastest in summer and slowest or negligible in winter. Water temperatures below 20°C (68°F) inhibit growth of juvenile shrimp (Etzold and Christmas 1977) and growth is virtually nil at 16°C (61°F) (St. Amant and Lindner 1966). Growth rates increase rapidly as temperatures increases above 20°C (68°F). Temperature and food supply limited the growth of white shrimp postlarvae more than did salinity differences between 2 and 35 ppt (Zein-Eldin 1964). Freshwater inflow may affect coastal water temperatures, which in turn affect the growth rates (White and Boudreaux 1977) and migration of white shrimp (Shipman 1983b). Increased water temperatures also affect molting rate (Perez-Farfante 1969)

Brown shrimp

Movement of brown shrimp appears to take place primarily at night with peak movement at, or shortly after dusk. In the South Atlantic, juvenile and adult brown shrimp are rarely affected by severe winter weather because most surviving shrimp have moved offshore prior to the onset of cold weather (SAFMC 1996b). Brown shrimp first enter the commercial fishery in North Carolina in June at about 100 mm TL (4 in).

Brown shrimp grow 0.5 to 2.5 mm (0.02 – 0.1 in) per day (SAFMC 1993). Salinity is a factor determining growth rate in brown shrimp. Temperature also affects brown (and pink) shrimp growth rates, with rates as high as 3.3 mm (0.13 in) per day recorded when temperature exceeded 25°C (77° F) but less than 1.0 mm (0.04 in) per day when water temperature was below 20°C (68° F). Gaidry and White (1973) stated that years of low commercial landings of brown shrimp were associated with prolonged estuarine temperatures of less than 20°C (68°F) at the time of postlarval immigration into the estuary. Aldrich et al. (1968) demonstrated in laboratory experiments that brown shrimp postlarvae burrowed in the sediment when water temperature was reduced to 12°-16.5°C (54°-62°F). Brown shrimp postlarvae may overwinter in offshore waters and migrate into estuaries the following spring (Aldrich et al., 1968).

Pink shrimp

Pink shrimp leave Florida estuaries two to six months after having arrived as postlarvae. In North Carolina, young pink shrimp enter the commercial catch in August. Recruitment to the area offshore of Cape Canaveral begins in April and May and again during October and November (SAFMC 1996b). In North Carolina, pink shrimp begin entering the estuaries in June and July. In Florida, larvae can take two routes to the estuarine nursery areas where they spend most of their life cycle. One route is directly to the shallow-water estuaries of 10,000 Island, Whitewater Bay, and Florida Bay. On the other route, larvae are swept southwesterly into the Florida Current by way of the Loop Current, and are carried northeasterly along the outer edge of the Florida Reef Tract or east coast of Florida (Ingle et al. 1959).

Pink shrimp that overwinter inside estuaries are susceptible to mortality induced by cold weather. However, pink shrimp bury deeply in the substrate with the onset of cold weather and are protected to some extent from winter mortalities (Purvis and McCoy 1972). Pink and white shrimp that survive the winter grow rapidly in late winter and early spring before migrating to the ocean. Pink shrimp that overwinter in estuaries migrate to sea in May and June, at which time spawning takes place. Recruitment to the area offshore of Cape Canaveral begins in April and May and again during October and November (SAFMC 1996b).

Pink shrimp grow 0.25 to 1.7 mm (0.01 – 0.07 in) per day (SAFMC 1993). In Florida Bay, pink shrimp were found to grow 3.5 mm Carapace Length (CL) (0.14 in) in winter and only 1.9 mm CL (0.07 in) in spring (SAFMC 1993). In North Carolina, maximum pink shrimp growth rates were recorded in summer (SAFMC 1993).

Ecological relationships

The inshore phase of the penaeid life cycle is perhaps the most critical because this is a period of rapid growth. Estuarine nursery areas, dominated by the marsh grass, *Spartina alterniflora*, provide abundant food, suitable substrate, and shelter from predators for postlarval shrimp.

Juvenile shrimp appear to be most abundant at the *Spartina* grass-water interface. This "estuarine edge" is the most productive zone in many estuaries. Because there is a minimum of wind generated turbulence and stabilization of sediments, rich bands of organic material are found along the edges of marshes (Odum 1970). Furthermore, Odum (1970) found the percentages of organic detritus in sediments along the shore in the Everglades estuary are several times greater than a few meters offshore. Mock (1967) examined two estuarine habitats, one natural and one altered by bulkheading. He found a 0.6 m (2 ft) band of rich organic material along the natural shore and very little organic material along the bulkheaded shore. White shrimp were 12.5 times and brown shrimp 2.5 times more numerous in the natural area as in the altered area. Loesch (1965) found that juvenile white shrimp in Mobile Bay were most abundant nearshore in water less than 0.6 m (2 ft) deep containing large amounts of organic detritus. Brown shrimp were congregated in water 0.6 to 0.9 m (2-3 ft) deep where there was attached vegetation.

White shrimp appear to prefer muddy or peaty bottoms rich in organic matter and decaying vegetation when in inshore waters. Offshore they are most abundant on soft muddy bottoms (Lindner and Cook, 1970). Brown shrimp appear to prefer a similar bottom type and as adults may also be found in areas where the bottom consists of mud, sand, and shell. Pink shrimp are found most commonly on hard sand and calcareous shell bottom (Williams 1955, 1984). Both brown and pink shrimp generally bury in the substrate during daylight, being active at night. White shrimp do not bury with the regularity of pink or brown shrimp.

Juvenile and adult penaeids are omnivorous (eating both plants and animals) bottom feeders, with most feeding activity occurring at night, although daytime feeding may occur in turbid waters (Darnell 1958; Broad 1965). Food items may consist of polychaetes, amphipods, nematodes, caridean shrimps, mysids, copepods, isopods, amphipods, ostracods, mollusks, foraminiferans, chironomid larvae, and various types of organic debris. In addition, aggregations of shrimp have been shown to increase community metabolism and inorganic nitrogen available to phytoplankton (Vetter and Hopkinson 1985).

Shrimp are preyed on by a wide variety of species at virtually all stages in their life history (Gunter 1957). Predation on postlarvae has been observed by sheepshead minnows, water boatmen, and insect larvae. Grass shrimp, killifishes, and blue crabs prey on young penaeid shrimp, and a wide variety of finfish are known to prey heavily on juvenile and adult penaeid shrimp (Minello and Zimmerman 1983).

Abundance and status of stocks

Population sizes of brown, pink, and white shrimp are believed to be primarily regulated by environmental conditions and available habitat. Penaeid (brown, pink and white) shrimp have an annual life cycle, where adults spawn offshore and the larvae are transported to coastal estuaries. Recruitment to the estuaries and eventually to the fishing grounds is extremely dependent on fluctuations of environmental conditions within estuaries. Poor recruitment to the fishery may occur because of excessively cold winters or heavy rains that reduce salinities and cause high mortality of post-larvae. Conversely, high recruitment to the fishery may occur when environmental conditions are favorable for postlarval development. Effort in the penaeid fishery has been relatively stable over the last 20 years; therefore, catches in any given year may show large fluctuations depending on the magnitude of successful recruitment of young shrimp as they emigrate from the estuaries to offshore waters.

Although shrimp trawling certainly reduces population size over the course of a season, the impact of fishing on subsequent year-class strength is unknown. Natural mortality rates are very high, and coupled with fishing mortality, most of the year class may be removed by the end of a season. Because annual variation in catch is presumed to be due to a combination of prevailing environmental conditions, fishing effort, price and relative abundance of shrimp (SAFMC 1996b), fishing is not believed to have any impact on subsequent year class strength unless the spawning stock has been reduced below a minimum threshold level by environmental conditions. Nevertheless, due to high fecundity and migratory behavior, the three penaeid species are capable of rebounding from very low population sizes in one year to large population sizes in the next, provided environmental conditions are favorable (SAFMC 1996b).

Fluctuations in abundance resulting from changes in environmental conditions will continue to occur. Perhaps the most serious potential threat to the stocks is loss of habitat due to pollution or physical alteration. For white and brown shrimp, salt marsh habitat is especially important as juvenile nursery areas. Inshore seagrass beds are important nursery areas for juvenile pink shrimp. The quality and availability of these habitat areas to the juvenile penaeid shrimp species is critical to overall shrimp production (SAFMC 1996b).

During years when inshore overwintering white shrimp stocks are greatly reduced due to cold water temperature or heavy rain, management action may accelerate recovery of the stocks and increase fall production by protecting the few remaining spawners that survive a freeze. Also, elimination of winter and spring fishing mortality off southern Georgia and Florida may enable a greater quantity of potential spawners to move north, possibly resulting in larger regional white shrimp stocks the following fall. An offshore or deep estuarine water reserve of overwintering white shrimp may also contribute significantly to the spawning stock. In either case, while fishing does not by itself appear to be a factor in determining subsequent year class strength for white shrimp, in years when the overwintering adult population is significantly reduced due to severe winter weather, the additional mortality caused by fishing can result in a further reduction in subsequent fall production (SAFMC 1996b).

(from Shrimp Amendment 6)
For the South Atlantic shrimp fishery, only historical catch records and limited effort information is available. Current data gaps preclude the estimation of B_{MSY}. Furthermore, because of high

fluctuations in annual recruitment and landings, F_{MSY}, or even F_{CURR}, cannot be estimated. This limited information makes it difficult to use standard procedures to establish an overfishing threshold based on F_{MSY}. Nevertheless, the Council has stated, that although estimates of population size are not available, effort in the fishery is known to be high and the fishery may be fishing at near-maximum levels. Therefore, it can be assumed to be operating at or near B_{MSY} and F_{MSY}. Based on that assumption, the Council has established targets and thresholds using annual landings as an indication of relative abundance (health) of the parent stock.

The limitation to this approach, especially for annual species such as shrimp, is its total dependence on catch, without accounting for external factors such as economic or social conditions that might influence the overall annual landings of a particular species. It is possible that the fishery might not target a species to the extent possible during a given year, and low landings could result from a lack of effort instead of a reduced stock size. Similarly, a stock might undergo a poor recruitment year, but still be relatively healthy, but reduced catch rates combined with economic or social factors might inhibit fishery effort on that stock, and annual landings would decline. Conversely, because of good prices or exceptionally good recruitment, landings might be exceptionally high during a given year, or two-year period. In either situation, the Council would want to further evaluate all the conditions before making a determination regarding the status of the stock, which could delay effective remedial action.

The National Standard Guidelines (50 CFR 600.310[c][2][i]) identify alternatives for establishing MSY to include removal of a constant catch each year that allows the stock size to remain above an identified lower level, or to allow a constant level of parent stock escapement each year. For penaeid shrimp stocks, it is appropriate to establish an MSY control rule based on maintaining a constant level of escapement each year that will produce sufficient recruits to maintain harvest at historical levels. This approach would relate MSY in terms of catch to a quantifiable level of escapement in each stock, where a proxy for B_{MSY} is established as the minimum parent stock size known to have produced MSY the following year. MFMT, as a fishing mortality that drives the stock below B_{MSY} in a given year when exceeded, would define overfishing. MSST, or the overfished level, would represent a biomass level lower than $0.5*B_{MSY}$ (i.e., one-half the parent stock size or other proxy). In other words, this would be an MSY control rule that relied on constant escapement of B_{MSY}.

In accordance with the Technical Guidelines (Restrepo et al., 1998), CPUE data can be used as a proxy for biomass-based parameters including B_{MSY} and current biomass. Until those data become available from the fishery, CPUE-based abundance estimates from fishery-independent Southeast Area Monitoring and Assessment Program - South Atlantic (SEAMAP-SA) data can serve as a proxy to indicate parent stock (escapement).

The SEAMAP-SA Shallow Water Trawl Survey is funded by NOAA Fisheries and conducted by the South Carolina Department of Natural Resources - Marine Resources Division (SCDNR-MRD). This survey provides long-term, fishery-independent data on seasonal abundance and biomass of all finfish, elasmobranchs, decapod and stomatopod crustaceans, sea turtles, horseshoe crabs and cephalopods that are accessible by high-rise trawls. Samples are taken by trawl from Cape Hatteras, North Carolina to Cape Canaveral, Florida. Cruises are conducted in spring (early April - mid-May), summer (mid-July - early August) and fall (October - mid-

November). Stations are randomly selected from a pool of stations within each stratum. Strata are delineated by the 4 m depth contour inshore and the 10 m depth contour offshore.

SEAMAP data for the period 1990-1992 indicate that the average escapement results in annual abundance estimates ranging from 1.975 to 10.277 shrimp per hectare for brown shrimp, 0.211 to 1.728 shrimp per hectare for pink shrimp and 5.665 to 34.799 shrimp per hectare for white shrimp (Table 4.1-1).

Table 4.1-1. Annual shrimp CPUE (nos/ha) estimates derived from the SEAMAP Shallow water Trawl Survey.

Year	Brown Shrimp	Pink Shrimp	White Shrimp
1990	4.022	0.568	9.028
1991	2.469	0.873	12.880
1992	2.000	0.511	5.868
1993	5.899	0.673	5.665
1994	5.568	0.594	10.606
1995	3.104	1.728	17.535
1996	10.277	0.461	12.913
1997	2.275	0.948	7.447
1998	1.975	0.853	18.256
1999	2.972	0.450	34.799
2000	7.697	0.211	13.060
2001	8.637	0.502	10.454
2002	3.347	0.867	9.186
2003	9.640	0.418	7.372

Because of their high sensitivity to certain environmental factors, South Atlantic shrimp show extreme fluctuations in population size. Annual sampling of shrimp from the southeast region indicate that density per hectare have varied by a factor of 5 to 10 and can more than double from one year to the next (Table 4.1-1).

The current stock status determination criteria for white, brown and pink shrimp were calculated from landings information. The data used to generate these parameters are presented in Table 4.1-2. These landings statistics were compiled in the original plan and Amendment 2 to the South Atlantic Shrimp Plan (SAFMC 1993; SAFMC 1996b).

Table 4.1-2. Landings data used to calculate the current MSY values for the penaeid species in the South Atlantic. (SAFMC 1996b).

Year	White Shrimp	Brown Shrimp	Pink Shrimp
1957	14,712,461	9,740,164	2,157,243
1958	11,092,893	9,189,603	823,467
1959	12,823,217	9,434,893	2,061,216
1960	18,788,016	9,038,236	1,226,496
1961	14,033,378	2,495,614	1,747,822
1962	12,133,840	11,532,694	2,246,510

1963	7,268,926	7,646,291	554,339
1964	8,119,217	7,089,616	1,948,048
1965	16,304,005	8,126,345	1,687,237
1966	9,162,164	11,604,450	531,230
1967	10,902,104	7,978,838	1,579,998
1968	16,945,887	5,919,510	1,337,930
1969	16,914,732	8,570,168	1,698,021
1970	12,491,819	7,133,124	860,584
1971	18,810,304	9,764,458	1,914,656
1972	16,635,560	7,725,422	788,277
1973	18,241,500	4,502,900	1,518,395
1974	13,375,345	11,088,656	2,118,261
1975	15,910,990	6,713,349	2,015,874
1976	14,370,316	9,651,432	1,815,048
1977	4,961,115	10,605,268	801,227
1978	8,913,478	6,601,646	561,297
1979	17,014,249	6,643,381	1,775,764
1980	14,255,717	13,368,442	1,573,926
1981	8,367,526	4,372,667	871,121
1982	10,517,276	8,915,451	1,749,785
1983	12,404,793	6,711,871	2,699,625
1984	4,088,105	7,209,256	1,391,292
1985	7,727,811	16,318,704	1,438,953
1986	10,968,861	8,702,924	2,101,628
1987	13,086,952	3,024,169	3,139,447
1988	10,909,691	8,143,448	2,929,585
1989	13,851,605	9,231,743	3,393,081
1990	12,613,723	8,734,294	1,651,188
1991	18,272,539	10,680,481	2,699,144

White shrimp

Maximum Sustainable Yield

The existing definition of MSY established by the original Shrimp Plan was calculated as mean total landings for the South Atlantic during 1957 to 1991 adjusted for recreational landings. In calculating total landings, an additional ten percent (an estimate made by state shrimp biologists) was added to the commercial catch to account for recreational landings that were unreported. There were other adjustments based on more accurate recreational landings information when the shrimp baiting permit went into effect in South Carolina. Using this methodology, MSY is estimated to be 14.5 million pounds for white shrimp (SAFMC 1993).

Optimum Yield

OY for the white shrimp fishery is defined as the amount of harvest that can be taken by U.S. fishermen without reducing the spawning stock below the level necessary to ensure adequate reproduction. This level has been estimated only for the central coastal area of South Carolina, and only in terms of subsequent fall production (assumed to represent recruitment). Therefore, in actual application, OY for the white shrimp fishery is the amount of harvest that can be taken by the U.S. fishery during the fishing season which may vary from year to year based on both state regulations and regulations promulgated pursuant to the Shrimp FMP (i.e., closures due to cold kills) (SAFMC 1993).

Overfished Definition

The Council has not established an overfished definition for white shrimp. Nevertheless, the overfishing definition, indicating when population sizes have declined below a minimum threshold would also represent an overfished definition.

Overfishing Definition

Overfishing is indicated when the overwintering white shrimp population within a state's waters declines by 80% or more following severe winter weather resulting in prolonged cold water temperatures. Continued fishing following such a decline may reduce the reproductive capacity of the stock affecting subsequent recruitment and would be considered overfishing. Relative population abundance will be determined by catch per unit effort (CPUE) during standardized assessment sampling (SAFMC 1993).

Brown shrimp

Maximum Sustainable Yield

The existing definition of MSY established by the original Shrimp Plan was calculated as the mean total landings for the South Atlantic during 1957 to 1991 adjusted for recreational landings. In calculating total landings, an additional ten percent (an estimate provided by state shrimp biologists) was added to the commercial catch to account for recreational landings that are unreported. Using this methodology, MSY was estimated to be 9.2 million pounds for brown shrimp (SAFMC 1993).

Optimum Yield

OY for brown shrimp was defined in Amendment 2 to the Shrimp Plan as the amount of harvest that can be taken by U.S. fishermen without annual landings falling two standard deviations below the mean landings during 1957 through 1993 for three consecutive years (SAFMC 1996b). This value is 2,946,157 pounds (heads on).

Overfished Definition

The South Atlantic brown shrimp resource is considered to be overfished when annual landings fall below two standard deviations below mean landings for the period 1957 to 1993 for three consecutive years (2,946,157 pounds (heads on)). The brown shrimp stocks in the South Atlantic are not considered overfished. Annual production appears to be most influenced by late winter and early spring environmental conditions as has been observed in the Gulf of Mexico (SAFMC 1996b).

Overfishing Definition

The Council has not established an overfishing definition for brown shrimp. If landings fall below the overfished threshold, it can be assumed that overfishing is also occurring.

Pink shrimp

Maximum Sustainable Yield

The existing definition of MSY established by the original Shrimp Plan was calculated as mean total landings for the South Atlantic during 1957 to 1991 adjusted for recreational landings. In calculating total landings, an additional ten percent (an estimate provided by state shrimp biologists) was added to the commercial catch to account for recreational landings that are unreported. Using this methodology, MSY was estimated to be 1.8 million pounds for pink shrimp (SAFMC 1993).

Optimum Yield
OY for pink shrimp was defined as the amount of harvest that can be taken by U.S. fishermen without annual landings falling two standard deviations below the mean landings during 1957 through 1993 for three consecutive years. This value is 286,293 pounds (heads on) for pink shrimp (SAFMC 1996b).

Overfished Definition
The South Atlantic pink shrimp resource is overfished when annual landings fall below two standard deviations below mean landings during 1957 to 1993 for three consecutive years (286,293 pounds (heads on)). There are indications that pink shrimp abundance may be reduced by prolonged cold water conditions. However, unlike with white shrimp, there does not appear to be a biological justification for closing the fishery following cold kills. It is believed that overwintering shrimp that are not harvested before reaching the ocean may simply be lost to the fishery. Further, being at the northern end of their range, larvae produced by overwintering North Carolina pink shrimp may be carried north by prevailing currents and lost to the system (SAFMC 1993).

Overfishing Definition
The Council has not established an overfishing definition for pink shrimp. If landings fall below the overfished threshold, it can be assumed that overfishing is also occurring.

4.1.1.2 Deepwater Shrimp

Description and distribution

Rock Shrimp
Rock shrimp, *Sicyonia brevirostris*, (Figure 4.1-5) are very different in appearance from the three penaeid species. Rock shrimp can be easily separated from penaeid species by their thick, rigid, stony exoskeleton. The body of the rock shrimp is covered with short hair and the abdomen has deep transverse grooves and numerous tubercles.

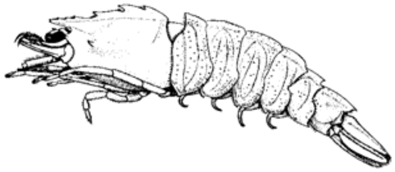


Figure 4.1-5. Rock shrimp, *Sicyonia brevirostris*.

Recruitment to the area offshore of Cape Canaveral occurs between April and August with two or more influxes of recruits entering within one season (Kennedy et al. 1977).

Keiser (1976) described the distribution of rock shrimp in coastal waters of the southeastern United States. Whitaker (1982) presented a summary of information on rock shrimp off South Carolina. The only comprehensive research to date on rock shrimp off the east coast of Florida was by Kennedy et al. (1977). This section presents some of the more significant findings by Kennedy et al. (1977) regarding the biology of rock shrimp on the east coast of Florida.

Rock shrimp are found in the Gulf of Mexico, Cuba, the Bahamas, and the Atlantic Coast of the U.S. up to Virginia (SAFMC, 1993). The center of abundance and the concentrated commercial fishery for rock shrimp in the south Atlantic region occurs off northeast Florida south to Jupiter Inlet. Rock shrimp live mainly on sand bottom from a few meters to 183 m (600 ft), occasionally deeper (SAFMC 1993). The largest concentrations are found between 25 and 65 m (82 and 213 ft).

Although rock shrimp are also found off North Carolina, South Carolina, and Georgia and are occasionally landed in these states, no sustainable commercially harvestable quantities of rock shrimp comparable to the fishery prosecuted in the EEZ off Florida are being exploited.

Royal Red Shrimp

Royal red shrimp, *Pleoticus robustus*, (Figure 4.1-6) are members of the family Solenoceridae, and are characterized by a body covered with short hair and a rostrum with the ventral margin toothless. Color can range from orange to milky white. Royal red shrimp are found on the continental slope throughout the Gulf of Mexico and South Atlantic area from Cape Cod to French Guiana. In the South Atlantic they are found in large concentrations primarily off northeast Florida. They inhabit the upper regions of the continental slope from 180 m (590 ft) to about 730 m (2,395 ft), but concentrations are usually found at depths of between 250 m (820 ft) and 475 m (1,558 ft) over blue/black mud, sand, muddy sand, or white calcareous mud. Royal red shrimp are not burrowers but dig grooves in the substrate in search of small benthic organisms (Carpenter 2002). They have been commercially harvested in a relatively limited capacity.

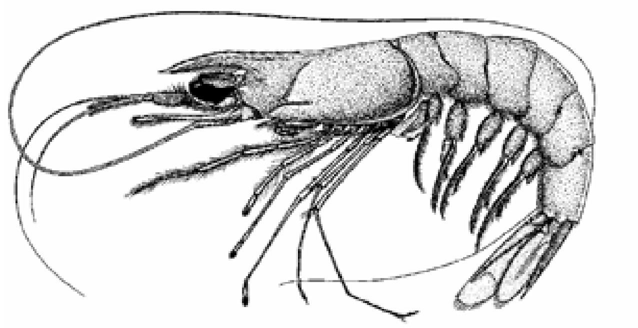


Figure 4.1-6. Royal red shrimp, *Pleoticus robustus* (Perez-Farfante and Kenlsey 1997)

Reproduction

Rock Shrimp

Rock shrimp are dioecious (separate sexes). Female rock shrimp attain sexual maturity at about 17 mm carapace length (CL), and all males are mature by 24 mm CL. Seasonal temperature initiates maturation. Rock shrimp have ovaries that extend from the anterior end of the cephalothorax to the posterior end of the abdomen.

Female rock shrimp attain sexual maturity at about 0.7 in (17 mm) carapace length (CL), and all males are mature by 0.9 in (24 mm) CL. Rock shrimp, as with most shrimp species, are highly fecund. Fecundity most probably, as with penaeids, increases with size. In rock shrimp, copulation is believed to take place between hard-shelled individuals. During copulation, similar to penaeid shrimp, the male anchors the spermatophore to the female's thelycum by the petasma and other structures and a glutinous material. Fertilization is believed to take place as ova and spermatozoa are simultaneously expulsed from the female. The spawning season for rock shrimp is variable with peak spawning beginning between November and January and lasting 3 months (Kennedy et al. 1977). Individual females may spawn three or more times in one season. Peak spawning activity seems to occur monthly and coincides with the full moon (Kennedy et al. 1977).

Kennedy et al. (1977) found rock shrimp larvae to be present year round with no trend relative to depth, temperature, salinity, and length or moon phase. The development from egg to postlarvae takes approximately one month. Subsequently the development from postlarvae to the smallest mode of recruits takes two to three months.

Development, growth and movement patterns

Rock Shrimp

For rock shrimp the development from egg to postlarvae takes approximately one month. Subsequently, the development from postlarvae to the smallest mode of recruits takes two to three months. The major transport mechanism affecting planktonic larval rock shrimp is the shelf current systems near Cape Canaveral, Florida (Bumpus, 1973). These currents keep larvae on the Florida Shelf and may transport them inshore during spring. Recruitment to the area offshore of Cape Canaveral occurs between April and August with two or more influxes of recruits entering within one season (Kennedy et al., 1977).

Rates of growth in rock shrimp are variable and depend on factors such as season, water temperature, shrimp density, size, and sex. Rock shrimp grow about 2 to 3 mm CL (0.08 – 0.1 in) per month as juveniles and 0.5 - 0.6 mm CL (0.02 in) per month as adults (Kennedy et al. 1977).

Density is thought to also affect growth of rock shrimp. In 1993, the industry indicated that rock shrimp were abundant but never grew significantly over 36/40 count that was the predominant size class harvested during July and August of that year. During years of low densities, the average size appears to be generally larger.

Since rock shrimp live between 20 and 22 months, natural mortality rates are very high, and with fishing, virtually the entire year class will be dead at the end of the season. The intense fishing effort that exists in today's fishery, harvests exclusively the incoming year class. Three year classes were present in sampling conducted between 1973 and 1974 by Kennedy et al. (1977). Fishing mortality in combination with high natural mortality and possibly poor environmental conditions may be high enough to prevent any significant escapement of adults to constitute a harvestable segment of the population. The better than average rock shrimp production in the 1996 season possibly resulted from better environmental conditions more conducive to rock shrimp reproduction and spawning.

Ecological relationships

Rock Shrimp

Along the Florida Atlantic coast, the predominant substrate inside of 200 m depth is fine to medium sand with small patches of silt and clay (Milliman 1972). Juvenile and adult rock shrimp are bottom feeders. Rock shrimp are most active at night (Carpenter 2003). Stomach contents analyses indicated that rock shrimp primarily feed on small bivalve mollusks and decapod crustaceans (Cobb et al. 1973). Kennedy et al. (1977) found the relative abundance of particular crustaceans and mollusks in stomach contents of rock shrimp corresponding to their availability in the surrounding benthic habitat. The diet of *Sicyonia brevirostris* consists primarily of mollusks, crustaceans and polychaete worms. Also included are nematodes, and foraminiferans. Ostracods, amphipods and decapods made up the bulk of the diet, with lesser amounts of tanaidaceans, isopods, cumaceans, gastropods, and other bivalves also present (Kennedy et al. 1977).

Kennedy et al. (1977) characterized rock shrimp habitat and compiled a list of crustacean and molluscan taxa associated with rock shrimp benthic habitat. The bottom habitat on which rock shrimp thrive is limited and thus limits the depth distribution of these shrimp. Cobb et al. (1973) found the inshore distribution of rock shrimp to be associated with terrigenous and biogenic sand substrates and only sporadically on mud. Rock shrimp also utilize hardbottom and coral, more specifically *Oculina*, habitat areas. This was confirmed with research trawls capturing large amounts of rock shrimp in and around the Oculina Bank HAPC prior to its designation.

Abundance and status of stocks

Rock Shrimp

(from Shrimp Amendment 6)
For stocks such as rock shrimp information from which to establish stock status determination criteria are limited to measures of catch. Nevertheless, with the development of a permitting system and reporting requirements associated with the permit, better information will be collected on the effort and catch in this fishery. Data should be reviewed periodically to determine if better inferences can be drawn to address $B_{MSY.}$ Additionally, any time that annual catch levels trigger one of the selected thresholds, new effort should be made to infer B_{MSY} or a reasonable proxy.

The current stock status determination criteria for rock shrimp were calculated from catch estimates as reported in Amendment 1 of the Shrimp Plan (SAFMC 1996a) during the period 1984-1996 (Table 4.1-3).

Table 4.1-3. Landings data used to calculate the current MSY value for rock shrimp in the South Atlantic.

Year	Landings
1986	2,514,895
1987	3,223,692

1988	1,933,097
1989	3,964,942
1990	3,507,955
1991	1,330,919
1992	2,572,727
1993	5,297,197
1994	6,714,761

Note: Data for the period 1986 to 1994 are taken from Shrimp Amendment 1 (SAFMC 1996a).

Maximum Sustainable Yield

Because rock shrimp live only 20 to 22 months, landings fluctuate considerably from year to year depending primarily on environmental factors. Although there is a good historical time series of catch data, the associated effort data were not considered adequate to calculate a biologically realistic value for MSY. Nevertheless, two standard deviations above the mean total landings was considered to be a reasonable proxy for MSY (SAFMC 1996a). The MSY proxy for rock shrimp, based on the state data from 1986 to 1994, is 6,829,449 pounds heads on (SAFMC 1996a).

Optimum Yield

OY is equal to MSY. The intent is to allow the amount of harvest that can be taken by U.S. fishermen without reducing the spawning stock below the level necessary to ensure adequate reproduction. This is appropriate for an annual crop like rock shrimp when recruitment is dependent on environmental conditions rather than female biomass. A relatively small number of mature shrimp can provide sufficient recruits for the subsequent year's production (SAFMC 1996a).

Overfished Definition

The South Atlantic rock shrimp resource is overfished when annual landings exceed a value two standard deviations above mean landings during 1986 to 1994 (mean=3,451,132 lb., s.d. =1,689,159), or 6,829,449 pounds heads on (SAFMC 1996a). In other words, the stock would be overfished if landings exceeded MSY. The status of rock shrimp stocks in the South Atlantic are not considered overfished at this time. High fecundity enables rock shrimp to rebound from a very low population size in one year to a high population size in the next when environmental conditions are favorable (SAFMC 1996a).

Overfishing Definition

There is no designation of overfishing for rock shrimp. The overfished definition, which is based on landings (and fishing effort) in excess of average catch is, in essence, an overfishing definition.

4.1.2 Snapper Grouper Complex

4.1.2.1 Species Descriptions

Sea basses and Groupers (Serranidae)

(all species' descriptions updated from the Snapper Grouper SAFE Report Nov. 2005)

All serranids described in this document are reported to be protogynous hermaphrodites meaning that all individuals change sex from female to male at a certain size and/or age. This size and age at sex transition is species-dependent and can vary considerably within species.

Gag

Gag, *Mycteroperca microlepis*, occur in the Western Atlantic from North Carolina to the Yucatan Peninsula, and throughout the Gulf of Mexico. Juveniles are sometimes observed as far north as Massachusetts (Heemstra and Randall 1993). Gag commonly occurs at depths of 39-152 m (131-498 ft) (Heemstra and Randall 1993) and prefers inshore-reef and shelf-break habitats (Hood and Schlieder 1992). Bullock and Smith (1991) indicated that gag probably do not move seasonally between reefs in the Gulf of Mexico, but show a gradual shift toward deeper water with age. McGovern et al. (2005) reported extensive movement of gag along the Southeast United States. In a tagging study, 23% of the 435 recaptured gag moved distances greater that 185 km. Most of these individuals were tagged off South Carolina and were recaptured off Georgia, Florida, and in the Gulf of Mexico (McGovern et al. 2005).

Gag are considered estuarine dependent (Keener et al. 1988; Ross and Moser 1995; Koenig and Coleman 1998; Strelcheck et al. 2003). Juveniles (age 0) occur in shallow grass beds along Florida's east coast during the late spring and summer (Bullock and Smith 1991). Sea grass is also an important nursery habitat for juvenile gag in North Carolina (Ross and Moser 1995). Post-larval gag enter South Carolina estuaries when they are 13 mm TL and 40 days old during April and May each year (Keener et al. 1988), and utilize oyster shell rubble as nursery habitat. Juveniles remain in estuarine waters throughout the summer and move offshore as water temperatures cool during September and October. Adults are often seen in shallow water 5-15 m (16-49 ft) above the reef (Bullock and Smith 1991) and as far as 40-70 km (25-44 ft) offshore.

Huntsman et al. (1999) indicated that gag are vulnerable to overfishing since they are long-lived, late to mature, change sex, and aggregate to spawn. The estimated natural mortality rate is 0.15 (Potts et al. 1998a). Maximum reported size for gag is 145 cm (57.5 in) TL and 36.5 kg (81 lbs) (Heemstra and Randall 1993), and maximum reported age is 26 years (Harris and Collins 2000). Almost all individuals less than 87.5 cm (34.7 in) TL are females. At 105.0 cm (41.6 in) TL, 50% of fishes are males, while almost all gag are males at sizes greater than 120.0 cm (47.5 in) TL (McGovern et al. 1998).

Along the southeastern United States (1994-1995), size at first maturity is 50.8 cm (20.2 in) TL, and 50% of gag females are sexually mature at 62.2 cm (24.7 in) (McGovern et al. 1998). According to Harris and Collins (2000), age-at-first-maturity is 2 years, and 50% of gag are mature at 3 years. For data that were collected during 1978-1982 off the southeastern United States, McGovern et al. (1998) reported that the smallest mature females were 58.0 cm (22.9 in) TL and 3 years old. Hood and Schlieder (1992) indicated that most females reach sexual maturity at ages 5-7 in the Gulf of Mexico. Off the southeastern United States, gag spawn from December through May, with a peak in March and April (McGovern et al., 1998). Duration of planktonic larvae is about 42 days (Keener et al. 1988; Koenig and Coleman 1998; Lindeman et al. 2000). McGovern et al. (1998) reported that the percentage of male gag landed by commercial fishermen decreased from 20% during 1979-1981 to 6% during 1995-1996. This coincided with a decrease in the mean length of fish landed. A similar decrease in the percentage of males was reported in the Gulf of Mexico (Hood and Schleider 1992; Coleman et al. 1996).

Adults are sometimes solitary, or can occur in groups of 5 to 50 individuals, especially during the spawning season. They feed primarily on fishes, but also prey on crabs, shrimps, and cephalopods (Heemstra and Randall 1993), and often forage in small groups far from the reef ledge (Bullock and Smith 1991). Juveniles feed primarily on crustaceans, and begin to consume fishes when they reach about 25 mm (1 in) in length (Bullock and Smith 1991; Mullaney 1994).

Red grouper

Red grouper, *Epinephelus morio*, is primarily a continental species, mostly found in broad shelf areas (Jory and Iversen 1989). Distributed in the Western Atlantic, from North Carolina to southeastern Brazil, including the eastern Gulf of Mexico and Bermuda, but can occasionally be found as far north as Massachusetts (Heemstra and Randall 1993). The red grouper is uncommon around coral reefs; it generally occurs over flat rock perforated with solution holes (Bullock and Smith 1991), and is commonly found in the caverns and crevices of limestone reef in the Gulf of Mexico (Moe 1969). It also occurs over rocky reef bottoms (Moe 1969).

Adult red grouper are sedentary fish that are usually found at depths of 5-300 m (16-984 ft). Fishermen off North Carolina commonly catch red grouper at depths of 27-76 m (88-249 ft) for an average of 34 m (111 ft). Fishermen off southeastern Florida also catch red grouper in depths ranging from 27-76 m (88-249 ft) with an average depth of 45 m (148 ft) (Burgos, 2001; McGovern et al., 2002a). Moe (1969) reported that juveniles live in shallow water nearshore reefs until they are 40.0 cm (16 in) and 5 years of age, when they become sexually mature and move offshore. Spawning occurs during February-June, with a peak in April (Burgos 2001). In the eastern Gulf of Mexico, ripe females are found December through June, with a peak during April and May (Moe 1969). Based on the presence of ripe adults (Moe 1996) and larval red grouper (Johnson and Keener 1984) spawning probably occurs offshore. Coleman et al. (1996) found groups of spawning red grouper at depths between 21-110 m (70-360 feet). Red grouper do not appear to form spawning aggregation or spawn at specific sites (Coleman et al. 1996). They are reported to spawn in depths of 30-90 m (98-295 ft) off the Southeast Atlantic coast (Burgos 2001; McGovern et al. 2002a).

Off North Carolina, red grouper first become males at 50.9 cm (20.1 in) TL and males dominate size classes greater than 70.0 cm (27.8 in) TL. Most females transform to males between ages 7 and 14. Burgos (2001) reported that 50% of the females caught off North Carolina are undergoing sexual transition at age 8. Maximum age reported by Heemstra and Randall (1993) was 25 years. Burgos (2001) and McGovern et al. (2002a) indicated that red grouper live for at least 20 years in the Southeast Atlantic and a maximum age of 26 years has been reported for red grouper in the Gulf of Mexico (L. Lombardi, NMFS Panama City, personal communication). Natural mortality rate is estimated to be 0.20 (Potts and Brennan 2001). Maximum reported size is 125.0 cm (49.2 in) TL (male) and 23.0 kg (51.1 lb). For fish collected off North Carolina during the late 1990s, age at 50% maturity of females is 2.4 years and size at 50% maturity is 48.7 cm (19.3 in) TL. Off southeastern Florida, age at 50% maturity was 2.1 years and size at 50% maturity was 52.9 cm (21.0 in) TL (Burgos 2001; McGovern et al. 2002a). These fish eat a wide variety of fishes, octopuses, and crustaceans, including shrimp, lobsters, and stomatopods (Bullock and Smith 1991; Heemstra and Randall 1993).

Scamp

Scamp, *Mycteroperca phenax*, occurs in the Western Atlantic, from North Carolina to Key West, in the Gulf of Mexico, and in the southern portion of the Caribbean Sea. Juveniles are sometimes encountered as far north as Massachusetts (Heemstra and Randall 1993). Its reported depth range is 30-100 m (98-328 ft) (Heemstra and Randall 1993). Juveniles are found in estuarine and shallow coastal waters (Bullock and Smith 1991; Heemstra and Randall 1993).

Scamp are protogynous, with females dominating sizes less than 70.0 cm (27.8 in) (Harris et al. 2002). Scamp live for at least 30 years (Harris et al. 2002), and attain sizes as great as 107.0 cm (42.4 in) TL and 14.2 kg (31.3 lbs) (Heemstra and Randall 1993). Natural mortality rate is estimated to be 0.15 (Potts and Brennan 2001). Harris et al. (2002) report that the length and age at first spawning of females off North Carolina to southeast Florida was 30.0-35.0 cm (11.9-13.8 in) TL and age 1. Length and age at 50% maturity was 35.3 cm (13.9 in) TL and 1.28 years, respectively (Harris et al. 2002). In a study conducted in the eastern Gulf of Mexico, all fish larger than 35.0 cm TL were sexually mature (M. Godcharles and L. Bullock unpublished data).

Spawning occurs from February through July in the South Atlantic Bight and in the Gulf of Mexico, with a peak in March to mid-May (Harris et al., 2002). Hydration of eggs occurs primarily during the morning and late afternoon, which indicates that scamp spawn during late afternoon and evening. Spawning individuals have been captured off South Carolina and St. Augustine, Florida at depths of 33 to 93 m. Scamp aggregate to spawn. Spawning locations and time of spawning overlap with those of gag (Gilmore and Jones 1992). Fish are the primary prey of this species (Matheson et al. 1986).

Black grouper

The black grouper, *Mycteroperca bonaci*, occurs in the Western Atlantic, from North Carolina to Florida, Bermuda, the Gulf of Mexico, West Indies, and from Central America to Southern Brazil (Crabtree and Bullock 1998). Adults are found over hard bottom such as coral reefs and rocky ledges. Black grouper occur at depths of 9 to 30 m (30 to 98 ft). Juveniles sometimes occur in estuarine seagrass and oyster rubble habitat in North Carolina and South Carolina (Keener et al. 1988; Ross and Moser 1995). In the Florida Keys, juveniles settle on patch reefs (Sluka et al. 1994). Commercial landings of black grouper exceed landings of any other grouper in the Florida Keys.

Natural mortality (M) is estimated to be 0.15 (Potts and Brennan 2001). Crabtree and Bullock (1998) found that black grouper live for at least 33 years and attain sizes as great as 151.8 cm (60.1 in) TL. Females ranged in length from 15.5 to 131.0 cm (6.1-51.9 in) TL and males range in length from 94.7 to 151.8 cm (38.3-60.1 in) TL. Black grouper are protogynous. Approximately 50% of females are sexually mature by 82.6 cm (32.7 in) TL and 5.2 years of age. At a length of 121.4 cm (48.1 in) TL and an age of 15.5 years, approximately 50% of the females have become males. Black grouper probably spawn throughout the year. However, peak spawning of females occurs from January to March.

Off Belize, black grouper are believed to spawn in aggregations at the same sites used by Nassau grouper (Carter and Perrine 1994). Eklund et al. (2000) describe a black grouper spawning aggregation discovered during winter 1997-1998, less than 100 m outside a newly designated marine reserve. Adults feed primarily on fishes.

Rock hind

Rock hind, *Epinephelus adcensionis*, are found in the western Atlantic from Massachusetts to southern Brazil, Bermuda, the Gulf of Mexico, and the Caribbean, (Smith 1997). They also occur in the eastern Atlantic from Ascension Island and St. Helena Island (Smith 1997). The rock hind is a demersal species, inhabiting rocky reef habitat to depths of 120 m (394 ft). It is usually solitary.

Maximum reported size is 61.0 cm (24.2 in) TL (male) and 4.1 kg (9.1 lbs) (Heemstra and Randall 1993). Size at maturity and age at first maturity are estimated as 28.0 cm (11.1 in) TL and 6.1 years, respectively. Maximum reported age is 12 years (Potts and Manooch 1995). The natural mortality rate is estimated as 0.25 (Ault et al. 1998).

Rock hind has been observed to spawn in aggregations near the shelf edge off the southwest coast of Puerto Rico in January at depths of 20-30 m (66 – 98 ft) (Rielinger 1999). Off Cuba, rock hind spawn during January through March (García-Cagide et al. 1994). Off South Carolina, females in spawning condition (hydrated oocytes or postovulatory follicles) have been collected during May through August (Unpublished MARMAP data). Crabs comprise the majority of their diet, but rock hind have also been observed to feed on fishes and young sea turtles (Heemstra and Randall 1993).

Red hind

Red hind, *Epinephelus guttatus*, is found in the Western Atlantic from North Carolina to Venezuela and is the most common species of *Epinephelus* in Bermuda and the West Indies (Smith 1997). The red hind is found in shallow reefs and rocky bottoms, at depths of 2-100 m (7 – 328 ft) (Heemstra and Randall 1993). It is usually solitary and territorial.

Maximum reported size is 76.0 cm (30.0 in) TL (male) and 25.0 kg (55.5 lbs) (Heemstra and Randall 1993). Natural mortality rate is estimated to be 0.18 (Ault et al. 1998). Potts and Manooch (1995) examined 146 otoliths of red hind that were collected from North Carolina to the Dry Tortugas during 1980-1992 and report a maximum age of 11 years and maximum sizes of 49.0 cm (19.4 in) TL. Sadovy et al. (1992) conducted an age and growth study of red hind from Puerto Rico (n = 624) and St. Thomas, USVI (n = 162) and report a maximum age of 18 and a maximum size of 47.5 cm (18.8 in) TL. Luckhurst et al. (1992) captured a red hind off Bermuda that was 72.0 cm (28.5 in) TL and 22 years old.

Females (n = 390) off Puerto Rico become sexually mature at 21.5 cm (9.7 in) TL, the size at 50% maturity is 28.5 cm (11.3 in) TL, and they range in size from 11.0 to 48.0 cm (4.4 to 19.0 in) TL Sadovy et al. (1994). Males (n = 120) range in size from 27.3 to 51.0 cm (10.8 to 20.2) TL and transitional individuals (n = 7) were from 27.5 to 34.5 cm (10.9 to 13.7 in) TL. Annual spawning aggregations occur during the full moon in January and February off the southwest coast of Puerto Rico and during the summer in Bermuda with no relation to lunar periodicity

(Shapiro et al. 1993; Sadovy et al. 1994). Spawning off Jamaica, Puerto Rico, and USVI occurs from December to February (Thompson and Munro 1978; Colin et al. 1987; Sadovy et al. 1992; Sadovy et al. 1994). Burnett-Herkes (1975) reports that red hind spawn from April to July off Bermuda. Red hind spawn during the summer off the southeastern United States (MARMAP unpublished data).

This species aggregates in large numbers during the spawning season (Coleman et al. 2000; Sadovy et al. 1994). A number of spawning aggregation sites have been documented in the Caribbean. The timing of aggregations is somewhat variable. Aggregations off Puerto Rico generally occur from January through March in association with the full moon, while those off the USVI generally occur from December through March in association with the full moon (Rielinger 1999). The red hind feeds mainly on crabs and other crustaceans, fishes, such as labrids and haemulids, and octopus (Randall, 1967, Heemstra and Randall 1993).

Graysby

Graysby, *Cephalopholis cruentata*, occur from North Carolina to south Florida and in the Gulf of Mexico, Caribbean and Bermuda. The graysby inhabits seagrass (*Thalassia*) beds and coral reefs, and is found as deep as 170 m (557 ft). It is sedentary, solitary, and secretive, usually hiding during the day, and feeding at night. This small grouper is rare in landings off the southeast United States, and is more commonly seen in the Caribbean (Potts and Manooch 1999). Graysby are probably most often landed as unclassified grouper by commercial fishermen off the southeastern United States.

Maximum reported size is 42.6 cm (16.9 in) TL (male) and 1.1 kg (2.4 lbs). In the northeastern Caribbean, individuals in spawning condition have been observed in March, and from May to July (Erdman 1976). Nagelkerken (1979) determined that graysby collected in the Caribbean spawn from July through October. Graysby spawn during summer off the Southeastern United States (MARMAP unpublished data). Size at maturity and age at first maturity are estimated as 14.0 cm (5.5 in) TL and 3.5 years (Nagelkerken 1979). Sexual transition occurs at sizes ranging from 14.0 to 26.0 cm (5.5-10.3 in) TL with most transitional individuals occurring between the sizes of 20.0-23.0 cm (7.9-9.1 in) TL and ages 4-5 (Nagelkerken 1979).

Potts and Manooch (1999) examined otoliths from 118 graysby that were collected from 1979 to 1997. Maximum reported age is 13 years and maximum size is 40.5 cm (16.0 in) TL. Juveniles feed on shrimp, while adults eat primarily fishes. Natural mortality rate is estimated as 0.20 (Ault et al. 1998). Adult graysby eat bony fish, shrimp, stomatopods, crabs, and gastropods (Randall 1967).

Yellowfin grouper

Yellowfin grouper, *Mycteroperca venenosa*, occur in the Western Atlantic, ranging from Bermuda to Brazil and the Guianas, including the Gulf of Mexico and Caribbean Sea at depths of 2-137 m (7-449 ft). Juveniles are commonly found in shallow sea grass beds, while adults occur over rocky areas and coral reefs.

Maximum reported size is 100.0 cm (39.6 in) TL (male) and 18.5 kg (41.1 lbs) (Heemstra and Randall 1993). Thompson and Munro (1978) reported that yellowfin grouper off Jamaica are 4 years old between 46.0-57.0 cm (18.1-22.4 in) TL, and by 80.0 cm (31.5 in) TL, they are 10 years of age. Manooch (1987) reported a maximum age of 15 years for yellowfin grouper. Natural mortality rate is estimated to be 0.18 (Ault et al. 1998). Yellowfin grouper aggregate at some of the same sites utilized by tiger grouper, Nassau grouper, and black grouper (Sadovy et al. 1994). Spawning occurs during March in the Florida Keys (Taylor and McMichael 1983), and from March and May to August in the Gulf of Mexico (Bullock and Smith, 1991). Most spawning occurs in Jamaican waters between February and April (Thompson and Munro 1978), and during July off Bermuda (Smith 1958). Yellowfin grouper feed mainly on fishes (especially coral reef species) and squids (Heemstra and Randall 1993).

Coney

Coney, *Cephalopholis fulva*, is a small grouper that occurs in the Western Atlantic, ranging from South Carolina (USA) and Bermuda to southern Brazil, including Atol das Rocas. The coney is a sedentary species. It prefers coral reefs and clear water, and can be found to depths as great as 150 m (492 ft). Coney are most commonly taken in the Caribbean, where they are found associated with patch reefs. Most commercial landings of coney are off southeast Florida and are often labeled as unclassified grouper.
Maximum reported length is 41.0 cm (16.2 in) TL (male). This species is protogynous (Heemstra and Randall 1993). Size at 50% maturity for females sampled off the west coast of Puerto Rico was 13.0 cm (5.1 in) FL (Figuerola and Torrez Ruiz 2000). Heemstra and Randall (1993) report that females mature at 16.0 (6.3 in) cm TL and transform to males at about 20.0 (7.9 in) cm TL.

Potts and Manooch (1999) examined the otoliths from 55 coney that were collected during 1979-1997 from North Carolina to the Dry Tortugas, Florida. The maximum reported age is 11 years and maximum size is 39.7 cm (15.7 in) TL. Natural mortality rate is estimated as 0.18 (Ault et al. 1998).

Spawning occurs in small groups composed of one male and multiple females. Although ripe ovaries are found from November to March off the west coast of Puerto Rico, spawning activity appears to be limited to several days around the last quarter and new moon phases during January and February (Figuerola et al. 1997). The diet is composed primarily of small fishes and crustaceans (Randall 1967).

Yellowmouth grouper

Yellowmouth grouper, *Mycteroperca interstitialis*, occur along the eastern U.S. coast, Bermuda, Bahamas, Gulf of Mexico, and in the Caribbean south to Brazil (Smith 1971). Adults are found over rocky hard bottom and coral reefs near the shoreline as deep as 55 m (100 ft). Individuals have been found as deep as 150 m (275 ft). Young commonly occur in mangrove lined lagoons.

The maximum reported size of yellowmouth grouper is 84.0 cm (33.2 in) TL (male) and 10.2 kg (22.6 lbs) (IGFA data base, 2001 http://www.igfa.org in FISHBASE www.fishbase.org). In the Gulf of Mexico, maximum reported age for yellowmouth grouper is 28 years (Bullock and Murphy 1994), while in Trinidat and Tobago the maximum reported age was 41 years (Maninckhand-Heilman and Phillip 2000). Males (2-28 years) are generally older than females (2-17 years). Females become sexually mature between 40.0-45.0 cm (15.8-17.7 in) TL and ages 2-4 years. Fifty percent are males at 60.0-64.9 cm (23.6-25.6 in) TL. Fish undergo sexual transition from female to male at lengths from 50.3 to 64.3 cm (19.8-25.3 in) TL, between the ages of 5 and 14 years. Yellowmouth grouper may spawn all year, but peak spawning of females in the Gulf of Mexico occurs during March to May (Bullock and Murphy 1994). Finfish constitute a large part of the diet of yellowmouth grouper (Randall 1967).

Tiger grouper

Tiger grouper, *Mycteroperca tigris*, occur in the Western Atlantic, ranging from Bermuda and south Florida to Venezuela and, possibly Brazil, including the Gulf of Mexico and the Caribbean Sea. It inhabits coral reefs and rocky areas at depths of 10 to 40 m (33-131 ft).

Maximum reported size is 101.0 cm (40.0 in) TL (male) and 10 kg (22.2 lbs) (Heemstra and Randall 1993). Approximate life span is 26 years, and M is estimated at 0.12 (Ault et al. 1998).

The size-sex ratios described in a study conducted off Bermuda indicate this fish is probably protogynous (Heemstra and Randall 1993). It forms aggregations at specific times and locations each year, but only during the spawning season (Coleman et al. 2000; White et al. 2002). White et al. (2002) reported that spawning aggregations of tiger grouper occurred one week after the full moon during January through April off Puerto Rico. Tiger grouper spawn from December through April off southwest Cuba (García-Cagide et al. 1999). The tiger grouper preys on a variety of fishes, and frequents cleaning stations (Heemstra and Randall 1993).

Goliath grouper

Goliath grouper, *Epinephelus itajara* -- formerly known as the “jewfish,” occurs in the Western and Eastern Atlantic, and in the Eastern Pacific Ocean. In the Western Atlantic, its range extends from Florida to southern Brazil, including the Gulf of Mexico and the Caribbean Sea. A solitary species, goliath grouper inhabits rock, coral, and mud bottom habitats in both shallow, inshore areas and as deep as 100 m (328 ft) (Heemstra and Randall 1993). Juveniles are generally found in mangrove areas and brackish estuaries. Large adults also may be found in estuaries. They appear to occupy limited home ranges with little movement (Heemstra and Randall 1993).

The goliath grouper is the largest grouper in the Western North Atlantic. Maximum reported size is 250 cm (99 in) TL (male) and 455 kg (1,003 lbs) (Heemstra and Randall 1993). Bullock et al. (1992) indicated that fish taken from exploited populations have a maximum age of 37 years. However, it is likely that this species could live much longer if left unexploited. Froese and Pauly (2003) estimate M to be 0.13. Porch et al. (2003) use M between 0.04 and 0.19.

There is some evidence that males may transform from immature females (Bullock et al. 1992). Males exhibit a similar testicular structure to those of other serranids that are protogynous, however, mature males are observed at smaller lengths than those of mature females. Bullock et al. (1992) found that males become mature at slightly smaller sizes and at younger ages than females. They first become mature at 110.0 cm (43.6 in) TL and age 4. All males are mature by 115.2 cm (45.6 in) and age 7. Females first become mature at 120.0 cm (47.0 in) TL and age 6, and all are mature by 135.0 cm (53.1 in) TL and age 8.

Goliath grouper form consistent aggregations (always containing the largest, oldest individuals in the population), but only during the spawning season (Sadovy and Eklund 1999; Coleman et al. 2000). Aggregations off Florida declined in the 1980s from 50 to 100 fish per site to less than 10 fish per site. Since the harvest prohibition, aggregations have rebounded somewhat to 20-40 fish per site. Spawning off Florida occurs July through September during the full moon. Fish may move distances as great as 100 km from inshore reefs to the offshore spawning aggregations in numbers of up to 100 or more on shipwrecks, rock ledges, and isolated patch reefs along the southwest coast. In the northeastern Caribbean, individuals in spawning condition have been observed in July and August (Erdman 1976). Bullock et al. (1992) reported that goliath grouper spawn during June through December with a peak in July to September in the eastern Gulf of Mexico.

Goliath grouper feed primarily on crustaceans, particularly spiny lobsters, as well as turtles and fishes, including stingrays. It is a territorial species, and larger individuals have reportedly stalked and attempted to eat human divers (Heemstra and Randall 1993).

Nassau grouper

The Nassau grouper, *Epinephelus striatus*, occurs in the tropical Western Atlantic, ranging from Bermuda, the Bahamas, and Florida to southern Brazil. It has not been found in the Gulf of Mexico, except at the Campeche Bank off the coast of Yucatan, at Tortugas, and off Key West. The Nassau grouper occurs from the shoreline to depths of at least 90 m (295 ft). It is a sedentary, reef-associated species and usually encountered close to caves, although juveniles are common in seagrass beds (Heemstra and Randall 1993). Adults lead solitary lives, except when they aggregate to spawn (Sadovy and Eklund 1999).

Maximum reported size is 122 cm (48.3 in) TL (male) and 23-27 kg (51.1-29.9 lbs), and maximum reported age is 29 years (Sadovy and Eklund 1999). M has been estimated at 0.18 (Ault et al. 1998).

Unlike most other serranids where males are derived from females (protogyny), Sadovy and Colin (1995) indicated that Nassau grouper is primarily a gonochoristic species (separate sexes) with a potential for sex change. Male and female Nassau grouper mature between 40.0-50.0 cm (15.8-19.8 in) SL and 4-8 years of age. Most individuals attain maturity by 50.0 cm (19.8 in) SL and 7 years.

This species aggregates to spawn at specific times and locations each year (Coleman et al. 2000; Sadovy et al. 1994), reportedly at some of the same sites utilized by the tiger grouper, yellowfin grouper, and black grouper (Sadovy et al. 1994). Concentrated aggregations of from a few dozen to 30,000 Nassau grouper have been reported off the Bahamas, Jamaica, Cayman Islands, Belize, and the Virgin Islands (Heemstra and Randall 1993). Spawning aggregations composed of about 2,000 individuals have been documented north and south of St. Thomas, USVI at depths of 10-40 m, from December through February, around the time of the full moon (Rielinger 1999).

The spawning season is brief and associated with water temperature and the moon phase. At lower latitudes, reproductive activity lasts for about one week per month during December-February. In more northern latitudes (e.g. Bermuda), reproduction occurs between May and

August, with a peak in July. Spawning aggregations in the Caribbean occurs at depths of 20-40 m on the outer reef shelf edge, in December and January around the time of the full moon in waters 25-26° C (Sadovy and Eklund 1999).

Juveniles feed primarily on crustaceans (Eggleston et al. 1998), while adults forage on fishes, bivalves, lobsters, and gastropods (Sadovy and Eklund 1999).

Snowy grouper

Snowy grouper, *Epinephelus niveatus*, occur in the Eastern Pacific and the Western Atlantic from Massachusetts to southeastern Brazil, including the northern Gulf of Mexico (Robins and Ray 1986 in Froese and Pauly 2003). It is found at depths of 30-525 m (98-1,722 ft). Adults occur offshore over rocky bottom habitat. Juveniles are often observed inshore and occasionally in estuaries (Heemstra and Randall 1993).

The snowy grouper is a protogynous species. The smallest, youngest male examined by Wyanski et al. (2000) was 72.7 cm (28.8 in) TL and age 8. The median size and age of snowy grouper was 91.9 cm (34.5 in) and age 16. The largest specimen observed was 122 cm (48 in) TL and 30 kg (66 lbs), and 27 years old (Heemstra and Randall 1993). The maximum age reported by Wyanski et al. (2000) is 29 years for fish collected off of North Carolina and South Carolina. Radiocarbon techniques indicate that snow grouper may live for as long as 40 years (Harris, South Carolina Department of Natural Resources, personal communication). Wyanski et al. (2000) reported that 50% of the females are mature at 54.1 cm (21.3 in) TL and 5 years of age. The smallest mature female was 46.9 cm (18.5 in) TL, and the largest immature female was 57.5 cm (22.6 in) TL.

Females in spawning condition have been captured off western Florida during May, June, and August (Bullock and Smith 1991). In the Florida Keys, ripe individuals have been observed from April to July (Moore and Labinsky 1984). Spawning seasons reported by other researchers are as follows: South Atlantic (north of Cape Canaveral), April through September (Wyanski et al. 2000) and April through July (Parker and Mays 1998); and South Atlantic (south of Cape Canaveral), May through July (Manooch 1984). Wyanski et al. (2000) reported that snowy grouper spawn at depths from 176 to 232 m (577 to 761 ft) off South Carolina. Adults feed on fishes, gastropods, cephalopods, and crustaceans (Heemstra and Randall 1993).

Yellowedge grouper

Yellowedge grouper, *Epinephelus flavolimbatus*, occur in the Western Atlantic from North Carolina to southern Brazil, including the Gulf of Mexico. A solitary, demersal, deepwater species, the yellowedge grouper occurs in rocky areas and on sand mud bottom, at depths ranging from 64 to 275 m (210 to 902 ft). On soft bottom habitats, this fish is often seen in or near trenches or burrow-like excavations (Heemstra and Randall 1993).

Maximum reported size is 114 cm (45.3 in) TL (male) and 18.6 kg (41 lbs). Manickchand-Heileman and Phillip (2000) reported a maximum age for yellowedge grouper of 35 years in Trinidad and Tobage, but Cass-Calay and Bahnick (2002) observed a maximum age of 85 years that was validated by the use of radiocarbon dating. M is estimated to be 0.05 (Cass-Calay and Bahnick 2002).

Bullock et al. (1996) in the Gulf of Mexico reported that 50% of fishes are mature at 22.4 in, and that 50% of females transform into males by 81 cm (32.2 in) TL. Spawning occurs from April through October in the South Atlantic (Keener 1984; Manooch 1984; Parker and Mays 1998). Ripe females were found in the eastern Gulf of Mexico from May through September (Bullock et al. 1996). Yellowedge grouper eat a wide variety of invertebrates (mainly brachyuran crabs) and fishes (Bullock and Smith 1991; Heemstra and Randall 1993).

Warsaw grouper

Warsaw grouper, *Epinephelus nigritus*, occur in the Western Atlantic from Massachusetts to southeastern Brazil (Robins and Ray 1986), and in the Gulf of Mexico (Smith 1971). The Warsaw grouper is a solitary species (Heemstra and Randall 1993), usually found on rocky ledges and seamounts (Robins and Ray 1986), at depths from 55 to 525 m (180-1,722 ft) (Heemstra and Randall 1993). Juveniles are sometimes observed in inshore waters (Robins and Ray 1986), on jetties and shallow reefs (Heemstra and Randall 1993).

Maximum reported size is 230 cm (91 in) TL (Heemstra and Randall 1993) and 263 kg (580 lbs) (Robins and Ray 1986). The oldest specimen was 41 years old (Manooch and Mason 1987). M was estimated by the SEDAR group during November 2003 to range from 0.05 to 0.12 (SEDAR 4 2004). The Warsaw grouper spawns during August, September, and October in the Gulf of Mexico (Peter Hood, NOAA Fisheries, personal communication), and during April and May off Cuba (Naranjo 1956). Adults feed on benthic invertebrates and on fishes (Heemstra and Randall 1993).

Speckled hind

Speckled hind, *Epinephelus drummondhayi*, occur along the southeast coast of United States from North Carolina to Florida, around Bermuda and in the northern and eastern Gulf of Mexico (Heemstra and Randall, 1993. Speckled hind are found at depths from 25 m to 400 m but most commonly occur at depths of 60 to 120 m (Heemstra and Randall, 1993). They have been caught at depths of 28 to 165 m (Roe, 1976; Sedberry, et al., 2006). Bullock and Smith (1991) reported that most commercial catches are taken from depths of 50 m or more. Juveniles occur in the shallower portions of the depth range.

The largest speckled hind on record is 110 cm total length and 30 kg (Matheson and Huntsman, 1984; Heemstra and Randall, 1993). Matheson and Huntsman (1984) observed a recruitment age of 3.3 years and a maximum age of at least 25 years. The von Bertalanffy equation calculated by Matheson and Huntsmen (1984) indicate that this species reaches maximum size slowly (L_t=967{1-exp[-0.13(t+1.01]}).

Histological examination of gonads collected from speckled hind revealed that it is a protogynous hermaphrodite (Brule et al., 2000). The estimated age at maturity for females is 4 to 5 years and the estimated size at maturity is 45 to 60 cm. The estimated age at transition from female to male is 8 to 12 years. It is thought that although speckled hind is a solitary species, they do form spawning aggregations (G. Gilmore, ECOS, personal communication). Spawning reportedly occurs between April and September (Brule et al., 2000; Heemstra and Randall, 1993).

Prey items include fishes, crustaceans, and squids (Bullock and Smith, 1991).

Prior to 1976, commercial landings of speckled hind were infrequent but increased in the late 70s and early 80s (Matheson and Huntsmen, 1984). Commercial landings of speckled hind reached a maximum of 14.8 metric tons in 1984. Landings of speckled hind steadily decreased until 1994 when a one fish per vessel limit was put into place. Commercial landings of speckled hind have averaged less than 1 metric ton annually from 1995 to 2004. Huntsmen *et al*. (1999) reported that in 1990 the population size was 10% and biomass was 5% of what they were in 1973 off North Carolina and South Carolina. The South Atlantic Fishery Management Council considers the speckled hind population in the South Atlantic to be overfished and currently experiencing overfishing (SAFMC, 1991).

Misty grouper

Misty grouper, *Epinephelus mystacinus*, occur in the Western and Eastern Atlantic Ocean (Heemstra and Randall 1993 in Froese and Pauly 2003). In the Western Atlantic, it ranges from Bermuda and the Bahamas to Brazil (Robins and Ray 1986). The misty grouper is a solitary, bathydemersal species. Adults generally occur at depths from about 100 to 550 m (327 to 1,803 ft) (Robins 1967). Juveniles occur in shallower waters (e.g., 30 m (98 ft)).

Little is known about the age, growth, and reproduction of this species. Maximum reported size is 160 cm (63 in) TL and 100 cm (39 in) TL for males and females, respectively. Maximum reported weight is 107 kg (236 lbs) (Heemstra and Randall 1993). The estimated size at maturity is 81.1 cm (31.9 in), and M is 0.14 (Froese and Pauly 2003). This species feeds primarily on fishes, crustaceans, and squids (Heemstra and Randall 1993).

Black sea bass

Black sea bass, *Centropristis striata*, occur in the Western Atlantic, from Maine to northeastern Florida, and in the eastern Gulf of Mexico. It can be found in extreme south Florida during cold winters (Robins and Ray 1986). Separate populations were reported to exist to the north and south of Cape Hatteras, North Carolina (Wenner et al. 1986). However, genetic similarities suggest that this is one stock (McGovern et al. 2002b). This species is common around rock jetties and on rocky bottoms in shallow water (Robins and Ray 1986) at depths from 2-120 m (7-394 ft). Most adults occur at depths from 20-60 m (66-197 ft) (Vaughan et al. 1995).

Maximum reported size is 66.0 cm (26.1 in) TL and 3.6 kg (7.9 lbs) (McGovern et al. 2002b). Maximum reported age is 10 years (SEDAR 2 2003a). Natural mortality is estimated to be 0.30 (SEDAR 2-SAR1 2003). The minimum size and age of maturity for females studied off the southeastern U.S. coast is 10.0 cm (3.6 in) SL and age 0. All females are mature by 18.0 cm (7.1 in) SL and age 3 (McGovern et al. 2002). Wenner et al. (1986) reported that spawning occurs from March through May in the South Atlantic Bight. McGovern et al. (2002) indicated that black sea bass females are in spawning condition during March-July, with a peak during March through May (McGovern et al., 2002). Some spawning also occurs during September and November. Spawning takes place in the evening (McGovern et al. 2002). Black sea bass change sex from female to male (protogyny). McGovern et al. (2002b) noted that the size at maturity and the size at transition of black sea bass was smaller in the 1990s than during the early 1980s.

Black sea bass appear to compensate for the loss of larger males by changing sex at smaller sizes and younger ages.

In the eastern Gulf of Mexico and off North Carolina, females dominate the first 5-year classes. Individuals over the age of 5 are more commonly males. Black sea bass live for at least 10 years. The diet of this species is generally composed of shrimp, crab, and fish (Sedberry 1988). Sedberry (1988) indicated that black sea bass consume primarily amphipods, decapods, and fishes off the Southeastern United States. Smaller black sea bass ate more small crustaceans and larger individuals fed more on decapods and fishes.

Bank sea bass

The bank sea bass, *Centropristis ocyurus*, is a small demersal serrarid occuring in reefs or rocky offshore habitats from Cape Lookout, North Carolina, to the Yucatan banks of the southern Gulf of Mexico (Miller 1957). In the South Atlantic Bight it is more common in shelf edge habitats than the black sea bass, which is found more on inner- and mid-shelf reefs (Wyanski et al. 1992). Bank sea bass ranked between fifth and eight in abundance in chevron trap catches of the 1990-2005 MARMAP reef fish surveys in sponge-coral hard bottom habitat (Wyanski et al. 1992; MARMAP unpublished data). Unlike the larger and more abundant black sea bass (*C. striata*), it is of limited direct economic interest and is captured incidentally by anglers and commercial fishermen (Wyanski et al. 1992).

Little is known about the life history of ban sea bass. Most information comes from unpublished documents by Link (1980, unpubl. dissertation) and Wyanski et al (1992, unpubl. analytical MARMAP report). Maximum reported age is 7 (Link 1980) or 8 years (Wyanski et al. 1992). Maximum reported length in the off the SE coast of the US is 39 cm (15.4in) and 778 g (unpubl. data MARMAP). Sexual transition occurs over a wide range of sizes and ages, but most frequently between 12.5 and 17.4 cm TL (Wyanski et al. 1992). Peak spawning occurs in February, March, and April, but ripe females were collected in January through April and in October and November (Wyanski et al. 1992).

Link (1980) reported that food off the bank sea bass of North Carolina consisted of crustaceans (frequency of occurrence 63%), mollusks (42%), fishes (12%) and echinoderms (8%).

Rock sea bass

Rock sea bass, *Centropristis philadelphica*, occurs in the Western Atlantic from North Carolina to Palm Beach, Florida as well as the northern Gulf of Mexico (Froese and Pauly 2003). It prefers hard bottom, rocks, jetties, and ledges. Maximum reported size is 30.0 cm (11.9 in).

Link (1980) reported that food of the rock sea bass off North Carolina consisted of crustaceans (frequency of occurrence 75%), fishes (46%), and mollusks (35%).

Wreckfish (Polyprionidae)

The wreckfish, *Polyprion americanus*, is a large grouper-like fish that has a global anti-tropical distribution, but it was rarely captured in the western North Atlantic until the late 1980s, when a bottom hook-and-line fishery that targets wreckfish developed on the Blake Plateau (Vaughan et al. 2001). Wreckfish occur in the Eastern and Western Atlantic Ocean, on the Mid-Atlantic

Ridge, on Atlantic islands and seamounts, and in the Mediterranean Sea, southern Indian Ocean, and southwestern Pacific Ocean (Heemstra 1986; Sedberry et al. 1994; Sedberry 1995). In the western Atlantic, they occur from Grand Banks (44°50' N) off Newfoundland (Scott and Scott 1988) to the Valdes Peninsula (43°30' S) in Argentina (Menni et al. 1981). Genetic evidence suggests that the stock encompasses the entire North Atlantic (Sedberry et al. 1996). Active adult migration is also possible as the frequent occurrence of European fishhooks in western North Atlantic wreckfish suggests migration across great distances (Sedberry et al. 2001).

Wreckfish have supported substantial fisheries in the eastern North Atlantic, Mediterranean, Bermuda, and the western South Atlantic, but concentrations of wreckfish adequate to support a fishery off the southeastern United States were not discovered until 1987. The fishery off the southeastern United States occurs over a complex bottom feature that has over 100 m of topographic relief, known as the Charleston Bump, that is located 130-160 km southeast of Charleston, South Carolina, at 31°30'N and 79°00'W on the Blake Plateau (Sedberry et al. 2001). Fishing occurs at water depths of 450-600 m. Primary fishing grounds comprise an area of approximately 175-260 km^2, characterized by a rocky ridge and trough feature with a slope greater than 15° (Sedberry et al. 1994; Sedberry et al. 1999; Sedberry et al. 2001).

Adults are demersal and attain lengths of 200 cm TL (79 in; Heemstra 1986) and 100 kg (221 lbs; Roberts 1986). Wreckfish landed in the southeastern United States average 15 kg (33 lbs) and 100 cm TL (39 inches TL) (Sedberry et al. 1994). Juvenile wreckfish (< 60 cm TL) are pelagic, and often associate with floating debris, which accounts for their common name. The absence of small pelagic and demersal wreckfish on the Blake Plateau has led to speculation that young wreckfish drift for an extended period, up to four years, in surface currents until reaching the eastern Atlantic, or perhaps that they make a complete circuit of the North Atlantic (Sedberry et al. 2001).

Vaughan et al. (2001) reported maximum ages of 35 years, however, off Brazil ages as great as 76 years have been reported for wreckfish (Peres and Haimovici 2004). In a recent MARMAP report, mature gonads were present in 60% of females at 751-800 mm, 57% at 801-850 mm, and 100% at larger sizes. The smallest mature female was 692 mm, and immature females were 576-831 mm. The estimate of length at 50% maturity was 790 mm (Gomperz model; 95% CI = 733-820). Mature gonads were present in 40% of males at 651-800 mm and 100% at larger sizes. The smallest mature male was 661 mm, and immature males were 518-883 mm. L50 was not estimated because transition to maturity was abrupt.

Wreckfish spawn from December through May, with a peak during February and March. The highest percentages of ripe males occurred during December through May, which corresponded with the female spawning season; however, males in spawning condition were collected throughout the year. The male spawning peak was also during February and March.

Snappers (Lutjanidae)

Queen snapper

The queen snapper, *Etelis oculatus*, occurs in the Western Atlantic, ranging from Bermuda and North Carolina to Brazil, including the Gulf of Mexico and Caribbean Sea. It is commonly found near oceanic islands, and is particularly abundant in the Bahamas and the Antilles. This species is bathydemersal species (Allen 1985) and moves offshore to deepwater reefs and rocky ledges as it grows and matures (SAFMC 1999). Allen (1985) indicated it is primarily found over rocky bottom habitat, in depths of 100 to 450 m (327 to 1,475 ft). Thompson and Munro (1974a) report it was caught on mud slopes of the south Jamaica shelf at a depth of 460 m (1,508 ft). Maximum reported size is 100 cm TL (39 inches, male). Maximum reported weight is 5,300 g (11.7 lbs) (Allen 1985). Size at maturity and age at first maturity are estimated as 53.6 cm TL (21 inches) and 1 year, respectively. Spawning is reported to occur during April and May off St. Lucia (Murray et al. 1998). Approximate life span is 4.7 years; natural mortality rate, 0.76 (Froese and Pauly 2003). Primary prey items include small fishes and squids (Allen 1985).

Yellowtail snapper

Yellowtail snapper, *Ocyurus chrysurus*, occurs in the Western Atlantic, ranging from Massachusetts to southeastern Brazil, including the Gulf of Mexico and Caribbean Sea, but is most common in the Bahamas, off south Florida, and throughout the Caribbean. Most U.S. landings are from the Florida Keys and southeastern Florida. The yellowtail snapper inhabits waters as deep as 180 m (590 ft), and usually is found well above the bottom (Allen 1985). Muller et al. (2003) state that adults typically inhabit sandy areas near offshore reefs at depths ranging from 10 to 70 m (33-230 ft). Thompson and Munro (1974a) indicate that this species is most abundant at depths of 20-40 m (66-131 ft) near the edges of shelves and banks off Jamaica. Juveniles are usually found over back reefs and seagrass beds (Thompson and Munro 1974a; Muller et al. 2003). Yellowtail snapper exhibits schooling behavior (Thompson and Munro 1974a).

Maximum reported size is 86.3 cm (34.2 in) TL (male) and 4.1 kg (9.1 lbs) (Allen 1985). Maximum age is 17 years (Manooch and Drennon 1987). M is estimated at 0.20 with a range of 0.15-0.25 (Muller et al. 2003). There is a truncation in the size and age structure of yellowtail snapper near human population centers.
Yellowtail snapper have separate sexes throughout their lifetime (i.e., they are gonochoristic). Figuerola et al. (1997) estimated size at 50% maturity as 22.4 cm (8.9 in) FL (males) and 24.8 cm (9.8 in) FL (females), based on fishery independent and dependent data collected off Puerto Rico.

Spawning occurs over a protracted period and peaks at different times in different areas. In southeast Florida, spawning occurs during spring and summer, while it may occur year-round in the Bahamas and Caribbean (Grimes 1987). Figuerola et al. (1997) reported that, in the U.S. Caribbean, spawning occurs during February to October, with a peak from April to July. Erdman (1976) reported that 80% of adult yellowtail snapper captured off San Juan spawn during March through May. Spawning occurs in offshore waters (Figuerola et al. 1997; Thompson and Munro 1974a) and during the new moon (Figuerola et al. 1997). Large spawning aggregations are reported to occur seasonally off Cuba, the Turks and Caicos, and USVI. A large spawning aggregation occurs during May-July at Riley’s Hump near the Dry Tortugas off Key West, Florida (Muller et al. 2003).

Yellowtail snapper are nocturnal predators. Juveniles feed primarily on plankton (Allen 1985; Thompson and Munro 1974a). Adults eat a combination of planktonic (Allen 1985), pelagic (Thompson and Munro 1974a), and benthic organisms, including fishes, crustaceans, worms, gastropods, and cephalopods (Allen 1985). Bortone and Williams (1986) stated that both juveniles and adults feed on fish, shrimp, and crabs.

Gray (mangrove) snapper

Gray snapper, *Lutjanus griseus*, occur in the Western Atlantic from Massachusetts to Brazil, including the Gulf of Mexico and Caribbean Sea. Most gray snapper landed in the U.S. South Atlantic are caught in Florida. This species occupies a variety of habitats during its life history (Burton 2001). It occurs at depths of 5-180 m (16-591 ft), in coral reefs, rocky areas, estuaries, mangrove areas, and in the lower reaches of rivers (especially the young). Gray snapper often forms large aggregations (Allen 1985).

Maximum reported size is 89.0 cm (35.2 in) TL (male) and 20.0 kg (44.4 lbs) (Allen 1985). Burton (2001) reported a maximum age of 24 year for gray snapper. M is estimated at 0.30 (Ault et al. 1998).

Gray snapper are gonochorists. Length and age at first maturity is estimated as 23.0 cm (9.1 in) FL and 2 years for females (Stark, 1971) and 22.0 cm (8.7 in) for males. Allen (1985) indicates that spawning occurs during summer near the time of the full moon. This species spawns during July and August in the Florida Keys (Thompson and Munro 1974a). In the northeastern Caribbean, individuals in spawning condition have been observed in May, August, and September (Erdman 1976). Off Cuba, gray snapper spawn during June through October with a peak in July (García-Cagide et al. 1994). In Key West, FL, female gray snapper spawn from June to September with a peak in July (Domeier et al. 1996).

The gray snapper feeds mainly at night on small fishes, shrimps, crabs, gastropods, cephalopods, and some planktonic items (Allen 1985). The stomachs of 18 juveniles collected off the south coast of Jamaica contained 60% by volume of larval fish and 40% crabs and shrimp (Thompson and Munro 1974a). Sierra et al. (1994) indicated that gray snapper feed on fish, mollusks, and benthic crustaceans.

Mutton snapper

Mutton snapper, *Lutjanus analis*, are found in the Western Atlantic from Massachusetts to southeastern Brazil, including the Caribbean Sea and the Gulf of Mexico. It is most abundant around the Antilles, the Bahamas, and off southern Florida. According to Allen (1985), mutton snapper can be found in both brackish and marine waters at depths of 25-95 m (82-312 ft). This species is captured on mud slopes off the southeast coast of Jamaica at depths of 100-120 m (328-656 ft) (Thompson and Munro 1974a). Juveniles generally occur closer to shore, over sandy, vegetated (usually *Thalassia*) bottom habitats, while large adults are commonly found offshore among rocks and coral habitat (Allen 1985).

Allen (1985), reported a maximum size of 94.0 cm (37.2 in) TL (male) and 15.6 kg (34.6 lbs). The largest male and female observed in a study conducted in Puerto Rico between February 2000 and May 2001 measured 70.0 cm (27.8 in) FL and 69 cm (27.3 in) FL, respectively (Figuerola et al. 1997). Burton (2002) reported a maximum age of 29 years for mutton snapper. M is estimated as 0.21 (Ault et al. 1998).

Mutton snapper are gonochorists (separate sexes). Size at 50% maturity is 33.0 cm (13.1 in) FL and 41.4 cm (16.4 in) FL for males and females, respectively, off Puerto Rico (Figuerola and Torrez Ruiz 2001). All males and females are probably mature by 43.1 cm (17.1 in) FL and 45.0 cm (17.8 in) FL, respectively. Spawning occurs in aggregations (Figuerola et al. 1997). Individuals have been observed in spawning condition in the U.S. Caribbean from February through July (Erdman 1976). Some spawning occurs during February to June off Puerto Rico, but spawning peaks during the week following the full moon in April and May. Spawning aggregations are known to occur north of St. Thomas, USVI, and south of St. Croix, USVI, in March, April, and May (Rielinger 1999). This species feeds on fishes, shrimps, crabs, cephalopods, and gastropods (Allen 1985).

Lane snapper

Lane snapper, *Lutjanus synagris*, occur in the Western Atlantic, ranging from North Carolina and Bermuda to southeastern Brazil, including the Gulf of Mexico and Caribbean Sea. It is most common near the Antilles, on the Campeche Bank, off Panama, and off the northern coast of South America. This species occurs over all bottom types, but is usually encountered near coral reefs and on vegetated sandy areas, in turbid as well as clear water, at depths of 10-400 m (33-1,311 ft) (Allen 1985). Larvae and juveniles can be found in sea grass beds and bays in the eastern Gulf of Mexico (Froese and Pauly 2003).

Maximum reported size is 60.0 cm (23.8 in) TL (male) and 3.5 kg (7.8 lbs) (Allen 1985). The world record is 8.3 lbs from Mississippi (Andy Strelcheck, Pers. Com.). Luckhurst et al. (2000) a maximum age of 19 years for lane snapper caught off Bermuda. In the northern Gulf of Mexico, the maximum reported age of lane snapper is 17 years (Johnson et al. 1995). Estimates of M ranged from 0.11 to 0.24 (Johnson et al. 1995).

Figuerola et al. (1997) estimated size at 50% maturity as 14.7 cm (5.8 in) FL (males) and 18.5 cm (7.3 in) FL (females) in the U.S. Caribbean. Mean size at maturity of lane snapper collected off Jamaica was 26.8 cm (10.6 in) and 22.1 cm (8.8 in) in males and females respectively. Lane snapper first become sexually mature at age 1 (Luckhurst et al. 2000).

This fish often forms large aggregations, especially during the spawning season (Allen 1985). Reproduction occurs over a protracted period, with some degree of reproductive activity occurring all year (Figuerola et al. 1997). Most spawning occurs from March to September in the U.S. Caribbean (Erdman 1976; Figuerola et al. 1997) with peak spawning during April to July. Spawning is believed to peak in June and July around the full moon off Jamaica (Figuerola et al. 1997). This species feeds at night on small fishes, benthic crabs, shrimps, worms, gastropods, and cephalopods (Allen 1985).

Cubera snapper

Cubera snapper, *Lutjanus cyanopterus*, occur in the Western Atlantic from Nova Scotia and Bermuda to Brazil. It also occurs throughout the Bahamas and Caribbean, including Antilles. It is rare north of Florida and in the Gulf of Mexico (Froese and Pauly 2003). Adults are found mainly around ledges over rocky bottoms or around reefs, at depths of 18-55 m (59-180 ft). Juveniles are reef-associated but also occur in brackish marine waters, and sometimes inhabit mangrove areas. Maximum reported sizes for cubera snapper are 160.0 cm (63.4 in) TL (male/unsexed) and 57.0 kg (126.5 lbs) (Froese and Pauly 2003). Appeldoorn et al. (1987) estimated the maximum length as 102.0 cm (40.4 in) TL. Cubera snapper spawn during July-August off Cuba (García-Cagide et al. 1994). Cubera snapper feed on fishes, crabs, and shrimp (Froese and Pauly 2003).

Dog snapper

Dog snapper, *Lutjanus jocu*, occur in the Western and Eastern Atlantic. In the Western Atlantic, it occurs from Massachusetts to northern Brazil, including the Gulf of Mexico and Caribbean. The dog snapper is found at depths of 5-30 m (16-98 ft). Adults are common around rocky or coral reefs. Young are found in estuaries, and occasionally enter rivers (Allen 1985).

Maximum reported size is 128.0 cm (50.7 in) TL (male) and 28.6 kg (63.4 lbs) (Allen, 1985). Approximate life span is 29 years, and M is estimated at 0.33 (Ault et al. 1998). Dog snapper are gonochorists. The mean length at sexual maturity off Cuba is 43.0 cm (17.0 in) for females and 48.0 cm (19.0 in) FL for males (García-Cagide et al. 1994). Dog snapper are reported to spawn throughout the year off Cuba (García-Cagide et al. 1999). In the Caribbean, females in spawning condition have been collected during February-March, and in November (Thompson and Munro 1974a). In the northeastern Caribbean, individuals in spawning condition have been observed in March (Erdman 1976). Spawning aggregations have been observed on the outer fore reef of a promontory along the central province of the Belize barrier reef (Carter and Perrine 1994).

The dog snapper feeds mainly on fishes and benthic invertebrates, including shrimps, crabs, gastropods, and cephalopods (Allen 1985). Sierra et al. (1994) indicate that 92% of the diet is fishes, 4% mollusks, and 4% benthic crustaceans.

Schoolmaster

Schoolmaster, *Lutjanus apodus*, are found in the Western and Eastern Atlantic Ocean. In the Western Atlantic, it is found from Massachusetts to Trinidad and northern Brazil, including the Gulf of Mexico and Caribbean Sea. The schoolmaster snapper is found in shallow, clear, warm, coastal waters over coral reefs, from 2 to 63 m (7-207 ft) deep. Adults often seek shelter near elkhorn corals and gorgonians. Juveniles are encountered over sand bottoms with or without seagrass (*Thalassia*), and over muddy bottoms of lagoons or mangrove areas. Young sometimes enter brackish waters (Allen 1985).

Allen (1985) reported maximum sizes as 67.2 cm (26.6 in) TL and 75.0 cm (29.7 in) FL for males and females, respectively. The maximum reported weight is 10.8 kg (24.0 lbs) (Allen 1985). Estimated M is 0.25 (Ault et al. 1998). Off Jamaica, the smallest mature female was 25.0 cm (9.9 in) long (García-Cagide et al. 1994).

The schoolmaster is a gonochorist. Ripe and/or recently spent fishes have been collected in nearshore and oceanic habitats off Jamaica in February-June and August-November (Thompson and Munro, 1974a). Erdman (1976) reports the occurrence of ripe males and females in September. Schoolmaster is reported to spawn during April-June off Cuba (García-Cagide et al. 1994).

Schoolmaster sometimes form resting aggregations during the day (Allen 1985). Schools of this species observed over reefs off Florida dispersed at dusk in search of food (Thompson and Munro 1974a). Prey items include fishes, shrimps, crabs, worms, gastropods, and cephalopods (Allen 1985).

Mahogany snapper

Mahogany snapper, *Lutjanus mahogoni*, occur in the Western Atlantic from North Carolina to Venezuela, including the Gulf of Mexico and Caribbean Sea. This species is common in the Caribbean but is rare in US waters (Froese and Pauly 2003). The mahogany snapper occurs in nearshore water as deep as 100 m (328 ft). It is usually found in clear, shallow water over rocky bottoms near coral reefs but occurs less frequently in sandy areas or seagrass. It often forms large aggregations during the day (Allen 1985) and has been observed to school with white grunt, *Haemulon plumieri*, at Grand Cayman (Thompson and Munro 1974a).

Maximum reported size is 48.0 cm (19.0 in) TL (male) and 1.3 kg (2.9 lbs) (Allen 1985). M is estimated at 0.30 (Ault et al. 1998). Ripe females have been observed during August in the northeastern Caribbean (Erdman 1976). This fish feeds at night mainly on small fish, shrimps, crabs, and cephalopods (Allen 1985).

Vermilion snapper

Vermilion snapper, *Rhomboplites aurorubens*, occur in the Western Atlantic, from North Carolina to Rio de Janeiro. It is most abundant off the southeastern United States and in the Gulf of Campeche (Hood and Johnson 1999). The vermilion snapper is demersal, commonly found over rock, gravel, or sand bottoms near the edge of the continental and island shelves (Allen 1985). It occurs at depths from 18 to 122 m (59 to 400 ft), but is most abundant at depths less than 76 m (250 ft). Individuals often form large schools. This fish is not believed to exhibit extensive long range or local movement (SEDAR 2 2003b).

The maximum size of a male vermilion snapper, reported by Allen (1985), was 60.0 cm (23.8 in) TL and 3.2 kg (7.1 lbs). Maximum reported age in the South Atlantic Bight was 14 years (Zhao et al. 1997; Potts et al. 1998b). SEDAR 2-SAR2 (2003) recommends that M be defined as 0.25/yr, with a range of 0.2-0.3/yr.

This species spawns in aggregations (Lindeman et al. 2000) from April through late September in the southeastern United States (Cuellar et al. 1996). Zhao et al. (1997) indicated that most spawning in the South Atlantic Bight occurs from June through August. Eggs and larvae are pelagic.

Vermilion snapper are gonochorists. All vermilion snapper are mature at 2 years of age and 20.0 cm (7.9 in) (SEDAR 2 2003b). Cuellar et al. (1996) collected vermilion snapper off the southeastern United States and found that all were mature. The smallest female was 16.5 cm (6.5 in) FL and the smallest male was 17.9 cm (7.1 in) FL (Cuellar et al. 1996). Zhao and McGovern (1997) reported that 100% of males that were collected after 1982 along the southeastern United States were mature at 14.0 cm (5.6 in) TL and age 1. All females collected after 1988 were mature at 18.0 cm (7.1 in) TL and age 1.

This species preys on fishes, shrimps, crabs, polychaetes, and other benthic invertebrates, as well as cephalopods and planktonic organisms (Allen 1985). Sedberry and Cuellar (1993) reported that small crustaceans (especially copepods), sergestid decapods, barnacle larvae, stomatopods, and decapods dominated the diets of small (< 50 mm (2 in) SL) vermilion snapper off the Southeastern United States. Larger decapods, fishes, and cephalopods are more important in the diet of larger vermilion snapper.

Red snapper

The red snapper, *Lutjanus campechanus*, is found from North Carolina to the Florida Keys, and throughout the Gulf of Mexico to the Yucatan (Robins and Ray 1986). It can be found at depths from 10 to 190 m (33-623 ft). Adults usually occur over rocky bottoms. Juveniles inhabit shallow waters and are common over sandy or muddy bottom habitat (Allen 1985).

The maximum size reported for this species is 100 cm (39.7 in) TL (Allen 1985 and Robins and Ray 1986) and 22.8 kg (50 lbs) (Allen 1985). Maximum reported age in the Gulf of Mexico is 53 years (Goodyear 1995). For samples collected from North Carolina to eastern Florida, maximum reported age is 45 years (White and Palmer 2004). Potts and Brennan (2001) estimated M at 0.25.

Red snapper are gonochorists. In the U.S. South Atlantic Bight and in the Gulf of Mexico, Grimes (1987) reported that size at first maturity is 23.7 cm (9.3 in) FL. For red snapper collected along the Southeastern United States, White and Palmer (2004) found that the smallest mature male was 20.0 cm (7.9 in) TL, and the largest immature male was 37.8 cm (15 in) TL. 50% of males are mature at 22.3 cm (8.8 in) TL, while 50% of females are mature at 37.8 cm (15 in) TL. Males are present in 86% of age 1, 91% of age 2, 100% of age 3, 98% of age 4, and 100% of older age fish. Mature females are present in 0% of age 1, 53% of age 2, 92% of age 3, 96% of age 4, and 100% of older age individuals. Grimes (1987) found that the spawning season of this species varies with location, but in most cases occurs nearly year round. White and Palmer (2004) reported that the spawning season for female red snapper off the southeastern United States extends from May to October, peaking in July through September. Red snapper eat fishes, shrimps, crabs, worms, cephalopods, and some planktonic items (Szedlemayr and Lee 2004).

Silk snapper

Silk snapper, *Lutjanus vivanus*, occur in the Western Atlantic, from North Carolina to Brazil, including the Bahamas and the northern Gulf of Mexico. It is commonly found along rocky ledges, in depths of 91-242 m (299-794 ft) (Robins and Ray 1986). Adults are generally found further offshore than juveniles (SAFMC, 1999), and usually ascend to shallow water at night (Allen 1985). However, juveniles are sometimes observed on deep reefs (Robins and Ray 1986). Silk snapper form moving aggregations of similar-sized individuals (Boardman and Weiler 1980).

Maximum reported size is 83.0 cm (32.9 in) TL and 8.3 kg (18.3 lb) (Allen 1985). Size at maturity and age at first maturity are estimated at 43.4 cm (17.2 in) TL and 6.3 years, respectively (Froese and Pauly 2003). Silk snapper do not change sex. Spawning occurs in June, July, and August in waters off North and South Carolina (Grimes 1987).

Silk snapper eat primarily fishes, shrimps, crabs, gastropods, cephalopods, tunicates, and some pelagic items, including urochordates (Allen 1985).

Blackfin snapper

Blackfin snapper, *Lutjanus buccanella*, occur in the Western Atlantic, generally ranging from North Carolina, south throughout the Bahamas, and the northern Gulf of Mexico, to southeast Brazil (Robins and Ray 1986). This is a demersal species. Adults occur in deep waters over sandy or rocky bottoms, and near drop-offs and ledges (Allen 1985), ranging from 50-91 m (164-300 ft) depth (Robins and Ray 1986). Juveniles occur in shallower waters, often associated with reefs in depths of 35-50 m (115-164 ft) (Allen 1985).

Male blackfin snapper can reach sizes of 75.0 cm (29.8 in) and 14 kg (30.9 lbs). Blackfin snapper are gonochorists. Off Jamaica, the length at first maturity for males is 25.0-27.0 cm (9.9-10.7 in) FL and the mean length of females is 23.0-25.0 cm (9.1-9.9 in) FL (Thompson and Munro 1983). Allen (1985) identified fishes as the primary prey item of blackfin snapper.

Black snapper

Black snapper, *Apsilus dentatus*, occur in the Western Central Atlantic, off the Florida Keys, and in the western Gulf of Mexico and Caribbean Sea. A demersal species, the black snapper is primarily found over rocky bottom habitat, although juveniles are sometimes found near the surface (Allen 1985 in Froese and Pauly 2003). It moves offshore to deep-water reefs and rocky ledges as it matures (SAFMC 1999). Allen (1985) reported the depth range as 100-300 m (328-984 ft). Off Jamaica, it is most abundant at depths of 60-100 m (197-328 ft) (Thompson and Munro 1974a).

Maximum reported size is 65.0 cm (25.7 in) TL (male) and 3.2 kg (7.1 lbs) (Allen 1985). Observed maximum fork lengths are 56.0 cm (22.2 in) FL and 54.0 cm (21.4 in) FL for males and females, respectively (Thompson and Munro 1974a).

Black snapper have separate sexes throughout their lifetime. Size and age at maturity estimated in Froese and Pauly (2003) is 34.9 cm (13.8 in) TL and 1 year, respectively. Estimated mean size at maturity for fish collected off Jamaica is 43.0-45.0 cm (17.0-17.8 in) FL and 39.0-41.0 (15.4-16.2 in) cm FL for males and females, respectively (Thompson and Munro 1974a). Off Cuba the mean size at maturity is 44.0 cm (17.4 in) FL for males and 40.0 cm (15.8 in) FL for females (García-Cagide et al. 1994).
In the northeastern Caribbean, individuals in spawning condition have been observed from February through April and in September (Erdman 1976). Off Jamaica, the greatest proportions of ripe fishes were found from January to April and from September to November (Thompson and Munro 1974a).

Large catches occasionally obtained over a short period suggest a schooling habit for this species (Thompson and Munro 1974a). Prey includes fishes and benthic organisms, including cephalopods, tunicates (Allen 1985), and crustaceans (Thompson and Munro 1974a).

Porgies (Sparidae)

Red porgy

The red porgy, *Pagrus pagrus*, occurs in both the Eastern and Western Atlantic Oceans. In the Western Atlantic, it ranges from New York to Argentina, including the northern Gulf of Mexico. Adults are found in deepwater near the continental shelf, over rock, rubble or sand bottoms, to depths as great as 280 m (918 ft). Red porgy are most commonly captured at depths of 25-90 m (82-295 ft). Young occur in water as shallow as 18 m (59 ft) (Robins and Ray 1986), and are sometimes observed over seagrass beds (Bauchot and Hureau 1990).
Maximum reported size is 91.0 cm (36.0 in) (Robins and Ray 1986) and 7.7 kg (17.1 lbs) (Bauchot and Hureau 1990). Maximum reported age of red porgy in the South Atlantic is 18 years (Potts and Manooch 2002).

Maximum reported length is 73.3 cm (28.9 in) in the South Atlantic (Potts and Manooch 2002). Based on histological examination of reproductive tissue, it has been determined that red porgy spawn from December through May off the southeastern United States, with a peak in January and February (Harris and McGovern 1997; Daniel 2003). Manooch (1976) examined red porgy ovaries macroscopically and stated that peak spawning of red porgy was during March-April.

Based on data collected off the southeast United States from 1995-2000, females first mature at 20.1-22.4 cm (8.0-8.9 in) TL, and at age 0. Size and age at 50% maturity is 28.9 cm (11.5 in) TL and 1.5 years, respectively. Red porgy are protogynous. At 35.1-40.0 cm (13.9-15.9 in) TL, 72% of all individuals collected during 1995-2000 were male; by age 9, 100% of all individuals were males. Researchers observed a much greater percentage of males in smaller size classes during recent years, than during the early 1980s (Daniel 2003). This species feeds on crustaceans, fishes, and mollusks (Bauchot and Hureau 1990).

Sheepshead

The sheepshead, *Archosargus probatocephalus*, is a reef-associated species that occurs to depths as great as 15 m (49 ft) from Nova Scotia, Canada and northern Gulf of Mexico to Brazil. Sheepshead have been observed to depths as great as 24 m (80 ft) in the Gulf of Mexico (Andy Strelcheck, pers.com.). It is absent in the Bahamas, West Indies, Bermuda, and Grenada (Froese and Pauly 2003). Sheepshead inhabits bays and estuaries. It freely enters brackish waters and is sometimes found in freshwater. Sheepshead are commonly found around pilings. Maximum reported size is 91.0 cm (36.0 in) TL (male/unsexed) and 9.6 kg (21.3 lbs) and maximum reported age is 20 years (Schwartz 1990). Sheepshead feeds on crabs, other benthic crustaceans, and mollusks (Lieske and Myers 1994).

Knobbed porgy

Knobbed porgy, *Calamus nodosus*, occur in the Western Atlantic Ocean from North Carolina to Southern Florida, and throughout the Gulf of Mexico (Robins and Ray 1986). This fish is a demersal species, and typically occurs over hard bottom habitat at depths from 7-90 m (23-295 ft) (Robins and Ray 1986). Maximum reported size is 54.4 cm (21.4 in) TL (male/unsexed) (Horvath et al. 1990) and 2.63 kg (5.8 lb) (Froese and Pauly 2003).

Maximum reported age is 21 years off the southeastern United States (Sharp 2001). Few immature fish were sampled by Sharp (2001). Length and age at which 100% of sampled fish are mature is 6 years and 29.8 cm (11.8 in) FL, respectively. Male to female sex ratios increased with increasing length and age, and histological evidence of protogyny was found. Females changed sex at 26.5-37.7 cm (10.5-15.0 in) FL and 5-20 years, during any time of year. Females spawned during March-July with a peak during April and May, with an estimated spawning frequency of 1.46 days.

Jolthead porgy

Jolthead porgy, *Calamus bajonado*, occur in the Western Atlantic from Rhode Island and Bermuda, southward to Brazil, including the northern Gulf of Mexico (Robins and Ray 1986). This species inhabits coastal waters from 3 to more than 200 m (10–656 ft) in depth. It can be found on vegetated sand bottoms, but occurs more frequently on coral and hard bottom. Large adults are usually solitary. Maximum reported size is 76.0 cm (30.1 in) FL (male) and 10.6 kg (23.4 lbs) (Robins and Ray 1986). Crabs and mollusks constitute its primary prey items (Robins and Ray 1986).

Scup

Scup, *Stenotomus chrysops*, occur in the Western Atlantic from Nova Scotia in Canada to Florida. Maximum reported size is 46.0 cm (18.2 in) TL (male/unsexed) and 2.1 kg (4.6 lbs). Length at 50% maturity is 15.5 cm (6.1 in) TL (O'Brien et al. 1993). Spawning is reported to occur during June off North Carolina. Scup feeds on squid, polychaetes, amphipods, and other benthic invertebrates.

Whitebone porgy

Whitebone porgy, *Calamus leucosteus*, are found in the Western Atlantic from North Carolina to southern Florida in the USA and the entire Gulf of Mexico (Waltz et al. 1982). They are most frequently encountered in or near sponge-coral habitats at depths of 10-100 m (33-328 ft). Off the Southeastern United States, maximum reported size is 41.0 cm (16.2 in) and maximum reported age is12 years (Waltz et al. 1982).

Whitebone porgy are protogynous and approximately 60% of the females undergo sex reversal (Waltz et al. 1982). Spawning occurs during April-August off the Southeastern United States with peak during May (Waltz et al. 1982). Off the Southeastern United States, whitebone porgy feed mainly on small hard-shelled species of gastropods, pagurid decapods, and sipunculids (Sedberry 1989). Polychaetes, pelecypods, barnacles, and fishes are also eaten. Larger individuals consume fishes and echinoderms.

Saucereye porgy

Saucereye porgy, *Calamus calamus*, are a reef-associated species that occurs from North Carolina and Bermuda to Brazil at depths of 1-75 m (3-246 ft). Adults are frequently found in coral areas, while the young prefer seagrass (e.g. *Thalassia*) and sandy bottoms. Maximum reported size is 56.0 cm (22.2 in) TL (male/unsexed) and 0.68 kg (1.5 lbs). The diet of saucereye porgy includes polychaetes, echinoderms, mollusks, crabs, gastropods, and other benthic crustaceans (Randall 1967).

Grass porgy

Grass porgy, *Calamus arctifrons*, occur in the Western Central Atlantic from southern Florida to Louisiana. It is also found in the eastern Gulf of Mexico. Grass porgy occurs in sea grass beds from near shore to depths of at least 22 m (72 ft). Small individuals have been known to form small aggregations. Maximum reported size is 25.0 cm (9.9 in) TL. Diet includes benthic invertebrates.

Longspine porgy

The longspine porgy, *Stenotomus caprinus*, is found on mud bottom from North Carolina to Georgia in the USA and in the Gulf of Mexico from northern Florida to Yucatan, Mexico at depths of 5-185 m (16-607 ft) (Froese and Pauly 2003). Maximum reported size is 30.0 cm (11.9 in) TL. Maximum age is reported to be 3 years. Their diet includes polychaetes, crabs, other benthic invertebrates, shrimps, prawns, fishes, stomatopods, and amphipods (Sheridan and Trimm 1983).

Grunts (Haemulidae)

White grunt

The white grunt, *Haemulon plumieri*, is a demersal fish distributed in coastal waters of the Atlantic Ocean from the Chesapeake Bay to southeastern Brazil, including the Bahamas, West Indies, eastern Gulf of Mexico, and the Central American coast (Potts and Manooch 2001). It has also been introduced in Bermuda (Fischer 1978; Darcy 1983; Sadovy and Severin 1992; Bohlke and Chaplin 1993). The white grunt is found in tropical and subtropical waters (Johnson 1978; Miller and Richards 1979; Darcy 1983). It inhabits nearshore sponge-coral ("live-bottom") habitats or offshore rocky outcrop habitats on the continental shelf along the southeastern coast of the United States and the Gulf of Mexico (Powles and Barans 1980; Darcy 1983) in depths ranging from 18-55 m (59-180 ft) (Huntsman 1976).

Maximum reported size is 53.0 cm (21.0 in) TL (male/unsexed) and 4.4 kg (9.8 lbs). White grunt occurring off North and South Carolina live for at least 27 years (Padgett 1997). Potts and Brennan (2001) estimate natural mortality for white grunt at 0.25.

Males are significantly larger than females. In fishery-independent samples, mature females are present in 50% of age 1 females, 88% of age 2 females, 99% of age 3 females, and 100% of older age females. Mature males from fishery-independent samples were present in 0% of age 1 males, 73% of age 2 males, 95% of age 3 males, and 100% of older age males. Females mature at 16.9-24.1 cm (6.7-9.5 in) TL (L50 = 16.7 cm (6.6 in) TL) and males mature at 17.3-27.7 cm (6.9-11.0) TL (L50 of 18.6 cm (7.4 in) TL). Off the southeastern United States, females are in spawning condition from March-September with a peak during May and June (Padgett 1997). Males are in spawning condition throughout the year with most activity occurring from March-June. Padgett (1997) indicated that the sex ratio of white grunt taken with fishery-dependent and fishery-independent gear was skewed towards females. White grunt feed on mollusks, polychaetes, fishes, benthic crustaceans, stomatopods, echinoderms, and amphipods (Bowman et al. 2000).

Black margate

Black margate, *Anistotremus surinamensis*, is found in the Western Atlantic from Florida, Bahamas, Gulf of Mexico Caribbean, and south American coast (Froese and Pauly 2003). It inhabits larger patch reefs and sloping rocky bottoms at depths of 3-20 m (10-66 ft). It attains sizes as large as 76.0 cm (30.1 in) TL and 5.8 kg (12.8 lbs). Spawning occurs May-July off Cuba (García-Cagide et al. 1994). Black margate feeds on echinoderms, gastropods, crabs, shrimp, prawns, fishes, and benthic invertebrates.

Margate

Margate, *Haemulon album*, occurs in the Western Atlantic from the Florida Keys to Brazil, including the Caribbean Sea. Margate are found in pairs or larger schools, over seagrass beds, sand flats, coral reefs, and wrecks in depths of 20-60 m (66-197 ft). Maximum reported size is 79.0 cm (31.3 in) TL (male) and 7.1 kg (2.1 lbs) (Cervigón 1993). Estimated natural mortality rate is 0.37 (Ault et al., 1998). García-Cagide et al. (1994) indicate that the mean size at maturity off Jamaica is 24.0 cm (9.5 in) FL. Peak spawning occurs during January and April off Jamaica, with a minor peak in September-November. In the northeastern Caribbean, individuals in spawning condition have been observed in February, March, April, and September (Erdman 1976). Margate off Cuba are in spawning condition throughout the year with a peak during March and April (García-Cagide et al. 1994). This fish feeds on benthic invertebrates, and has been observed to eat subsurface invertebrates such as peanut worms and heart urchins (Cervigón 1993).

Tomtate

The tomtate, *Haemulon aurolineatum*, occurs in the Western Atlantic from Massachusetts to Brazil, including the Gulf of Mexico and Caribbean Sea (Courtney, 1961). The tomtate inhabits seagrass beds, sand flats, patch reefs, rocky outcrops, and even muddy bottom habitat, to depths of 55 m (180 ft) (Manooch and Barans 1982; unpublished MARMAP data). Along the Southeastern United States, maximum reported length is 261.0 mm FL, female and the maximum reported age is 17 years (Mikell et al., 2007). Maximum reported age is 9 years along the Southeastern United States Estimated natural mortality rate is 0.33 (Ault et al. 1998).

Peak spawning occurs during January and April off Jamaica (Munro et al. 1973; Gaut and Munro 1983). In the northeastern Caribbean, individuals in spawning condition have been observed from January through May, and in July and August (Erdman 1976). Along the southeastern United States, female tomtate are in spawning condition from March through July, with peak spawning occurring in April through June. Nearly all females (99.4%) were mature within the 150-159 mm FL category and by age 2 (MARMAP unpublished data Mikell et al., 2007).

Prey items include small crustaceans, mollusks, other benthic invertebrates, plankton, and algae (Carpenter 2002). In the Southeast Atlantic, polychaetes and amphipods are the most important component of the diet (Sedberry 1985). Decapods are also frequently consumed, but make up a small percentage of the volume or number of prey items. Pelecypods are the most abundant prey and cephalochordates make up a large portion of the food volume.

Sailor's choice

The Sailor's choice, *Haemulon parra*, is a reef-associated species that occurs in the Western Atlantic including the Bahamas, Florida, northern Gulf of Mexico, throughout the Caribbean Sea, and Central and South American coasts (Froese and Pauly 2003). They inhabit shallow coastal reefs, with young occurring on seagrass beds at depths of 3-30 m (10-98 ft). Adults occur in schools in relatively open areas and the species is rare around oceanic islands. It attains a maximum size of 41.2 cm (16.3 in) TL. Sailor's choice feeds on annelids, benthic crustaceans, and echinoderms (Sierra et al. 1994).

Porkfish

The porkfish, *Anisotremus virginicus*, occurs in the Western Atlantic from Florida to Brazil, including the Gulf of Mexico and Caribbean Sea. It inhabits reef and rocky bottom habitats at depths of 2-20 m (7-65 ft). Maximum reported size is 40.6 cm (16.1 in) TL (male) and 0.93 kg (2.1 lbs) (Robins and Ray 1986). Estimated natural mortality rate is 0.43 (Ault et al. 1998). Peak spawning occurs during January and April offshore of Jamaica (Munro et al. 1973; Gaut and Munro 1983). In the northeastern Caribbean, individuals in spawning condition have been collected during April, July, October, and December (Erdman 1976). This species feeds at night on mollusks, echinoderms, annelids, and crustaceans. Juveniles pick parasites from the bodies of larger fishes (Robins and Ray 1986).

Bluestriped grunt

The bluestriped grunt, *Haemulon sciurus*, occurs in the Western Atlantic from Florida to Brazil, including the Gulf of Mexico and Caribbean. It is found in small groups over coral and rocky reefs to depth of 30 m (98.4 ft). Juveniles are abundant in seagrass (*Thalassia*) beds. Maximum reported size is 46.0 cm (18.2 in) TL (male) and 0.75 kg (1.7 lbs) (Froese and Pauly 2003).

Few fish are mature at sizes 18.0 cm (7.1 in) FL and that full maturity is probably at about 22.0 cm (8.7 in) FL (Munro et al. 1973; Gaut and Munro 1983). Peak spawning off Jamaica occurs during January-April, with a minor peak in September-November. In the northeastern Caribbean, individuals in spawning condition have been observed during January and March (Erdman 1976). Off Cuba, bluestriped grunt are reported to be in spawning condition during October through April with a peak during December and January (García-Cagide et al. 1994). The bluestriped grunt feeds on crustaceans, bivalves and, occasionally, on small fishes (Froese and Pauly 2003).

French grunt

The French grunt, *Haemulon flavolineatum*, occurs in the Western Atlantic from Bermuda, South Carolina, northern Gulf of Mexico, Caribbean, and Brazil. It occurs in large schools on rocky and coral reefs to depths of 60 m (197 ft). Juveniles are abundant in nearshore seagrass beds. Maximum reported size is 30.0 cm (11.9 in) TL (male) (Robins and Ray 1986).

French grunt become sexually mature at lengths of 12.0 cm (4.8 in) FL or less (Munro et al. 1973; Gaut and Munro 1983). Spawning probably occurs throughout the year off Jamaica. In the northeastern Caribbean, individuals in spawning condition have been observed in March and September (Erdman 1976). Small crustaceans are the primary prey (Robins and Ray 1986).

Cottonwick

Cottonwick, *Haemulon melanurum*, is found in the Western Atlantic from Bermuda, southeastern Florida, and the Bahamas to Brazil. It is also reported from Yucatan, Mexico (Froese and Pauly 2003). This reef-associated species occurs at depths ranging from 3-50 m (10-164 ft). Maximum reported size is 33.0 cm (13.1 in) TL (male/unsexed) and 0.55 kg (1.2 lbs).

The length at 50% maturity is 19.0 cm (7.5 in) FL off Jamaica (Billings and Munro 1974). Cottonwick feeds on benthic crustaceans and other benthic invertebrates.

Spanish grunt

Spanish grunt, *Haemulon macrostomum*, is found in the Western Atlantic from southern Florida and the Antilles to Brazil. This reef-associated species occurs in dense schools at depths of 5-25 m (16-82 ft) (Froese and Pauly 2003). The maximum size reported is 43.0 cm (17.0 in) TL (male/unsexed) and 0.85 kg (1.9 lbs). Spawning occurs during May and June off Cuba (García-Cagide et al. 1994). Spanish grunt feeds on benthic crustaceans and echinoderms (Froese and Pauly 2003).

Smallmouth grunt

The smallmouth grunt, *Haemulon chrysargeryum*, is a reef-associated species that occurs in the Western Atlantic in southern Florida, Bahamas, and Yucatan, Mexico to Brazil at depths of 0 - 25 m. They are of minor commercial importance and are more commonly used as bait and in aquariums. It inhabits exposed rocky areas and coral reefs often near elkhorn and staghorn corals. Smallmouth grunt commonly found in schools and juveniles are encountered in *Thalassia* beds. Adults are observed in coral reefs during the day but enter open waters at night to feed primarily on mainly on plankton, but also on small crustaceans and mollusks (Froese and Pauly 2003).

Jacks (Carangidae)

Greater amberjack

The greater amberjack, *Seriola dumerili*, is a pelagic and epibenthic member of the family Carangidae (Manooch and Potts 1997a). This species occurs in the Indo-West Pacific, and in the Western and Eastern Atlantic Oceans. In the Western Atlantic, it occurs as far north as Nova Scotia, Canada, southward to Brazil, including the Gulf of Mexico (Carpenter 2002; Manooch and Potts 1997a; Manooch and Potts 1997b). The greater amberjack is found at depths of 18-360 m (60-1,181 ft). It inhabits deep reefs, rocky outcrops or wrecks and, occasionally, coastal bays. Juveniles and adults occur singly or in schools in association with floating plants or debris in oceanic and offshore waters.

This species is the largest jack and the maximum reported size is 190 cm (75 in) and 80.6 kg (177.7 lbs) (Paxton et al. 1989). Sexual dimorphism was evident in greater amberjack, with females being larger at age than males, although females were significantly larger than males only for ages 3, 4, 7 and 9 (Harris et al. In press). Maximum reported age is 17 years (Manooch and Potts 1997a). The natural mortality rate is estimated to be 0.25 (Legault and Turner 1999).

Greater amberjack are gonochorists (separate sexes). The smallest mature female was 514 mm FL and the youngest was age 1, whereas the largest immature female was 826 mm FL and the oldest was age 5; the size at 50% maturity was 733 mm FL (95% CI = 719-745). Age at 50% maturity for females was 1.3 yr (95% CI = 0.7-1.7). All females were mature by 851-900 mm FL and age 6 (Harris et al. In press). The smallest mature male was 464 mm FL and the youngest was age 1, whereas the largest immature male was 755 mm FL and the oldest was age

5; the size at 50% maturity was 644 mm FL (95% CI = 610-666). All males were mature at 751-800 mm FL and age 6.

Based on the occurrence of migratory nucleus oocytes and postovulatory follicles (POFs), spawning occurs from January through June, with peak spawning in April and May. Although fish in spawning condition were captured from North Carolina through the Florida Keys, spawning appears to occur primarily off south Florida and the Florida Keys (Harris et al. In press). Greater amberjack in spawning condition were sampled from a range of depths, although the bulk of samples were from the shelf break. Given that annual fecundity in greater amberjack is indeterminate, estimates of spawning frequency and batch fecundity are necessary to estimate annual fecundity. Multiplying the estimated number of spawning events (n = 14) per year by batch fecundity (BF) estimates (BF = 7.955*FL – 6,093,049) for specimens 930-1296 mm FL produced estimates of potential annual fecundity that ranged from 18,271,400 to 59,032,800 oocytes (Harris et al. In press). Relative to age, estimates of potential annual fecundity ranged from 25,472,100 to 47,194,300 oocytes for ages 3-7.

Tagging data indicated that greater amberjack are capable of extensive movement that might be related to spawning activity. Greater amberjack tagged off South Carolina have been recaptured off Georgia, east Florida, Florida Keys, west Florida, Cancun Mexico, Cuba, and the Bahamas (MARMAP, unpublished data). Primary food items include fishes, such as bigeye scad, and invertebrates (Paxton et al. 1989 in Froese and Pauly 2003)

Crevalle jack

The crevalle jack, *Caranx hippos*, occurs in the Western Atlantic Ocean, ranging as far north as Nova Scotia, southward to Uruguay, including the northern Gulf of Mexico (Robins and Ray 1986).

This is a pelagic species, which is generally found over the continental shelf, although young are often found in brackish estuaries. The depth range is 1-350 m (3-1,148 ft) (Smith-Vaniz et al. 1990 in Froese and Pauly 2003). The crevalle jack forms schools, although large individuals may be solitary (Smith-Vaniz et al. 1990 in Froese and Pauly 2003). Maximum reported size is 150.0 cm (59.4 in) TL and 9.0 kg (20.0 lbs) (Robins and Ray 1986 in Froese and Pauly 2003).

Maximum reported age from Florida is 19 years (Snelson 1992). Males become sexually mature by age 4 or 5 and females are sexually mature when they are 5-6 years old. Its diet is composed of smaller fish, shrimp and other invertebrates (Saloman and Naughton 1984; Smith-Vaniz et al. 1990 in Froese and Pauly 2003).

Blue runner

The blue runner, *Caranx crysos*, occurs in the Eastern and Western Atlantic. In the Western Atlantic, it is found from Nova Scotia, Canada to Brazil, including the Gulf of Mexico and Caribbean. Blue runner is a pelagic species that occurs in water as deep as 100 m (328 ft), but generally stays close to the coast. Juveniles often occur in association with floating *Sargassum*. Maximum reported size is 70.0 cm (27.7 in) TL (male) and 5.1 kg (11.3 lbs) (Smith-Vaniz et al. 1990). Maximum reported age is 11 years (Smith-Vaniz et al. 1990). This species is believed to form spawning aggregations (Thompson and Munro 1974b). Thomas and Munro (1974b) indicate that blue runner spawn from February to September. Erdman (1976) indicate that off La Parguera, spawning occurs mainly during March through May. Prey items include fishes, shrimps, and other invertebrates (Smith-Vaniz et al. 1990).

Almaco jack

The almaco jack, *Seriola rivoliana*, occurs in the Indo-West Pacific, in the Eastern Pacific, and in the Western Atlantic, where it occurs from Massachusetts to northern Argentina. This species is thought to occur in the Eastern Atlantic as well, but the extent of its distribution there is not well established (Myers 1991). A benthopelagic species, the almaco jack inhabits outer reef slopes and offshore banks, generally at depths from 15-160 m (49-525 ft). It has been observed to occur in small groups. Juveniles are often seen around floating objects (Myers 1991).

Maximum reported size is 160.0 cm (63.4 in) FL (male) and 59.9 kg (132.1 lbs) (Myers 1991 in Froese and Pauly 2003). Size at maturity is estimated as 81.1 cm (32 in) FL (Froese and Pauly 2003). Fishes serve as its primary prey but invertebrates also make up a portion of its diet (Myers 1991).

Banded rudderfish

Banded rudderfish, *Seriola zonanta*, are found in the Western Atlantic from Nova Scotia, Canada to Santos, Brazil, including the Gulf of Mexico and the Caribbean Sea. They are absent from Bahamas and most islands (Froese and Pauly 2003). Adults are pelagic or epibenthic and confined to coastal waters over the continental shelf. Maximum reported size is 75.0 cm (29.7 in) TL (male/unsexed) and 5.2 kg (11.5 lbs). Banded rudderfish feed on shrimp and fishes.

Bar jack

The bar jack, *Caranx ruber*, occurs in the Western Atlantic from New Jersey to southern Brazil, including the Gulf of Mexico and throughout the Caribbean Sea. It is commonly found in clear insular areas or coral reef habitats off mainland coasts, from depths of 3-35 m (10-115 ft). Juveniles frequent areas with *Sargassum* (Berry and Smith-Vaniz 1978) and appear to be common in shallow water (0-15 m; 0-49 ft) reef habitats, but probably move to the outer margins of the shelf at or before maturity (Thompson and Munro 1974b). Bar jacks are sometimes solitary, but usually forms schools, possibly associated with spawning events (Berry and Smith-Vaniz 1978).

Maximum reported size is 69.0 cm (27.3 in) TL and 8.2 kg (18.2 lbs) (Berry and Smith-Vaniz 1978). The minimum size of maturity for both males and females off Jamaica is 22.0-23.9 cm (8.7-9.5 in) FL (Thompson and Munro 1974b). The mean length at maturity is 24.0 cm (9.5 in) TL for both sexes, and most fish are probably mature by 26.0-27.0 cm (10.3-10.7 in) FL. Spawning occurs during all year with peak spawning during April and October (Thompson and Munro 1974b). Peak spawning off Cuba occurs during April and July (García-Cagide et al. 1994). Prey items include fishes, shrimps, and other invertebrates (Berry and Smith-Vaniz 1978).

Lesser amberjack

The lesser amberjack, *Seriola fasciata*, occurs in the Eastern and Western Atlantic Oceans. In the Western Atlantic, it is found from Massachusetts to Brazil (Robins and Ray 1986). This is a benthopelagic species, primarily found in depths of 55-130 m (180-427 ft) (Smith-Vaniz et al. 1990). Maximum reported size is 68 cm (27 in) FL (Claro 1994). It feeds on squids and fishes (Smith-Vaniz et al. 1990).

Yellow jack

The yellow jack, *Caranx bartholomaei*, occurs in both the Western and Eastern Atlantic Oceans. In the Western Atlantic, its range extends from Massachusetts to Brazil, including the Gulf of Mexico and Caribbean Sea. It is usually found in offshore reef and open marine water habitat to depths of 50 m (164 ft). Yellow jack is solitary, but also has been observed to occur in small groups. Juveniles are often found near the shore on seagrass beds (Cervigón 1993), and probably move to the outer margins of the shelf at or before maturity (Thompson and Munro 1974b). They often occur in association with jellyfish or floating *Sargassum* (Cervigón 1993).

Maximum reported size is 100.0 cm (39.6 in) TL (male) and 14 kg (31.1 lbs) (Cervigón 1993). According to Cervigón (1993), yellow jack spawns offshore during February to October. Thompson and Munro (1974b) reported that fish in spawning condition have been collected in November off Jamaica. This species feeds on small fishes (Cervigón 1993).

Tilefishes (Malacanthidae)

Golden tilefish

Tilefish, *Lopholatilus chamaeleonticeps*, is distributed throughout the Western Atlantic, occurring as far north as Nova Scotia, to southern Florida, and in the eastern Gulf of Mexico (Robins and Ray 1986). According to Dooley (1978), the tilefish occurs at depths of 80-540 m (263-1,772 ft). Robins and Ray (1986) report the depth range of this fish as 82-275 m (270-900 ft). It is most commonly found at about 200 m (656 ft), usually over mud or sand bottom but, occasionally, over rough bottom (Dooley 1978).

Maximum reported size is 125 cm (50 in) TL and 30 kg (66 lbs) (Dooley 1978).. Maximum reported age is 40 years (Palmer et al. 2004). Radiocarbon aging indicates that tilefish may live for at least 50 years (Harris South Carolina Department of Natural Resources, personal communication). A recent SEDAR assessment estimated M at 0.07 (SEDAR 4 2004). Palmer et al. (2004) reported that this species spawns off the southeast coast of the United States from March through late July, with a peak in April. Grimes et al. (1988) indicated that peak spawning occurs from May through September in waters north of Cape Canaveral. Tilefish primarily prey upon shrimp and crabs, but also eat fishes, squid, bivalves, and holothurians (Dooley 1978).

Blueline tilefish

Blueline tilefish, *Caulolatilus microps*, occurs in the Western Atlantic Ocean, North Carolina to southern Florida and Mexico, including the northern (and probably eastern) Gulf of Mexico (Dooley 1978). Blueline tilefish are found along the outer continental shelf, shelf break, and upper slope on irregular bottom with ledges or crevices, and around boulders or rubble piles in depths of 30-236 m (98-774 ft) and temperatures ranging from 15 to 23°C (59-73.4° F) (Ross 1978; Ross and Huntsman 1982; Parker and Mays 1998).

Maximum reported size is 90 cm (35.7 in) TL and 7 kg (15 lbs) (Dooley 1978). Maximum reported age is 42 years. The SEDAR group estimated M is between 0.04 and 0.17 (SEDAR 4 2004). Spawning occurs at night, from February to October, with a peak in May at depths of 48-232 m (157-761 ft) (Harris et al. 2004). This species feeds primarily on benthic invertebrates and fishes (Dooley 1978).

Sand tilefish

Sand tilefish, *Malacanthus plumieri*, occur in the Western and Southeast Atlantic. In the Western Atlantic, the species ranges from North Carolina and Bermuda to Venezuela, Brazil, and to Rio de la Plata in Uruguay, including the Gulf of Mexico and Caribbean Sea. The sand tilefish occurs at depths of 10-153 m (33-502 ft), but is described as primarily a shallow-water benthic species. It generally occurs on sand and rubble bottoms, and is known to build mounds of rubble and shell fragments near reefs and grass beds. Maximum reported size is 70.0 cm (27.7 in) SL (male) and 1.1 kg (2.4 lbs) (Dooley 1978). There is little information on the life history of this species. Since blueline tilefish and other tilefish species are not hermaphroditic (Harris et al. 2004; Palmer et al. 2004), it is likely that sand tilefish is also a gonochorist. Prey items include stomatopods, fishes, polychaete worms, chitons, sea urchins, sea stars, amphipods, and shrimps (Dooley 1978).

Triggerfishes (Balistidae)

Gray triggerfish

Gray triggerfish, *Balistes capriscus*, are found in the Eastern Atlantic from the Mediterranean to Moçamedes, Angola and in the Western Atlantic from Nova Scotia to Bermuda, the northern Gulf of Mexico, and to Argentina. The gray triggerfish is associated with live bottom and rocky outcrops from nearshore areas to depths of 100 m (328 ft). It also inhabits bays, harbors, and lagoons, and juveniles drift at the surface with *Sargassum*.

Maximum reported size is 60 cm (23.76 in) TL (male/unsexed) and 6.2 kg (13.8 lbs; Froese and Pauly 2003). Males are significantly larger than females (Moore 2001). The maximum age of gray triggerfish collected from North Carolina to eastern Florida was 10 years (Moore 2001). The maximum age of gray triggerfish collected from the Northeastern Gulf of Mexico was 13 years (Johnson and Saloman 1984). Potts and Brennan (2001) estimated the natural mortality of gray triggerfish to be 0.30.

Gray triggerfish are gonochorists that exhibit nest-building and territorial reproductive behavior. Mature females from fishery-independent samples are found in 0% of age-0, 98 % of age-1 and age-2 fish, and 100% of fish older than age-3. Mature males from fishery-independent samples are present in 63% of age-1, 91% of age-2, 98% of age-3, 99% of age-4 and age-5, and 100% of older age fish. Females reach first maturity at 14.2 cm (5.6 in) FL, with an L50 of 15.8 cm (6.3 in) FL. Males first mature at 17.0 cm (6.7 in) FL, with a L50 of 18.0 cm (7.1 in) FL (Moore 2001).

Along the southeast United States, Moore (2001) determined that gray triggerfish spawn every 37 days, or 3-4 times per season. In contrast, Ingram (2001) estimated that gray triggerfish spawn every 3.7 days in the Gulf of Mexico. Off the southeast United States, female gray triggerfish are in spawning condition from April-August, with a peak of activity during June-

July. Male gray triggerfish are found in spawning condition throughout the year; however, there was a peak in activity during May-September (Moore 2001).

Ocean triggerfish

The ocean triggerfish, *Canthidermis sufflamen*, occurs in both the Western and Eastern Atlantic. In the Western Atlantic, it ranges from Massachusetts to South America, including the Gulf of Mexico and Caribbean. The ocean triggerfish is found at depths of 5-60 m (16-197 ft) (Robins and Ray 1986 in Froese and Pauly 2003), in mid-water or at the surface associated with *Sargassum* (Aiken 1983), near drop-offs of seaward reefs, and occasionally in shallow waters (Robins and Ray 1986 in Froese and Pauly 2003). This species is sometimes solitary, but also is known to form small groups in open water (Aiken 1983; Robins and Ray 1986 in Froese and Pauly 2003) of over 50 individuals. It is sometimes seen in association with the black durgon (Aiken 1983).

Maximum reported size is 65.0 cm (25.7 in) TL (male) and 6.1 kg (13.5 lbs) (Robins and Ray 1986). Off Jamaica, spawning occurs during January, May, August, September, and December, with a peak in September (Aiken 1983). In the northeastern Caribbean, individuals in spawning condition have been observed in April (Erdman 1976).

This species feeds primarily on large zooplankton (Robins and Ray 1986), but also has been observed to consume benthic invertebrates (Aiken 1983).

Queen triggerfish

The queen triggerfish, *Balistes vetula*, occurs in both the Eastern and Western Atlantic. In the Western Atlantic, its range extends from Massachusetts to southeastern Brazil, including the Gulf of Mexico and Caribbean (Robins and Ray 1986). It is generally found over rocky or coral areas at depths of 2-275 m (7-902 ft). It also has been observed over sand and grassy areas (Robins and Ray 1986). Juveniles tend to inhabit shallower waters, and then move into deeper water as they mature (Aiken 1983). This fish may school, but also has been observed alone and in small groups (Aiken 1983).

Maximum reported size is 60.0 cm (23.8 in) TL (male) and 5.4 kg (11.9 lbs) (Robins and Ray 1986). Aiken (1983) estimated mean size at maturity as 26.5 cm (10.5 in) fork length (FL) and 23.5 cm (9.3 in) for males and females, respectively, collected in a Jamaican study. Aiken (1983) reported that peak spawning occurs during January to February and from August to October. In the northeastern Caribbean, spawning reportedly occurs during February through June (Erdman 1976). Froese and Pauly (2003) estimate that queen triggerfish live for 12.5 years. The queen triggerfish feeds primarily on benthic invertebrates, such as sea urchins (Robins and Ray 1986).

Wrasses (Labridae)

Hogfish

Hogfish, *Lachnolaimus maximus*, occur in the Western Atlantic from Nova Scotia (Canada) to northern South America, including the Gulf of Mexico and Caribbean Sea (Robins and Ray 1986). Hogfish are primarily found in warm subtropical and tropical waters (SEDAR 6-SAR2

2004). Froese and Pauly (2003) reported that hogfish is found at depths of 3-30 m (10-98 ft) over open bottom or coral reef. However, hogfish have occasionally been captured by the MARMAP program at depths ranging from 23 to 53 m (75 to 174 ft) and have been observed during submersible dives off South Carolina at depths of 52 m (171 ft) (McGovern, Pers. Com.). Hogfish exhibit sexual dimorphism. Large males have an elongate pig-like snout that is lacking in females and small males. Males also exhibit dark markings on top of the head and along the base of the medial fins, as well as a dark spot behind the pectoral fin.

Maximum reported size is 91.0 cm (36.0 in) TL (male) and 10.0 kg (22.2 lbs) (Robins and Ray 1986). M is estimated as 0.13 (SEDAR6 - SAR2 2004). Maximum reported age in the eastern Gulf of Mexico is 23 years (McBride et al. 2001) and 13 years in the Florida Keys (McBride 2001). Ault et al. (2003) and McBride and Murphy (2003) indicated hogfish were experiencing overfishing, and increasing the minimum size could increase yield.

Hogfish are protogynous (McBride et al. 2001). Spawning aggregations have been documented to occur in water deeper than 16 m (52 ft) off La Parguera, Puerto Rico from December through April (Rielinger 1999). García-Cagide et al. (1994) reported that hogfish spawn off Cuba during May through July. Colin (1982) found that peak spawning of hogfish off Puerto Rico is during December through April. Off the Florida Keys, Davis (1976) reports that spawning occurs from September to April with a February and March peak. Hogfish primarily eat mollusks, but also feed on crabs and sea urchins (Robins and Ray 1986).

Puddingwife

Puddingwife, *Halichoeres radiatus*, occur in the Western and Eastern Central Atlantic. In the Western Atlantic, they are found from North Carolina and Bermuda to Brazil, including the Gulf of Mexico and Caribbean (Carpenter 2002). Adults are found on shallow patch or seaward reefs as deep as 55 m. Juveniles usually occur in shallower coral reefs.

Maximum reported size in the Atlantic is about 45cm (17.7 in) (Carpenter 2002). In the northeastern Caribbean, individuals in spawning condition have been observed in March, April, and December (Erdman 1976). Prey items include polychaetes, mollusks, sea urchins, crustaceans, and brittle stars (Carpenter 2002).

Spadefishes (Eppiphidae)

Atlantic spadefish

The Atlantic spadefish, *Chaetodipterus faber*, occurs in the Western Atlantic, from Massachusetts to southeastern Brazil, including the Gulf of Mexico and Caribbean (Robins and Ray 1986, Carpenter 2002). It has also been introduced to waters surrounding Bermuda (Hayse 1987). Atlantic spadefish is found in depths of 3-35 m (10-115 ft), and is abundant in shallow coastal waters, from mangroves and sandy beaches, to wrecks and harbors. Juveniles are common in estuaries. Adults often occur in large schools of up to 500 individuals (Carpenter 2002). Maximum reported size is 100 cm (39 in) TL (Carpenter 2002). Hayse (1987) reported that Atlantic spadefish live for at least 8 years off South Carolina.

Atlantic spadefish are gonochorists (Hayse 1987). Histological examination of gonads indicates that 64% of age 0 males are sexually mature and all males age 1 and older are mature. All age 0 females are immature, while all females age 1 and older are mature (Hayse 1987). Atlantic spadefish are in spawning condition off South Carolina during May-September with peak spawning occurring during May (Hayse 1987). In the northeastern Caribbean, individuals in spawning condition have been observed in May and September (Erdman 1976).

Atlantic spadefish feed on benthic invertebrates like crustaceans, mollusks, annelids, cnidarians, as well as on plankton (Robins and Ray 1986). Hayse (1987) reported that cannonball jellyfish is the dominant food item in Atlantic spadefish collected off South Carolina. Hydroids, epifaunal amphipods, and sea anemones are observed in considerably lower volumes.

4.1.2.2 Habitat

Inshore/estuarine habitat

Snapper grouper species utilize both pelagic (open ocean) and benthic (bottom) habitats during their life cycle. Free-swimming larval stages live in the water column and feed on zooplankton. Juveniles and adults are typically bottom dwellers and usually associate with hard structures on the continental shelf that have moderate to high relief; i.e., coral reefs, artificial reefs, rocky hard-bottom substrates, ledges and caves, sloping soft-bottom areas, and limestone outcroppings. More detail on these habitat types is found in Section 3.0 of this document. However, juveniles of some species, such as mutton snapper, gray snapper, dog snapper, lane snapper, yellowtail snapper, goliath grouper, red grouper, gag, snowy grouper, yellowfin grouper, black sea bass, Atlantic spadefish, and hogfish may occur in inshore seagrass beds, mangrove estuaries, lagoons, oyster reefs, and bay systems. In many species, various combinations of these habitats may be utilized during daily feeding migrations or seasonal shifts in cross-shelf distributions.

Offshore habitat

The principal snapper grouper fishing areas are located in live bottom and shelf-edge habitats; depths range from 54 to 90 feet or greater for live-bottom habitats, 180 to 360 feet for the shelf-edge habitat, and 360 to 600 feet for the lower-shelf habitat. Temperatures range from 11° to 27°C over the continental shelf and shelf-edge due to the proximity of the Gulf Stream, with lower shelf habitat temperatures varying from 11° to 14°C. The SEAMAP Bottom Mapping Project using a variety of data sources has mapped the extent and distribution of productive snapper grouper habitat on the continental shelf north of Cape Canaveral. Current data suggest that from 3% to 30% of the shelf is suitable bottom. These hard, live-bottom habitats may be low relief areas supporting sparse to moderate growth of immobile invertebrates, moderate relief reefs from 1.6 to 6.6 feet, or high relief ridges at or near the shelf break consisting of outcrops of rock that are heavily encrusted with immobile invertebrates such as sponges and sea fans. Live-bottom habitat is scattered irregularly over most of the shelf north of Cape Canaveral, but is most abundant off northeastern Florida. South of Cape Canaveral, the continental shelf narrows from 35 to 10 miles and less off the southeast coast of Florida and the Florida Keys. The lack of a large shelf area, presence of extensive, rugged living fossil coral reefs, and dominance of a tropical Caribbean fauna are distinctive characteristics.

Rock outcroppings occur throughout the continental shelf from Cape Hatteras, NC to Key West, FL. Generally, the outcroppings are composed of eroded limestone and carbonate sandstone and exhibit vertical relief ranging from less than ½ meter to over 10 meters. Ledge systems formed by rock outcrops and piles of irregularly sized boulders are common. It has been estimated that 24% (9,443 square kilometers) of the area between the 27 and 101 meter depth contours from Cape Hatteras to Cape Canaveral is reef habitat. Although the area of bottom between 100 and 300 meter depths from Cape Hatteras to Key West is small relative to the shelf as a whole, it constitutes prime reef fish habitat according to fishermen and probably contributes significantly to the total amount of reef habitat.

Man-made artificial reefs are also utilized to attract fish and increase fish harvests. Research on manmade reefs is limited and opinions differ as to whether or not artificial structures actually promote an increase of biomass or merely concentrate fishes by attracting them from nearby natural areas.

The distribution of coral and live hardbottom habitat as presented in the SEAMAP Bottom Mapping Project can be used as a proxy for the distribution of the species in the snapper grouper complex. These maps are available over the Council's Internet Mapping System under "Mapping/GIS" on the Habitat/Ecosystem section (www.safmc.net).

Additional information on use of offshore fish habitat by snapper grouper species has been obtained through the Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP). This fishery-independent survey program has been collecting data in the South Atlantic Bight region since 1973. The program began as a larval fish and groundfish survey of shelf and upper slope waters from Cape Fear to Cape Canaveral. However, since 1978, efforts of the South Carolina MARMAP program have concentrated on fishery-independent assessments of reef fish abundance and life history. The spatial distribution of sampling effort has varied considerably by gear type. Maps portraying the distribution of offshore species were created with this temporal and spatial variability in fishing effort in mind (see the Council's Habitat Plan). Maps of the distribution of snapper grouper species by gear type based on MARMAP data can be generated through the Council's Internet Mapping System under "Mapping/GIS" on the Habitat/Ecosystem section (www.safmc.net).

Spawning habitat

Along with habitat settlement patterns, spawning locations are a key demographic attribute of reef fish species. Protection of spawning habitats is an unquestionably logical component of managing essential fish habitat. Specific information on the spawning sites and component habitats for many snapper grouper species has been provided by the MARMAP Program (Sedberry et al. 2006). Several seasonal patterns are present: a) spawning is concentrated over one or two winter months (as in many groupers); b) spawning occurs at low levels year-round with one or two peaks in warmer months; and c) spawning occurs year-round with more than two significant peaks. In addition, spawning can occur in pairs or in various types of aggregations. Many species of groupers and snappers can form sizeable spawning aggregations. However, this may not be the case among all species in the snapper grouper management unit. In fact, some species that spawn in aggregations may also pair-spawn under certain conditions.

Species in the snapper grouper complex may form spawning aggregations in the same spawning locales for decades. One explanation for the choice of spawning sites has to do with the avoidance of egg predation. This assumes that the upward rush culminating the spawning act

takes place at structural features positioned in such a manner that eggs will be immediately carried offshore and away from predators on the reef. However, this hypothesis suffers from limited and sometimes contradictory experimental evaluation.
Spawning sites within Council's jurisdiction have been identified for many grouper and snapper species (Sedberry et al. 2006) and available information for other species suggests that shelf edge environments of moderate to high structural relief are sites of spawning for many species, perhaps throughout the entire South Atlantic region. In addition, shallow areas may also be spawning sites for some snapper grouper species such as goliath grouper. As new information becomes available, maps of all documented spawning areas will be created. In addition to pinpointing existing spawning information, this approach will allow the assessment of the spawning value of similar habitat types within Council's jurisdiction

4.1.2.3 Abundance and status of stocks

The Southeast, Data, Assessment, and Review process (SEDAR) process was initiated in 2002. Stocks in the Snapper Grouper Fishery Management Unit (FMU) that have gone through the SEDAR process include red porgy, black sea bass, vermilion snapper, yellowtail snapper, hogfish, goliath grouper, snowy grouper, and tilefish. Brief summaries of these assessments are provided below as well as links to the assessments.

Red porgy
Red porgy was the subject of the first SEDAR assessment that updated previous assessments conducted by Vaughan et al. (1991), Huntsman et al. (1994), Vaughan (1999), and Vaughan and Prager (2002). Data for the assessment were assembled and reviewed at a data workshop during the week of March 11, 2002, in Charleston, SC. The assessment utilized commercial and recreational landings, as well as abundance indices and life history information from fishery-independent and fishery-dependent sources. Four abundance indices were developed: two indices derived from CPUE in the NMFS headboat survey (1976-1991; 1992-1998), and two derived from CPUE observed by the South Carolina MARMAP fishery-independent monitoring program ("Florida" trap index, 1983-1987; and chevron trap index, 1990-2001) (SEDAR 1 2002).

At the assessment workshop (AW), age-structured and production models were applied to available data. Although the AW determined that the age-structured model provided the most definitive view of the population, both models provide a similar picture of the status of red porgy. SEDAR 1 (2002) indicated that, given the different assumptions used by each type of model and the lack of age structure in the production models, this degree of agreement increased confidence in the assessment results. It was concluded that the stock was overfished, but overfishing was not occurring (Table 4.1-4).

Table 4.1-4. Stock assessment parameters for red porgy.
Values are those recommended by SARC and SEFSC staff (SEDAR 1 2002).

Parameter	Value	Notes	Status
M	0.225		
F_{MSY}	0.19		

SSB_{MSY}	3,050	Metric Tons	
MSST	2,364	$(1-M)*B_{MSY}$; Metric Tons	
MSY	375	Metric Tons	
F_{2001}/F_{MSY}	0.45		Not Overfishing
SSB_{2001}/SSB_{MSY}	0.44		
$SSB_{2001}/MSST$	0.57		Overfished

The South Atlantic Council defined the rebuilding schedule for red porgy in Amendment 12 to the Snapper Grouper FMP. That schedule is 18 years, which is the maximum allowable rebuilding time frame based on the formula: TMIN (10 years) + one generation time (8 years) (SAFMC 2000). The schedule began with the implementation of a no harvest emergency rule in September of 1999 (64 FR 48324), and ends December 31, 2017.

Black Sea Bass

2003 Assessment

At the second SEDAR (SEDAR 2 2003a), assessments were conducted on black sea bass and vermilion snapper, which updated a black sea bass assessment conducted by Vaughan et al. (1996) and a vermilion snapper assessment conducted by Manooch et al. (1998). Data for the SEDAR assessment were assembled and reviewed at a data workshop held during the week of October 7, 2002 in Charleston, SC. The assessment utilized commercial and recreational landings, as well as abundance indices and life history information from fishery-independent and fishery-dependent sources. Six abundance indices were developed by the data workshop. Two CPUE indices were used from the NMFS headboat survey (1978-2001) and the MRFSS recreational survey (1992-1998). Four indices were derived from CPUE observed by the South Carolina MARMAP fishery-independent monitoring program ("Florida" trap index, 1981-1987; blackfish trap index, 1981-1987; hook and line index, 1981-1987; and chevron trap index, 1990-2001) (SEDAR 2 2003a).

Age-structured and age-aggregated production models were applied to available data at the assessment workshop. The age-structured model was considered the primary model, as recommended by participants in the data workshop. The stock assessment indicated that black sea bass was overfished and overfishing was occurring (Table 4.1-5).

Previously, the rebuilding clock for black sea bass was restarted with the effective date of the regulations implementing the Sustainable Fisheries Act (SFA) Comprehensive Amendment on December 2, 1999. Black sea bass rebuilt to Bmsy within 10 years (December 2, 2009). The stock assessment indicated that black sea bass could not be rebuilt to SSBmsy in 10 years in the absence of fishing mortality (SEDAR 2 2003a). The maximum rebuilding time is 18 years based on the formula: TMIN (11 years) + one generation time (7 years).

Table 4.1-5. Stock assessment parameters for black sea bass.

Note: M=0.3 and steep=free (SEDAR 2 2003a).

Parameter (Table 6-2	**Value**	**Notes**	**Status**
F_{2001}	1.04		
SSB_{2002}	1,755	As of January 1, 2002; Metric Tons	
F_{MSY}	0.2		
$F_{0.1}$	0.29		
F_{MAX}	0.83		
SSB_{MSY}	13,500	Metric Tons	
MSY	1,730	Metric Tons	
MSST	9,460	Metric Tons	
F_{2001}/F_{MSY}	5.22		Overfishing
SSB_{2002}/SSB_{MSY}	0.13		
SSB_{2002}/MSST	0.19		Overfished
Reduction Needed to End Overfishing	50-90%		
Rebuilding in Absence of Fishing	11 years	If F=0	

2005 Update

At the request of the SAFMC, the SEDAR panel convened to update the 2003 black sea bass stock assessment, using data through 2003, and to conduct stock projections based on possible management scenarios (SEDAR Update 1, 2005). The assessment indicated that the stock was overfished and overfishing was occurring (Table 4.1-6). However, the stock could be rebuilt to BMSY in 5 years when F = 0.

Table 4.1-6. Stock assessment parameters from black sea bass update 1 (SEDAR Update 1, 2005).

Parameter	**Value**	**Notes**	**Status**
F_{2003}	2.641		
SSB_{2004}	1,858	Metric Tons	

Parameter	Value	Notes	Status
F_{MSY}	0.429	Fully selected fishing mortality rate	
E_{MSY}	0.100	Ages 1+	
SSB_{MSY}	6,812	Metric Tons	
MSY	1,260	Metric Tons	
MSST	4,768	Metric Tons	
F_{2003}/F_{MSY}	6.151		Overfishing
E_{2003}/E_{MSY}	1.617		
SSB_{2004}/ SSB_{MSY}	0.273		Overfished
$SSB_{2004}/$ MSST	0.390		
Reduction Needed to End Overfishing	62%		
Rebuilding in Absence of Fishing	5 years	F = 0	

Vermilion snapper
The vermilion snapper assessment utilized commercial and recreational landings, as well as abundance indices and life history information from fishery-independent and fishery-dependent sources. Four abundance indices were developed by the data workshop. One CPUE index was developed from the NMFS headboat survey, 1973-2001. Three indices were derived from CPUE observed by the South Carolina MARMAP fishery-independent monitoring program ("Florida" trap index, 1983-1987; hook and line index, 1983-1987; and chevron trap index, 1990-2001) (SEDAR 2 2003b).

A forward-projecting model of catch at length was formulated for this stock. Two other models (forward-projecting catch at age and age-aggregated production model) were applied but neither could provide estimates. The assessment was based on the catch-at-length model, which was applied in a base run and eight sensitivity runs. The assessment indicated that the stock was undergoing overfishing but that there was a high level of uncertainty in the overfished condition as the stock recruitment relationship was poorly defined (Table 4.1-7).

Table 4.1-7. Stock assessment parameters for vermilion snapper (SEDAR 2, 2003b).

Parameter	Value	Notes	Status
$F_{PROJECTED}$	0.60	Averaged over the last 3 years	

F_{2001}	0.64		
F_{MSY}	0.36		
F_{MAX}	0.375		
$F_{40\%}$	0.33		
E_{MSY}	5.06×10^{11}	Eggs; E=Egg Production (Analogous to spawner biomass)	
MSST	3.8×10^{11}		
MFMT	0.36/year	= F_{MSY}	
E_{2002}/E_{MSY}	0.66	Eggs; E=Egg Production (Analogous to spawner biomass)	
F_{2001}/F_{MSY}	1.78		Overfishing

Yellowtail snapper

The stock assessment on yellowtail snapper was conducted by the State of Florida but went through the SEDAR review process (Muller et al. 2003). Abundance indices were developed from MRFSS data and from commercial CPUE data. Two age-structured models (Fleet-Specific and Integrated Catch at Age) were formulated for the stock. The results from both models were very similar and neither model was recommended to represent the status of the stock. It was concluded that yellowtail snapper was not overfished and was not experiencing overfishing (Table 4.1-8).

Table 4.1-8. Stock assessment parameters for yellowtail snapper (Muller et al., 2003).

Parameter	ICA Model	Fleet-Specific Model	Notes	Status
F_{2001}	0.19	0.24		
F_{MSY}	0.33	0.33		
F_{OY}	0.21	0.21		
MSY	946	1,388	Metric Tons	
MSST	2,947	4,288	(1-M)*(B_{MSY}); Metric Tons	
MFMT	0.33	0.33	F_{MSY}	
F_{2001}/MFMT	0.6	0.7		Not Overfishing

SSB_{2001}/B_{MSST}	1.5	1.2		Not Overfished

Goliath Grouper
The summary below is from NMFS. 2006. Status report on the continental United States distinct population segment of the goliath grouper (*Epinephelus itajara*). January 12, 2006. 49 pp.

This status report provides a summary of information gathered for the continental United States distinct population segment (DPS) of the goliath grouper (*Epinephelus itajara*), which was formerly on the 1999 Endangered Species Act (ESA) candidate species list and currently is considered a species of concern. The purpose of this status report is to investigate the current status of goliath grouper relative to the criteria for including a species on the species of concern list, in light of updated information about the status of and threats to the continental U.S. DPS of the goliath grouper.

Goliath grouper is a long-lived and late-maturing serranid. The species depends on mangrove habitat during its early development, and recovery of the species may be impacted by habitat loss and degraded water quality along the coast. Because goliath grouper readily strike at a baited hook or a struggling fish and are easily approached by divers (i.e., spearfishermen), large juvenile goliath grouper and adults are susceptible to harvest. Additionally, goliath grouper aggregate to spawn and are particularly vulnerable to fishing during this period.

Historically, the distribution of the species within the continental U.S. stretched from North Carolina through Texas, with the center of abundance extending from the central east coast of Florida through the Gulf of Mexico to the Florida Panhandle. The population showed a decline in abundance and a truncation of range during the late 1970s and 1980s, primarily due to overutilization by the recreational and commercial fisheries.
Because of goliath grouper population declines, fishery regulations and eventual prohibitions were enacted to conserve and manage the population. Both the Gulf of Mexico Fishery Management Council (GMFMC) and the South Atlantic Fishery Management Council (SAFMC) prohibited the harvest and possession of goliath grouper in 1990. Likewise, the state of Florida prohibited the harvest and possession of goliath grouper from state waters in 1990, followed by all other coastal states from North Carolina through Texas.

The declines in abundance and occurrence of goliath grouper also prompted several organizations to recognize the species' uncertain status in an effort to provide additional consideration related to its management. NMFS identified the species as a candidate for possible listing as threatened or endangered under the ESA in 1991 for the entire range of the species within continental U.S. waters (56 FR 26797). In 1996, the World Conservation Union (IUCN) recognized the species as "critically endangered" throughout its range and distribution based on the conclusion that the species has been "observed, estimated, inferred, or suspected" of a reduction in abundance of at least 80 percent over the last 10 years or three generations (IUCN, 2005). The IUCN considers a species "critically endangered" if it appears to be at an "extremely high risk of extinction in the wild in the immediate future." Furthermore, in reports submitted to Congress under the

Magnuson Stevens Fishery Conservation and Management Act (MSFCMA) on the status of fisheries in U.S. waters between 1999 and 2005, NMFS identified goliath grouper as "overfished," meaning the level of fishing mortality has jeopardized the capacity of the fishery to produce the maximum sustainable yield on a continuing basis (i.e., the population is below a level considered healthy, requiring management action to achieve an appropriate level and rate of rebuilding). However, in 2000, the American Fisheries Society identified goliath grouper as being conservation dependent, which is a category that recognizes the species is reduced but stabilized or recovering under a continuing conservation plan (Musick et al. 2000).

In 2004, a Southeast Data, Assessment, and Review (SEDAR) assessment indicated that the goliath grouper stock in south Florida waters was recovering, but that full recovery to the MSFCMA management target might not occur until 2020 or later (SEDAR 2004). Based on the results of the assessment and due to inquiries from numerous stakeholders, NMFS proceeded to evaluate whether the continental U.S. population of goliath grouper still warranted species of concern status.

After evaluating the most up-to-date data, the NMFS assessment team concludes that the continental U.S. DPS of goliath grouper has undergone significant increases in abundance since its identification in 1991 as a candidate species under the ESA. The species has also become re-established throughout its historical range. Due to management actions implemented via the MSFCMA, extraction of goliath grouper by commercial and recreational fisheries is currently not a threat to the species. While the team is concerned about the rate of habitat loss and modification, in particular the loss of mangrove habitat, we do not feel the current habitat loss is a factor affecting the species' status at this time. Therefore, the team believes inclusion of goliath grouper on the NMFS' species of concern list is no longer warranted due to the fact that it no longer meets the definition of a species of concern.

Hogfish

The hogfish assessment was conducted under contract to the State of Florida (SEDAR 6-SAR2 2004). It was reviewed by SEDAR because the Gulf of Mexico Fishery Management Council and the South Atlantic Fishery Management Council manage hogfish. The SEDAR Review Panel did not find a solid basis for accepting the quantitative assessment and had further reservations that, even if the problems with the assessment were corrected, the model was still limited in its geographic application to the Florida Keys.

Snowy Grouper

The data workshop convened in Charleston, SC during the week of November 3, 2003 to examine data from eight deep-water species for assessment purposes. The group determined that data were adequate to conduct assessments on snowy grouper and tilefish. Four indices were available for snowy grouper including a logbook index, headboat index, MARMAP trap index, and MARMAP short longline index. The assessment workshop chose not to use the logbook index for snowy grouper due to reasons listed below. Commercial and recreation landings as well as life history information from fishery-independent and fishery-dependent sources were used in the assessment.

A statistical catch-at-age model and a production model were used to assess the snowy grouper population (SEDAR 4 2004). The population was determined to be overfished and experiencing overfishing (Table 4.1-9). In the absence of fishing it was determined that it would take 13 years to rebuild the stock to SSBmsy. The maximum rebuilding time is 34 years based on the formula: TMIN (13 years) + one generation time (21 years).

Table 4.1-9. Stock assessment parameters for snowy grouper (SEDAR 4, 2004).

Parameter	**Value**	**Notes**	**Status**
E_{MSY}	0.037	Median estimate under current gear pattern $_{M}$. E=exploitation rate, the fraction of fish by number taking during one year of fishing. E=C/N, where C=catch in a fishing year and N=number of fish at beginning of year.	
$E_{30\%}$	0.046		
$E_{40\%}$	0.035		
B_{MSY}	2,481	Median value in metric tons	
SSB_{MSY}	2,116	Median value in metric tons	
MSST	1,587	0.75*SSB_{MSY} (metric tons)	
SSB_{2002}/ SSB_{virgin}	0.05		Overfished
E_{2002}/E_{MSY}	3.11		Overfishing
SSB_{2002}/ SSB_{MSY}	0.18	Median value	
Reduction Needed	68%	Reduction in fishing pressure needed to end overfishing	Reduction Needed
Rebuilding Projection	13 years	If no fishing, population will recover to SSB_{MSY} in 13 years based on 2002 data.	

Tilefish

There were two indices of abundance available for the tilefish stock assessment (SEDAR 4 2004). A fishery-independent index was developed from MARMAP horizontal longlines. A fishery-dependent index was developed from commercial logbook data during the data workshop. Commercial and recreation landings as well as life history information from fishery-independent and fishery-dependent sources were used in the assessment.

A statistical catch-at-age model and a production model were used to assess the tilefish population (SEDAR 4 2004). It was determined that this population was not overfished but overfishing was occurring (Table 4.1-10).

Table 4.1-10. Stock assessment parameters for tilefish (golden) (SEDAR 4 2004).

Parameter	**Value**	**Notes**	**Status**

Parameter	Value	Notes	Status
E_{MSY}	0.035 per year	Median estimate using average E among three$_{\%}$ fisheries for 1999-2002 and their respective selectivity patterns. E=exploitation rate, the fraction of fish by number taking during one year of fishing. E=C/N, where C=catch in a fishing year	
$E_{30\%}$	0.047	Based on ages 1+$_{\text{Y \%}}$	
$E_{40\%}$	0.035	Based on ages 1+$_{\text{Y \%}}$	
B_{MSY}	2,611.4	Median value in metric tons	
SSB_{MSY}	879.4	Median value in metric tons	
$MSST_{MSY}$	659.6	0.75*SSB_{MSY} (metric tons) Based on ages 1+	
E_{2002}/E_{MSY}	1.55	Median value	Overfishing
SSB_{2002}/SSB_{MSY}	0.95	Median value	
SSB_{2002}/ MSST	1.27		Not Overfished
Reduction Needed	35%	Reduction in fishing pressure needed to end overfishing.	Reduction Needed
Rebuilding Projection	1 year	If no fishing, population will recover to SSB_{MSY} in 1 year based on 2002 data.	

Gag
The SEDAR assessment for gag was completed in 2006 (Table 4.1-11) and based a statistical catch-at-age (primary model) and an age-aggregated production model. Data sources were fishery dependent indices.

Table 4.1-11. Stock assessment parameters for gag (SEDAR 10 2006).

Parameter	Value	Notes	Status
E_{MSY}	0.035 per year	Median estimate using average E among three$_{\%}$ fisheries for 1999-2002 and their respective selectivity patterns. E=exploitation rate, the fraction of fish by number taking during one year of fishing. E=C/N, where C=catch in a fishing year	
$E_{30\%}$	0.047	Based on ages 1+$_{\text{Y \%}}$	
$E_{40\%}$	0.035	Based on ages 1+$_{\text{Y \%}}$	
B_{MSY}	2,611.4	Median value in metric tons	
SSB_{MSY}	879.4	Median value in metric tons	
$MSST_{MSY}$	659.6	0.75*SSB_{MSY} (metric tons) Based on ages 1+	
E_{2002}/E_{MSY}	1.55	Median value	Overfishing
SSB_{2002}/SSB_{MSY}	0.95	Median value	
SSB_{2002}/ MSST	1.27		Not

Parameter	Value	Notes	Status
			Overfished
Reduction Needed	35%	Reduction in fishing pressure needed to end overfishing.	Reduction Needed
Rebuilding Projection	1 year	If no fishing, population will recover to SSB_{MSY} in 1 year based on 2002 data.	

4.1.3 Coastal Migratory Pelagics

Description and Distribution

(from CMP Am 15)
The coastal migratory pelagics management unit includes cero (*Scomberomous regalis*), cobia (*Rachycentron canadum*), king mackerel (*Scomberomous cavalla*), Spanish mackerel (*Scomberomorus maculatus*) and little tunny (*Euthynnus alleterattus*). The mackerels and tuna in this management unit are often referred to as "scombrids." The family Scombridae includes tunas, mackerels and bonitos. They are among the most important commercial and sport fishes. The habitat of adults in the coastal pelagic management unit is the coastal waters out to the edge of the continental shelf in the Atlantic Ocean. Within the area, the occurrence of coastal migratory pelagic species is governed by temperature and salinity. All species are seldom found in water temperatures less than 20°C. Salinity preference varies, but these species generally prefer high salinity. The scombrids prefer high salinities, but less than 36 ppt. Salinity prefence of little tunny and cobia is not well defined. The larval habitat of all species in the coastal pelagic management unit is the water column. Within the spawning area, eggs and larvae are concentrated in the surface waters.

(from PH draft Mackerel Am. 18)
King Mackerel
King mackerel is a marine pelagic species that is found throughout the Gulf of Mexico and Caribbean Sea and along the western Atlantic from the Gulf of Maine to Brazil and from the shore to 200 meter depths. Adults are known to spawn in areas of low turbidity, with salinity and temperatures of approximately 30 ppt and 27°C, respectively. There are major spawning areas off Louisiana and Texas in the Gulf (McEachran and Finucane 1979); and off the Carolinas, Cape Canaveral, and Miami in the western Atlantic (Wollam 1970; Schekter 1971; Mayo 1973).

(from PH draft Mackerel Am 18)
Spanish Mackerel
Spanish mackerel is also a pelagic species, occurring over depths to 75 meters throughout the coastal zones of the western Atlantic from southern New England to the Florida Keys and throughout the Gulf of Mexico (Collette and Russo 1979). Adults usually are found in neritic waters (area of ocean from the low-tide line to the edge of the continental shelf) and along coastal areas. They inhabit estuarine areas, especially the higher salinity areas, during seasonal migrations, but are considered rare and infrequent in many Gulf estuaries.

Cero Mackerel

(from the Florida Museum of Natural History website – see link below)
The elongate, streamlined body of the cero mackerel is well-adapted for swimming at speeds up to 30 mph (48 kph). The body is covered with small scales, with the lateral line sloping downwards toward the caudal peduncle. Another similar fish, the king mackerel, can be distinguished from the cero mackerel as it has a lateral line that curves downward below the second dorsal fin. The caudal fin is lunate and the pelvic fins are relatively long. Scales extend out onto the pectoral fins. This characteristic distinguishes it from the king mackerel and the Spanish mackerel, two scombrids lacking scales on the pectoral fins.

The range of the cero mackerel is limited to the western Atlantic Ocean, from Massachusetts south to Brazil, including the Bahamas and West Indies. It is common in the Caribbean, Bahamas, and Florida. Usually solitary, the cero mackerel occasionally forms schools over coral reefs, wrecks, and along ledges at depths ranging from 3.3 to 66 feet (1-20 m). It is usually seen in mid-water and near the water's surface.

Little Tunny
(from the Florida Museum of Natural History website – see link below)
The little tunny, *Euthynnus alletteratus*, is a member of the family Scombridae. It is steel blue with 3-5 broken, dark wavy lines, not extending below the lateral line. The belly is white and lacks stripes. There are 3-7 dark spots between the pelvic and pectoral fins. Spots below the pectoral fin are dusky. The little tunny has a robust, torpedo-shaped body built for powerful swimming. The mouth is large, slightly curved, and terminal with rigid jaws with the lower jaw slightly protruding past the upper jaw. Scales are lacking on the body except for the corselet and the lateral line. The corselet is a band of large, thick scales forming a circle around the body behind the head, extending backwards along the lateral line. The lateral line is slightly undulate with a slight arch below the front of the dorsal fin, then straight to the caudal keel. The caudal fin is deeply lunate, with a slender caudal penduncle including one short keel on each side.

The little tunny is found worldwide in tropical to temperate waters, between 56°N-30°S. In the western Atlantic Ocean, it ranges from Massachusetts south to Brazil, including the Gulf of Mexico, Caribbean Sea, and Bermuda. It is the most common scombrid in the western north Atlantic. This fish is typically found in nearshore waters, inshore over the continental shelf in turbid, brackish waters. Adult little tunny school according to size with other scombrid species at depths ranging from 1-150 m (3-490 feet). However, during certain times of the year the schools break apart with individuals scattering throughout the habitat. Juveniles form compact schools offshore.

Cobia
(from the FL Mus. of Natural History)
The cobia, *Rachycentron canadum*, is a member of the family Rachycentridae. It is managed under the Coastal Migratory Pelagics FMU because of its migratory behavior. The cobia is distributed worldwide in tropical, subtropical and warm-temperate waters. In the western Atlantic Ocean this pelagic fish occurs from Nova Scotia (Canada), south to Argentina, including the Caribbean Sea. It is abundant in warm waters off the coast of the U.S. from the Chesapeake Bay south and through out the Gulf of Mexico. Cobia prefer water temperatures between 68°-86°F. Seeking shelter in harbors and around wrecks and reefs, the cobia is often found off south

Florida and the Florida Keys. As a pelagic fish, cobia are found over the continental shelf as well as around offshore reefs. It prefers to reside near any structure that interrupts the open water such as pilings, buoys, platforms, anchored boats, and flotsam. The cobia is also found inshore inhabiting bays, inlets, and mangroves. Remoras are often seen swimming with cobia.

The body is dark brown to silver, paler on the sides and grayish white to silvery below, with two narrow dark bands extending from the snout to base of caudal fin. These dark bands are bordered above and below by paler bands. Young cobia have pronounced dark lateral bands, which tend to become obscured in the adult fish. Most fins are deep brown, with gray markings on the anal and pelvic fins. The body is elongate and torpedo-shaped with a long, depressed head. The eyes are small and the snout is broad. The lower jaw projects past the upper jaw. The skin looks smooth with very small embedded scales.

Reproduction

(from PH draft Mackerel Amendment 18)

King Mackerel

Spawning occurs generally from May through October with peak spawning in September (McEachran and Finucane 1979). Eggs are believed to be released and fertilized continuously during these months, with a peak between late May and early July with another between late July and early August. Maturity may first occur when the females are 450 to 499 mm (17.7 to 19.6 in) in length and usually occurs by the time they are 800 mm (35.4 in) in length. Stage five ovaries, which are the most mature, are found in females by about age 4 years. Males are usually sexually mature at age 3, at a length of 718 mm (28.3 in). Females in U.S. waters, between the sizes of 446-1,489 mm (17.6 to 58.6 in) released 69,000-12,200,000 eggs. Because both the Atlantic and Gulf populations spawn while in the northernmost parts of their ranges, there is some thought that they are reproductively isolated groups.

Larvae of the king mackerel have been found in waters with temperatures between 26-31°C (79-88°F). This stage of development does not last very long. Larva of the king mackerel can grow up to 0.02 to 0.05 inches (0.54-1.33 mm) per day. This shortened larval stage decreases the vulnerability of the larva, and is related to the increased metabolism of this fast-swimming species.

Spanish Mackerel

Spawning occurs along the inner continental shelf from April to September (Powell 1975). Eggs and larvae occur most frequently offshore over the inner continental shelf at temperatures between 20°C to 32°C and salinities between 28 ppt and 37 ppt. They are also most frequently found in water depths from 9 to about 84 meters, but are most common in < 50 meters.

Cero Mackerel

Spawning occurs offshore during April through October off Jamaica, and year round off the coast of Florida, Puerto Rico, and Venezuela. Females between 15-31 inches (38-80 cm) release from 160,000 to 2.23 million eggs each. This species has oviparous, buoyant eggs and pelagic larva.The eggs are usually 0.046-.048 inches (1.16-1.22 mm) in diameter and hatch at 0.013-0.014 inches (0.34-0.36 mm) (FL Museum of Nat. History website: http://www.flmnh.ufl.edu/fish/Gallery/Descript/CeroMackerel/CeroMackerel.html)

Little Tunny

(from the Fl Mus. of Nat. History)
Spawning occurs in April through November in the eastern and western Atlantic Ocean while in the Mediterranean Sea spawning takes place from late spring through summer. Little tunny spawn outside the continental shelf region in water of at least 25°C (77°F), where females release as many as 1,750,000 eggs in multiple batches. The males release sperm, fertilizing the eggs in the water column. These fertilized eggs are pelagic, spherical, and transparent, with a diameter of 0.8-1.1 mm.

Cobia

(from the FL Mus. of Nat. Hist.)
Cobia form large aggregations, spawning during daylight hours between June and August in the Atlantic Ocean near the Chesapeake Bay, off North Carolina in May and June, and in the Gulf of Mexico during April through September. Spawning frequency is once every 9-12 days, spawning 15-20 times during the season. During spawning, cobia undergo changes in body coloration from brown to a light horizontal-striped pattern, releasing eggs and sperm into offshore open water. Cobia have also been observed to spawn in estuaries and shallow bays with the young heading offshore soon after hatching. Cobia eggs are spherical, averaging 1.24mm in diameter. Larvae are released approximately 24-36 hours after fertilization.

Development, growth and movement patterns

(from PH draft Mackerel Amendment 18)

King Mackerel

Juveniles are generally found closer to shore at inshore to mid-shelf depths (to < 9 m) and occasionally in estuaries. Adults are migratory, and the CMP FMP recognizes two migratory groups (Gulf and Atlantic) that are shown in Figure 4.1-7. Typically, adult king mackerel are found in the southern climates (south Florida and extreme south Texas/Mexico) in the winter and in the northern Gulf in the summer. Food availability and water temperature are likely causes of these migratory patterns. King mackerel mature at approximately age 2 to 3 and have longevities of 24 to 26 years for females and 23 years for males (GMFMC/SAFMC 1985; MSAP 1996; Brooks and Ortiz 2004).

Spanish Mackerel

Juveniles are most often found in coastal and estuarine habitats and at temperatures >25°C and salinities >10 ppt. Although they occur in waters of varying salinity, juveniles appear to prefer marine salinity levels and generally are not considered estuarine dependent. Like king mackerel, adult Spanish mackerel are migratory, generally moving from wintering areas of south Florida and Mexico to more northern latitudes in spring and summer. Spanish mackerel generally mature at age 1 to 2 and have a maximum age of approximately 11 years (Powell 1975).

Figure 4.1-7. Gulf and Atlantic migratory groups.

Cero Mackerel

(from the FL Mus. of Nat. Hist.)
The cero mackerel grows to a maximum size of 72 inches (183 cm) in length and 17 pounds (7.76 kg) in weight. The record in Florida waters is 15.5 pounds (7 kg), although the fish commonly weighs up to 8 pounds (3.6 kg). Males reach maturity at lengths between 12.8-13.4 inches (32.5-34 cm), and females at lengths of approximately 15 inches (38 cm).

Little Tunny

The average size of the little tunny is up to 81 cm (32 in) in length, weighing up to 9.1 kg (20 lbs). The maximum recorded size is 122 cm (48 in) and 16 kg (35.3 lbs). The little tunny may live to 10 years of age. Females reach maturity at 27-37 cm (10.6-14.6 in) in length while males mature at approximately 40 cm (15.7 in).

Cobia

(from the FL Mus. of Natural History)

Newly hatched larvae are 2.5 mm long and lack pigmentation. Five days after hatching, the mouth and eyes develop, allowing for active feeding. A pale yellow streak is visible, extending the length of the body. By day 30, the juvenile takes on the appearance of the adult cobia with two color bands running from the head to the posterior end of the juvenile.

Weighing up to a record 61 kg (135 lbs), cobia are more common at weights of up to 23 kg (50 lbs). They reach lengths of 50-120 cm (20-47 in), with a maximum of 200 cm (79 in). Cobia grow quickly and have a moderately long life span. Maximum ages observed for cobia in the Gulf of Mexico were 9 and 11 years for males and females respectively while off the North Carolina coast maximum ages were 14 and 13 years. Females reach sexual maturity at 3 years of age and males at 2 years in the Chesapeake Bay region.

During autumn and winter months, cobia migrate south and offshore to warmer waters. In early spring, migration occurs northward along the Atlantic coast.

Ecological relationships

King Mackerel (Source: Florida Museum of Nat. History website).

Like other members of this genus, king mackerel feed primarily on fishes. They prefer to feed on schooling fish, but also eat crustaceans and occasionally mollusks. Some of the fish they eat include jack mackerels, snappers, grunts, and halfbeaks. They also eat penaeid shrimp and squid at all life stages (larvae to adult). Adult king mackerels mainly eat fish between the sizes of 3.9-5.9 inches (100-150 mm). Juveniles eat small fish and invertebrates, especially anchovies. The Atlantic and Gulf of Mexico populations differ significantly in their feeding habits. The Atlantic stock ate 58% engraulids, 1% clupeids, and 3.1% squid, the Gulf stock consumed 21.4% engraulids, 4.3% clupeids, and 7.1% squid. The Gulf population also showed more diversity in its feeding habits. In south Florida, the king mackerel's food of choice is the ballyhoo. On the east coast of Florida, the king mackerel prefers Spanish sardines, anchovies, mullet, flying fish, drums, and jacks. Larval and juvenile king mackerel fall prey to little tunny and dolphins. Adult king mackerel are consumed by pelagic sharks, little tunny, and dolphins. Bottlenosed dolphins have been known to steal king mackerel from commercial fishing nets.

The king mackerel is a host to 23 parasitic species. The copepods *Caligus bonito*, *Caligus mutabilis*, and *Caligus productus* are found on the body surface and on the wall of the branchial cavities. Other copepods including *Brachiella thynni*, located on the fins, and *Pseudocycnoides buccata*, found on the gill filaments, are also parasites of the king mackerel.

Other parasites include digenea (flukes), monogenea (gillworms), cestoda (tapeworms), nematoda (roundworms), acanthocephala (spiny-headed worms), copepods, and isopods. Sea lampreys (*Petromyzon marinus*) is an ectoparasite associated with the king mackerel

Spanish Mackerel

Like Gulf group king mackerel, Spanish mackerel primarily eat other fish species (herring, sardines, and menhaden) and to a lesser extent crustaceans and squid at all life stages (larvae to adult). They are eaten primarily by larger pelagic predators like sharks, tunas, and bottlenose dolphin.

Cero Mackerel

(from the FL Mus. of Nat. Hist.)
This swift, shallow water predator feeds primarily on clupeioid fish including herrings as well as silversides of the genus *Allanetta*. The diet of the cero mackerel also includes squid and shrimp. Predators of the cero mackerel include wahoo (*Acanthocybium solandri*), sharks, dolphins, and diving sea birds.

The cero mackerel hosts 21 documented parasites. Among these parasites is the copepod *Brachiella thynni*, which is found on the fins of this fish. Other parasitic copepods are *Caligus bonito* and *Caligus productus* which occur on the body surface and on the wall of the branchial cavities, as well as *Pseudocycnoides buccata* which occurs as a parasite on the gill filaments. Other parasites include protozoans, digenea (flukes), didymozoidea (tissue flukes), monogenea (gillworms), cestoda (tapeworms), nematoda (roundworms), and isopods.

Little Tunny

(from the FL Mus. of Nat. History)
Little tunny is an opportunistic predator, feeding on crustaceans, clupeid fishes, squids, and tunicates. It often feeds on herring and sardines at the surface of the water. Predators of little tunny inlcude other tunas, including conspecifics and yellowfin tuna (*Thynnus albacares*). Fishes such as dolphin fish (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), Atlantic sailfish (*Istiophorus albicans*), swordfish (*Xiphias gladius*), and various sharks as well as other large carnivorous fish all prey on the little tunny. Seabirds also prey on small little tunny.

Parasites of the little tunny include the copepods *Caligus bonito*, *Caligus coryphaenae*, and *Caligus productus*, all found on the body surface as well as on the wall of the branchial cavities. Another copepod, *Pseudocycnoides appendiculatus*, has been documented as parasitic on the gill filaments. Other parasites include digenea (flukes), monogenea (gillworms), cestoda (tapeworms), and isopods.

Cobia

(from the FL Mus. of Nat. History)
Cobia are voaracious feeders often engulfing their prey whole. Their diet includes crustaceans, cephalopods, and small fishes such as mullet, eels, jacks, snappers, pinfish, croakers, grunts, and herring. A favorite food is crabs, hence the common name of "crabeater." Cobia often cruise in packs of 3-100 fish, hunting for food during migrations in shallow water along the shoreline. They are also known to feed in a manner similar to remoras. Cobia will follow rays, turtles, and sharks; sneaking in to scavenge whatever is left behind. Little is known about the feeding habits of larvae and juvenile cobia.

Not much is known regarding the predators of cobia, however they are presumably eaten by larger pelagic fishes. Dolphin (*Coryphaena hippurus*) have been reported to feed on small cobia.

The majority of parasites found on cobia are host-specific, suggesting this fish is not closely related to any other fishes. Parasites include a variety of trematodes, cestodes, nematodes, acanthocephalans, and copepods as well as barnacles. Thirty individuals of a single trematode species, *Stephanostomum pseudoditrematis*, were found in the intestine of a single cobia taken from the Indian Ocean. Infestations of the nematode *Iheringascaris inquies* are quite common in the stomachs of cobia.

Abundance and status of stocks

(from Habitat Plan)
NOAA's Estuarine Living Marine Resource Program (ELMR), through a joint effort of National Ocean Service and NMFS, conducts regional compilations of information on the use of estuarine habitat by select marine fish and invertebrates. A report prepared through the ELMR program (NOAA 1991b) and revised information (NOAA 1998), provided the Council during the Habitat Plan development process, present known spatial and temporal distribution and relative abundance of fish and invertebrates using southeast estuarine habitats. Twenty southeast estuaries selected from the National Estuarine Inventory (NOAA 1985) are included in the analysis which resulted from a review of published and unpublished literature and personal consultations. The resulting information emphasizes the importance and essential nature of estuarine habitat to all life stages of Spanish mackerel.

Regional salinity and relative abundance maps for use in determining EFH for two estuarine dependent coastal migratory pelagic species included in the data, Spanish mackerel and cobia. Maps are included in Appendix F of the Council's Habitat Plan (SAFMC 1998a). Figures 43-46 in the Habitat Plan present a representative sample of the distibution maps for juvenile Spanish mackerel.

King Mackerel

In 2003, the first SEDAR assessment of Atlantic and Gulf of Mexico king mackerel was conducted using data from 1981 to 2002. The SEDAR 5 Advisory Report (April 2004) concluded that the Atlantic king mackerel stock was not overfished and overfishing was not occurring in 2002/2003. Current estimates indicate the fishing mortality rate of Atlantic king mackerel in fishing year 2002/2003 was well below MFMT and spawning biomass was well above MSST at the beginning of fishing year 2003/2004. The Base model resulted in only a 2% probability that B2003 was less than MSST, and there was only a 1% probability that F2002/2003 was greater than MFMT (FMSY). Combined mean landings of king mackerel were 7.37 million pounds between 1981/1982 and 2001/2002, with a range of 5.66 million pounds (1999/2000) to 9.62 million pounds (1985/1986) (Table 4.1-12). Estimated Atlantic king mackerel stock size has increased since the mid-1990s but not to the higher levels seen in the early 1980s. Recently, recruitment has been highly variable with a low and highly uncertain value in the most recent data year (2001/2002).

Table 4.1-12. Atlantic migratory group king mackerel management regulations and harvest. Pounds are in millions.

Fishing Year	ABC Range (M lbs)	TAC (M lbs)	Rec. Allocation (lbs. /	Rec. Bag Limit	Commercial Quota	Annual Com.	Harvest Rec.	Levels Total

			numbers)					
1986/87	6.9 -15.4	9.68		3	3.59 (PS=0.40)	2.837	5.980	8.817
1987/88	6.9 -15.4	9.68	6.09	3	3.59 (PS=0.40)	3.448	3.905	7.353
1988/89	5.5 -10.7	7.00	4.40	2 in FL, 3 GA-NC	2.60 (PS=0.40)	3.091	4.881	7.972
1989/90	6.9 -15.4	9.00	5.66 / 666,000	2 in FL, 3 GA-NC	3.34	2.619	3.400	6.019
1990/91	6.5 -15.7	8.30	5.22 / 601,000	2 in FL, 3 GA-NY	3.08	2.675	3.718	6.393
1991/92	9.6 -15.5	10.50	6.60 / 735,000	5 in FL-NY	3.90	2.515	5.822	8.337
1992/93	8.6 -12.0	10.50	6.60 / 834,000	2 in FL, 5 GA-NY	3.90	2.254	6.251	8.505
1993/94	9.9 -14.6	10.50	6.60 / 854,000	2 in FL, 5 GA-NY	3.90	2.018	4.438	6.456
1994/95	7.6 -10.3	10.00	6.29 / 709,000	2 in FL, 5 GA-NY	3.71	2.182	3.728	5.910
1995/96	7.3 -15.5	7.30	4.60 / 454,000	2 in FL, 3 GA-NY	2.70	1.866	4.153	6.019
1996/97	4.1 - 6.8	6.80	4.28 / 438,525	2 in FL, 3 GA-NY	2.52	2.703	3.990	6.693
1997/98	4.1 - 6.8	6.80	4.28 / 438,525	2 in FL, 3 GA-NY	2.52	2.683	5.158	7.841
1998/99	8.4 - 11.9	8.40	5.28 / 504,780	2 in FL, 3 GA-NY	3.12	2.549	4.268	6.817
1999/00	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	2.236	3.424	5.660
2000/01	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	2.107	5.338	7.445
2001/02	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	2.022	3.240	5.263
2002/03	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	1.745	2.672	4.417
2003/04	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	1.730	4.100	5.831
2004/05	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	2.820	3.287	6.107
2005/06	8.9 - 13.3	10.0	6.29 / 601,338	2 in FL, 3 GA-NY	3.71	2.424	3.954	6.378

Notes: 1) The range has been defined in terms of acceptable risk of achieving the FMP's fishing mortality rate target; the Panel's best estimate of ABC has been intermediate to the end-points of this range; 2) Recreational allocation in numbers is the allocation divided by an estimate of annual average weight; 3) Sums within rows may not appear to equal the total value shown due to rounding of numbers before printing; 4) Bag limit not reduced to zero when allocation reached, beginning fishing year 1992; 5) Bag limit reduced from 5 to 3 effective 1/1/96; and 6) Season is April through March for 2001/02 through 2004/05 and March through the end of February for 2005/06.

Source: ALS data, August 9, 2006; Data provided by the Southeast Fisheries Science Center, October 2006.

The SAMFC's stated objective is to select a TAC for Atlantic king mackerel that has a median probability of achieving its management target, Optimum Yield (OY), defined as the yield associated with a fishing mortality rate of F40%SPR. The SEDAR 5 Advisory Report (April 2004) only provided a point estimate of ABC for Atlantic king mackerel and not a range as was done for Gulf king mackerel. The point estimate provided in the Advisory Report was 5.6 million pounds. The Advisory Report did provide information on a range of yields at F40%SPR. The median estimate of yield at F40%SPR is 5.8 million pounds (20th - 80th percentile range = 4.5 – 7.9 million pounds). Catches above 5.8 million pounds would exceed 50% probability of future F> F40%SPR, conditional on projection assumptions. F40%SPR is the SAFMC's target mortality rate while the actual fishing mortality threshold (MFMT) is F30%SPR (FMSY). [Note: These recommendations are based on assuming 100% of the fish in the mixing zone are Gulf king mackerel. The alternatives included here are based on a 50/50 mixing rate.]

Spanish Mackerel

The Mackerel Stock Assessment Panel (MSAP 1996) conducted a full stock assessment for Atlantic Group Spanish mackerel in 2003, which included data through the 2001/2002 fishing year; projected landings through 2002/2003 also were included. Estimated fishing mortality for Atlantic Group Spanish mackerel has been below FMSY and FOY since 1995. Estimated stock abundance has increased steadily since 1995 and is now at a high for the analysis period. Stock biomass has increased from about 19 million to 24 million fish (Figure 4.1-8). Probabilities that Spanish mackerel is overfished are less than 1% and that overfishing has occurred in the most recent fishing year of the assessment are 3%; therefore the MSAP concluded that Atlantic Group Spanish mackerel were not overfished and overfishing did not occur in 2002/2003. Although all measures of stock status are well within desirable ranges, the median estimate of MSY dropped from 6.4 million pounds in the last full assessment in 1998 to 5.2 million pounds in the 2003 assessment. Much of the decline is believed to be due to the lower estimates of recruitment between the 2003 and the 1998 assessments. The MSAP recommended ABC as the median estimate of catch at F 40% SPR, which is 6.7 million pounds (20th –80th percentile range = 5.2 - 8.4 million pounds).

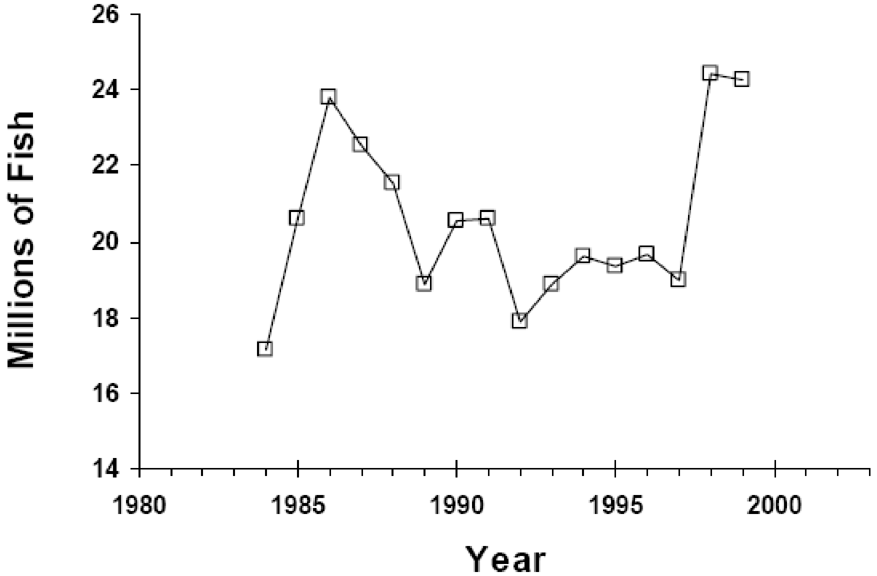


Figure 4.1-8. Estimated Atlantic Spanish mackerel stock abundance from the 2003 base model (MSAP 2003).

The Council staff presented the 2003 MSAP stock assessment and a variety of management options to the South Atlantic Council. The Council voted to defer framework action on Spanish mackerel until after the SEDAR stock assessment. Therefore the existing regulation of a TAC of 7.04 million pounds remained in effect for the 2005/2006 and 2006/07 fishing years. The estimate of landings for the 2000/2001 fishing year was 5.08 million pounds (Table 4.1-13), well below the TAC of 7.04 million pounds. If the fishery developed greater capacity and TAC was realized at a level of 7.04 million pounds for several years, fishing mortality rates would increase and eventually may exceed F 30% SPR. Consequently, fishing at this level over time would eventually reduce spawning stock biomass to a level below that which is capable of producing MSY on a continuing basis.

Table 4.1-13. Spanish mackerel estimated landings by fishing year (1987-2006).

Fishing Year	ABC Range (M lbs)	TAC (M lbs)	Rec. Allocation (lbs. / numbers)	Rec. Bag Limit	Commercial Quota	Annual Com.	Harvest Rec.	Levels Total
1987/88	1.7 - 3.1	3.1	0.74	4 in FL, 10 GA-NC	2.36	3.475	1.474	4.949
1988/89	1.3 - 5.5	4.0	0.96	4 in FL, 10 GA-NC	3.04	3.521	2.740	6.261
1989/90	4.1 - 7.4	6.0	2.76 / 1,725,000	4 in FL, 10 GA-NC	3.24	3.941	1.569	5.51
1990/91	4.2 - 6.6	5.0	1.86 / 1,216,000	4 in FL, 10 GA-NC	3.14	3.535	2.075	5.61
1991/92	5.5 - 13.5	7.0	3.50 / 2,778,000	5 in FL, 10 GA-NC	3.50	4.707	2.287	6.994
1992/93	4.9 - 7.9	7.0	3.50 / 2,536,000	10 FL - NY	3.50	3.727	1.995	5.722
1993/94	7.3 - 13.0	9.0	4.50 / 3,214,000	10 FL - NY	4.50	4.811	1.493	6.304
1994/95	4.1 - 9.2	9.2	4.60 / 3,262,000	10 FL - NY	4.60	5.254	1.378	6.632
1995/96	4.9 - 14.7	9.4	4.70 / 3,113,000	10 FL - NY	4.70	1.834	1.089	2.923
1996/97	5.0 - 7.0	7.0	3.50 / 2,713,000	10 FL - NY	3.50	3.098	0.849	3.947
1997/98	5.8 - 9.4	8.0	4.00 / 2,564,000	10 FL - NY	4.00	3.057	1.660	4.717
1998/99	5.4 - 8.2	8.0	4.00 / 2,564,000	10 FL - NY	4.00	3.272	0.817	4.089
1999/00	5.7 - 9.0	7.04	3.17 /	10 FL - NY	3.52	2.370	1.505	3.875
2000/01	5.7 - 9.0	7.04	3.17 / 2,032,000	15 FL - NY	3.87	2.794	2.699	5.493
2001/02	5.7 - 9.0	7.04	3.17 / 2,032,000	15 FL - NY	3.87	3.036	2.008	5.044

2002/03	5.7 - 9.0	7.04	3.17 / 2,032,000	15 FL - NY	3.87	3.207	2.072	5.279
2003/04	5.7 - 9.0	7.04	3.17 / 2,032,000	15 FL - NY	3.87	3.741	1.994	5.735
2004/05	5.7 - 9.0	7.04	3.17 / 2,032,000	15 FL - NY	3.87	3.678	1.371	5.049
2005/06	5.7 - 9.0	7.04	3.17 / 2,032,000	15 FL - NY	3.87	3.579	1.985	5.564

Notes: 1) The range has been defined in terms of acceptable risk of achieving the FMP's fishing mortality rate target; the Panel's best estimate of ABC has been intermediate to the end-points of this range; 2) Recreational allocation in numbers is the allocation divided by an estimate of annual average weight (not used prior to fishing year 1989); 3) Sums within rows may not appear to equal the total value shown due to rounding of numbers before printing; 4) Allocations and rec. quota are as revised October 14, 1989; 5) Bag limit not be reduced to zero when allocation reached, beginning fishing year 1992; and 6) Season is April through March for 2001/02 through 2004/05 and March through the end of February for 2005/06.
Source: ALS data, August 9, 2006; Data provided by the Southeast Fisheries Science Center, October 2006.

The Atlantic States Marine Fisheries Commission Plan Review Team (PRT) believes harvest reductions are due to management measures in state and federal waters as well as the recreational fishery targeting other species. The low level of harvest in relation to the stock size is encouraging for stock rebuilding, which is reflected in the increase in transitional SPR. Cooperative State/Federal management has achieved a successful stock recovery.

TAC is currently 7.04 million pounds, and based on the most recent assessment, the Stock Assessment Panel recommended an ABC range of 5.2 to 8.4 million pounds, with a median value of 6.7 million pounds. This yield would be in excess of the best point estimate of maximum sustainable yield (5.2 million pounds); however, the Atlantic migratory group Spanish mackerel fishery is not overfishing the available stock, and the stock is not overfished. This is because the current biomass is estimated to be above the biomass at MSY. Therefore, the difference in the current stock size and the MSY stock size could be harvested, reducing the stock size to the MSY level.

4.1.4 Golden Crab

Description and Distribution

The golden crab, *Chaceon fenneri*, is a large gold or buff colored species whose diagnostic characters include an hexagonal carapace; five anterolateral teeth on each side of carapace; well-developed, large frontal teeth; shallow, rounded orbits; chelipeds unequal; and the dactyli of the walking legs laterally compressed (Manning and Holthuis 1984, 1989). Golden crab inhabit the continental slope of Bermuda (Luckhurst 1986; Manning and Holthuis 1986) and the southeastern United States from off Chesapeake Bay (Schroeder 1959), south through the Straits of Florida and into the eastern Gulf of Mexico (Manning and Holthuis 1984, 1986; Otwell et al. 1984; Wenner et al. 1987, Erdman 1990).

Figure 4.1-9. Golden Crab, *Chaceon fenneri*.

Reported depth distributions of *C. fenneri* range from 205 m off the Dry Tortugas (Manning and Holthuis 1984) to 1007 m off Bermuda (Manning and Holthuis 1986). Size of males examined range from 34 to 139 mm carapace length (CL) and females range from 39 to 118 mm CL. Ovigerous females have been reported during September, October and November, and range in size from 91 to 118 mm CL (Manning and Holthuis 1984, 1986).

The following text is from Lockhart et al. (1990):
"The distribution patterns of *Chaceon fenneri* and possibly *C. quinquedens* in the eastern Gulf of Mexico suggest a causal role for the Loop Current System (Maul 1977) in basic life history adaptations. Female distribution within these species' geographic ranges and the timing of larval release supports this hypothesis. Ours was the first study to discover female golden crabs in any significant numbers and was also the first to find a major population of female red crabs in the Gulf of Mexico. Both of these concentrations of females were seemingly shifted counter-current to the Loop Current circulation. We hypothesize that this counter-current shift is linked to larval release and transport, and serves to maximize recruitment into the parent population by minimizing risk of larval flushing.

Similar counter-current shifts of other female decapods have been reported or hypothesized. In the Gulf of Mexico, spawning female blue crabs (*Callinectes sapidus*) have been hypothesized to undergo a late summer spawning migration in the northeastern Gulf of Mexico that is counter to the Loop Current system (Oesterling and Adams 1979). Female western rock lobsters (*Panulirus cygnus*) are hypothesized to undergo migration to favor recruitment back into the parent population (Phillips et al. 1979). Kelly et al. (1982) proposed that only those red crab larvae (*Chaceon quinquedens*) released up-current in the species' range will recruit back into the parent population. Melville-Smith (1987a, 1987b, 1987c) in a tagging study of red crabs (*C. maritae*) off the coast of southwest Africa, showed that the only segment of the population exhibiting significant directional movement were adult females: 32% of recaptures had moved greater than 100 km and the greatest distance traveled was 380 km over 5 yr. This directional movement was later shown to be counter to the prevailing surface currents (Melville-Smith 1990).

Thus, within decapods in general, and the genus in particular, adult females are capable of, and appear to undergo, long-distance directional movement in their lifetimes.
A similar migration of adult female golden crabs, counter-current to Loop Current circulation in the Gulf of Mexico, would produce the geographic population structure observed off the southeastern United States. Females would be most common farthest up-current whereas males

would be most common intermediate in the species geographic range. Wenner et al. (1987) reported a 15:1 (M:F) sex ratio in the South Atlantic Bight and in this study, we had an overall sex ratio of 1:4 — both consistent with hypothesized net female movements to accommodate larval retention and offset the risk of larval flushing.

In fact, given this, two female strategies could maximize recruitment in a prevailing current. The first is for females to position themselves far enough up current so that entrainment would return larvae to the parent population (Sastry 1983). The second is to avoid larval entrainment altogether and thus avoid flushing of the larvae out of the system. Female *Chaceon fenneri*, and perhaps *C. quinquedens*, appear to use both strategies but rely mainly on the latter.

Female golden crabs release larvae offshore in depths usually shallower than 500 m. If larvae were released directly into the Loop Current-Gulf Stream System, they would be entrained for their entire developmental period. Given a developmental time of 33-40 d at 18°C (K. Stuck, Gulf Coast Research Laboratories, Ocean Springs, Mississippi, pers. comm.) and current speeds of 10-20 cm/sec (Sturges and Evans 1983), transport of the larvae would be 285 km to 690 km downstream. Thus, larvae released on the Atlantic side of Florida are in danger of being flushed out of the species' range before recruiting to the benthic stock. Likewise, larvae released directly into the current in the southeastern Gulf of Mexico would be flushed from the Gulf.

Female golden crabs release larvae from February to March (Erdman and Blake 1988; Erdman et al., 1989) and the greatest concentration of female golden crabs to date found in this study was in the northeastern Gulf of Mexico off central Florida. Only during this period and in this region (Maul, 1977), can female golden crabs avoid complete entrainment and possible flushing of larvae out of the system. Partial entrainment of larvae might still occur, but its duration should be much reduced, and the risk of larval flushing minimal. This hypothesis predicts that most larvae should be found near the concentrations of females we found in the northeastern Gulf of Mexico with decreasing settlement further downstream. The abundance of juveniles should show a similar pattern.

One need not invoke similar counter-current movements for male geryonid crabs. In particular, males moving perpendicular to adult females (i.e. males moving up and down the continental slope) would have a greater encounter rate with females than males moving along the slope with females. Given low female reproductive frequency (Erdman et al. 1989), intense male-female competition (Lindberg and Lockhart 1988), and probability of multiple broods (Hinsch 1988) from a single protracted copulation (H. M. Perry, pers. obs.), the male strategy should be to intercept relatively rare receptive females all along the species' range, not to aggregate with presumably inseminated females. This hypothesis would predict a relatively uniform abundance of males along their geographic range. In addition, the incidence of inseminated females should be high farthest upstream with an ever decreasing percentage down-stream. Our study supports the former hypothesis but we cannot address the latter.

The distributional patterns of geryonid crabs we observed are consistent with those reported from elsewhere. Furthermore, these patterns lead us to suggest that the Loop Current System has had a causal role in life history adaptations of *Chaceon fenneri* and perhaps *C. quinquedens*. In general, females are expected to release larvae during a time and in a region where risk of larval flushing is minimal (Sinclair 1988), whereas males are expected to compete intensely for rare, receptive mates."

The coastal physical oceanography in the Florida Keys was described by Yeung (1991) in a study of lobster recruitment:
"The strong, northward-flowing Florida Current is the part of the Gulf Stream system confined within the Straits of Florida. It continues from the Loop Current in the Gulf of Mexico, and proceeds beyond Cape Hatteras as the North Atlantic Gulf Stream.
The mean axis of the Florida Current is approximately 80 km offshore of Key West and 25 km off Miami (Lee et al., 1991). Mean annual cross-stream surface current speed in the Straits of Florida is approximately 100 cm/s (U.S. Naval Oceanographic Office, 1965).

Brooks and Niller (1975) observed a persistent countercurrent near Key West extending from surface to the bottom, and from nearshore to approximately 20 km seaward. They believed that it was part of the cyclonic recalculation of the Florida Current between the Lower and Middle Keys.

The presence of a cold, cyclonic gyre was confirmed by physical oceanographic data collected in the SEFCAR cruises. It was named the Pourtales Gyre since it occurs over the Pourtales Terrace -- that area of the continental shelf off the Lower and Middle Keys (Lee et al., 1991). When the Florida Current moves offshore, the Pourtales Gyre forms over the Pourtales Terrace, and can last for a period of 1-4 weeks.

The Pourtales Gyre could entrain and retain locally spawned planktonic larvae for a short period. The combination of the cyclonic circulation and enhanced surface Ekman transport could also advect foreign arrivals into, and concentrate them at, the coastal boundary (Lee et al., 1991).

Vertical distribution of the larvae within the 3-dimensional circulation will subject them to complicated hydrographic gradients, which might influence their development time, and hence their dispersal potential (Kelly et al., 1982; Sulkin and McKeen, 1989). Thus, variability in the circulation features and water mass properties can lead to variability in larval transport and recruitment."

The Pourtales Gyre may provide a mechanism for entrainment of golden crab larvae spawned on the Florida east coast, and also as a mechanism to entrain and advect larvae from the Gulf and Caribbean (e.g., Cuba). This possibility is supported by the conclusion of Yeung (1991) suggesting that larvae of a foreign origin supply recruits to the Florida spiny lobster population:
"The foreign supply of pre-recruits arriving with the Florida Current might easily meet the same fate as the locally spawned larvae, that is, passing on with the Florida Current. The Pourtales Gyre may play a significant role in recruitment by providing a physical mechanism to entrain and advect larvae into the coastal boundary.

The Pourtales Gyre, even if linked with the Dry Tortugas gyre or the Florida Bay circulation, may not be able to provide a pathway much more than 2 months in period. For locally spawned Panulirus larvae to be retained for their entire development would require several circuits -- not impossible, but unlikely."

The timing of the Pourtales Gyre provides a mechanism for local recruitment of *Scyllarus* larvae (Yeung, 1991) and may also provide a similar mechanism for golden crab larvae. Golden crab larvae from the Gulf of Mexico, Cuba, and possibly other areas of the Caribbean, probably provide larvae to the South Atlantic population. The proportion of local recruitment is unknown but could be significant.

Wenner et al. (1987) note: "Other studies have described an association of *G. quinquedens* with soft substrates. Wigley et al. (1975) noted that bottom sediments throughout the area surveyed for red crab from offshore Maryland to Corsair Canyon (Georges Bank) consisted of a soft, olive-green, silt-clay mixture. If golden crabs preferentially inhabit soft substrates, then their zone of maximum abundance may be limited within the South Atlantic Bight. Surveys by Bullis and Rathjen (1959) indicated that green mud occurred consistently at 270-450 m between St. Augustine and Cape Canaveral, FL (30°N and 28°N). This same depth range from Savannah, GA to St. Augustine was generally characterized by Bullis and Rathjen (1959) as extremely irregular bottom with some smooth limestone or "slab" rock present. Our study indicates, however, that the bottom due east between Savannah and St. Catherines Island, GA at 270-540 m consists of mud and biogenic ooze. Further north from Cape Fear, NC to Savannah, bottom topography between 270 and 450 m is highly variable with rocky outcrops, sand and mud ooze present (Low and Ulrich, 1983)."

In a subsequent study using a submersible, Wenner and Barans (1990) found the greatest abundance in rock outcrops:
"Observations on density and a characterization of essential habitat for golden crab, *Chaceon fenneri*, were made from a submersible along 85 transects in depths of 389-567 m approximately 122 km southeast of Charleston, South Carolina. Additional observations on habitat were made on 16 transects that crossed isobaths between 293-517 m.

Seven essential habitat types can be identified for golden crab from observations:

- A flat foraminiferon ooze habitat (405-567 m) was the most frequently encountered habitat. This habitat type is characterized by pteropod-foraminiferan debris mixed with larger shell fragments, a sediment surface mostly covered with a black phosphorite precipitate;

- Distinct mounds, primarily of dead coral at depths of 503 to 555 meters and constituted 20% of the bottom surveyed on dives to count crabs. Coral mounds rose approximately 15 to 23 meters in height above the surrounding sea floor and included several that were thinly veneered with a fine sediment and dead coral fragments, as well as a number that were thickly encrusted with live branching ahermatypic corals (*Lophelia prolifera* and *Enallopsammia profunda*). Fan-shaped sponges, pennatulids and crinoids were oriented into the northerly 1.4-1.9 km- h-1 current. The decapod crustaceans *Bathynectes longispina*, *Eugonatonotus crassus* and *Eumunida pita*, the black-bellied rosefish, *Helicolenus dactylopterus*, and the wreckfish, *Polyprion americanus*, were frequently sighted along transects in the coral mound habitat.

- Ripple habitat (320-539 m); dunes (389-472 m); black pebble habitat (446-564 m); low outcrop (466-512 m); and soft-bioturbated habitat (293-475 m). A total of 109 *C. fenneri* were sighted within the 583,480 m^2 of bottom surveyed. Density (mean no. per 1,000 m^2) was significantly different among habitats, with highest values (0.7 per 1,000 m^2) noted among low rock outcrops. Lowest densities were observed in the dune habitat (<0.1 per 1,000 m^2), while densities for other habitats were similar (0.15-0.22 per 1,000 m^2)."

A similar submersible study in the eastern Gulf of Mexico (Lindberg and Lockhart, 1993) found similar results with higher abundance on hardbottom: "Within the bathymetric range of golden crabs, crab abundance may be related more to habitat type than to depth. The greatest density (36.5 crabs/ha) occurred on or near hardbottom canyon features."

Golden crabs occupy offshore oceanic waters along the Atlantic and Gulf of Mexico coasts as adults. Offshore areas used by adults are probably the least affected by habitat alterations and water quality degradation. Currently, the primary threat comes from oil and gas development and production, offshore dumping of dredged material, disposal of chemical and other wastes, and the discharge of contaminants by river systems.

Reproduction

Reproduction and anatomy of the reproductive tracts of males and females of the golden crab *Geryon fenneri* were studied by Hinsch (1988) in specimens collected from deep water of the eastern Gulf of Mexico.

"The male crab is larger than female. Their reproductive tracts are typical of brachyurans. Light and electron microscopic studies of the testes and vasa deferentia at various times during the year indicate that *G. fenneri* has a single reproductive season. Spermatogenesis begins in the fall. By January, many acini of the testes are filled with mature sperm and spermatophores and seminal fluids accumulate in the anterior and middle vasa deferentia. In March all portions of the vasa deferentia are swollen with seminal products. Mating occurs during March and April. The reproductive organs of males are reduced in size from May through September.

The fully developed ovary of golden crabs is purple in color. Females oviposit in September and October. Females undergo vitellogenesis at the same time that they carry eggs undergoing embryonic development. Females with broods have ovaries which vary in color and size. They release their larvae during February and March. Females may be reproductive for several seasons and appear to be capable of mating while in the hardened condition"

Also see Erdman, R.B., N.J. Blake, F.D. Lockhart, W.J. Lindberg, H.M. Perry, and R.S. Waller. 1991. Comparative reproduction of the deep-sea crabs *Chaceon fenneri* and *C. quenquedens* (Brachyura: Geryonidae) from the northeastern Gulf of Mexico. Journal of Invertebrate Reproduction and Development 19:175-184.

Development, growth and movement patterns

Wenner et al. (1987) found in the South Atlantic Bight that:

"Size-related distribution of *C. fenneri* with depth, similar to that reported for red crab, may occur in the South Atlantic Bight. We found the largest crabs in the shallowest (274-366 m) and deepest (733-823 m) strata. A clear trend of size-related up-slope migrations such as Wigley et al. (1975) reported for *C. quinquedens* is not apparent, however, because of trap bias for capture of larger crabs of both sexes. Otwell et al. (1984) also noted no pattern in size of golden crab by depth for either sex. Tagging studies of red crab off southern New England provided no evidence for migration patterns and indicated instead that tagged crabs seldom moved more than 20 km from their site of release (Lux et al., 1982)."

Lindberg and Lockhart (1993) found in the Gulf of Mexico:
"The golden crab *Chaceon fenneri* in the eastern Gulf of Mexico exhibits a typical bathymetric pattern of partial sex zonation and an inverse size-depth relationship, as first reported for red crabs (*C. quinquedens*: Wigley et al., 1975; *C. maritae*: Beyers and Wilke, 1980). Sex segregation, with females shallower than most males, was more evident in our results than in those of Wenner et al. (1987) from the South Atlantic Bight, primarily because our trap catch had a higher proportion of females (25.9% compared to 5.2%)." Also see above section on distribution for details on movement patterns.

Ecological relationships

Feeding habits are very poorly known. Golden crabs are often categorized as scavengers that feed opportunistically on dead carcasses deposited on the bottom from overlying waters (Hines, 1990).

Abundance and status of stocks

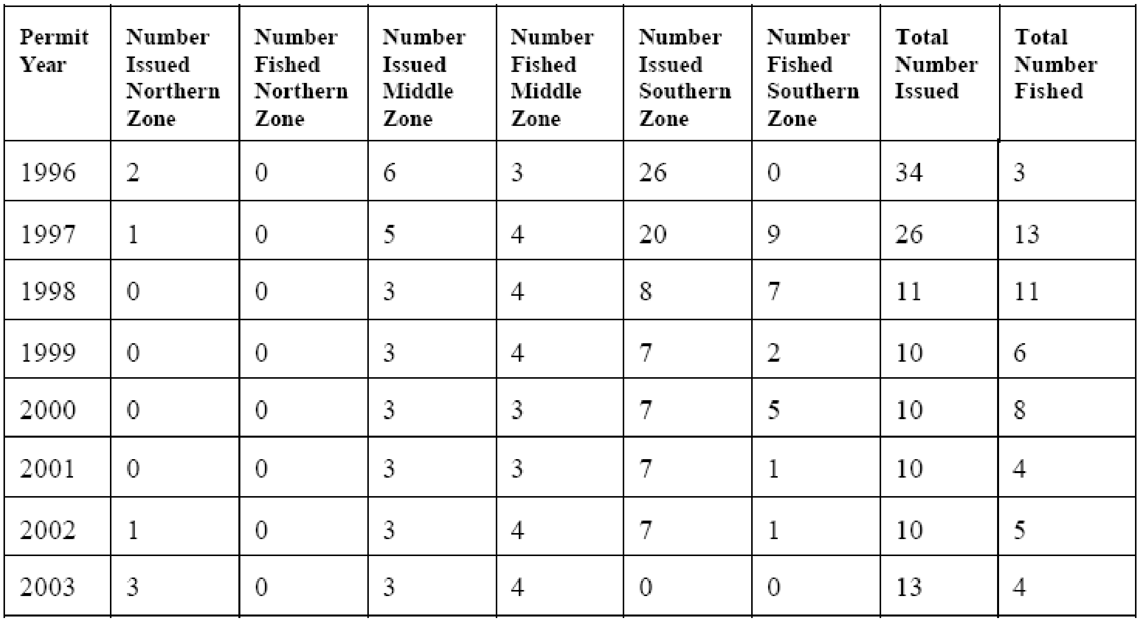
Golden crab abundance studies are limited. Data from the South Atlantic Bight (Wenner et al., 1987) estimated abundance from visual assessment was 1.9 crabs per hectare while traps caught between 2 and 10 kg per trap. Wenner and Barans (1990) estimated the golden crab population in small areas of 26-29 square km between 300-500 m off Charleston to be 5,000-6,000 adult crabs. In the eastern Gulf of Mexico adult standing stock was estimated to be 7.8 million golden crabs and the biomass was estimated to be 6.16 million kg (13.6 million pounds) (Lindberg et al., 1989). Experimental trapping off Georgia yielded an average catch of 7 kg per trap (Kendall, 1990).

Based on exploratory trapping, golden crab maximum abundance occurs between 367 and 549 meters in the South Atlantic Bight. Information on sediment composition suggests that golden crab abundance is influenced by sediment type with highest catches on substrates containing a mixture of silt-clay and foraminiferan shell (Wenner et al., 1987).

Participation in the Fishery (Source: Golden Crab SAFE 2004)
Thirty-four permits were issued in permit year 1996, but during that year only three vessels landed golden crab (Table 4.1-14). More vessels landed golden crab in permit years 1997 and 1998 (13 and 11, respectively) (Table 4.1-14). There was then a decline to five or less vessels reporting landings during each of permit years 2001-2003. Although at least 10 permits have been issued annually since 1996, at most 50% of permit holders actually fished for golden crab in a given year from 2001 to 2003 (Table 4.1-14). By 2003 there were three permits issued for the Northern Zone (after the addition of two permits in Amendment 3), but no fishermen have

reported landing golden crab there since the beginning of the permit process in 1996 (Table 4.1-14). Of the five companies processing golden crab in 1995, only one was still processing in 2002 (Antozzi, 2002; NMFS 2004, Appendix 4). Antozzi (2002, Appendix 4) thought that implementation of Amendment 3 may encourage permit holders to re-enter the fishery, but the number of fishermen participating in the fishery has been fairly stable from 2001 through 2003.

Table 4.1-14. Number of permitted golden crab vessels and the number that reported landings, 1996-2003. Permit year begins November 1 of the previous year. Source: Sadler 2004 and NMFS Logbook Database.



Permit Year	Number Issued Northern Zone	Number Fished Northern Zone	Number Issued Middle Zone	Number Fished Middle Zone	Number Issued Southern Zone	Number Fished Southern Zone	Total Number Issued	Total Number Fished
1996	2	0	6	3	26	0	34	3
1997	1	0	5	4	20	9	26	13
1998	0	0	3	4	8	7	11	11
1999	0	0	3	4	7	2	10	6
2000	0	0	3	3	7	5	10	8
2001	0	0	3	3	7	1	10	4
2002	1	0	3	4	7	1	10	5
2003	3	0	3	4	0	0	13	4

Landings and Effort

Middle Zone

Eighty-seven months of landings and effort data were added (from May 1996 to August 2003), reflecting 426 additional trips (NMFS 2004, Appendix 1). Overall, catches continued to occur primarily in the Middle Zone (Figure 4.1-10). Landings fell by 40% from 2000 to 2003, from 587,330 lbs to 351,987 lbs (Figure 4.1-10). Monthly catches generally decreased from January to July, then increased beginning in August (Figure 4.1-11a). This trend did not hold in 2001, when landings started out very high but decreased consistently over most of the year.

Annual CPUE has been fairly consistent from 1995 to 2003, ranging from 39 to 59 lbs per trap (Figure 4.1-12). CPUE in 2003 was the highest since records began in 1995 (Figure 4.1-12). Monthly CPUE has been relatively consistent during the last five years (Figure 4.1-13). Record high CPUE in 2001 was primarily due to unusually high CPUE from January through May. CPUE in 2003 was higher than in most other years measured, during the months for which data were available (Figure 4.1-13).

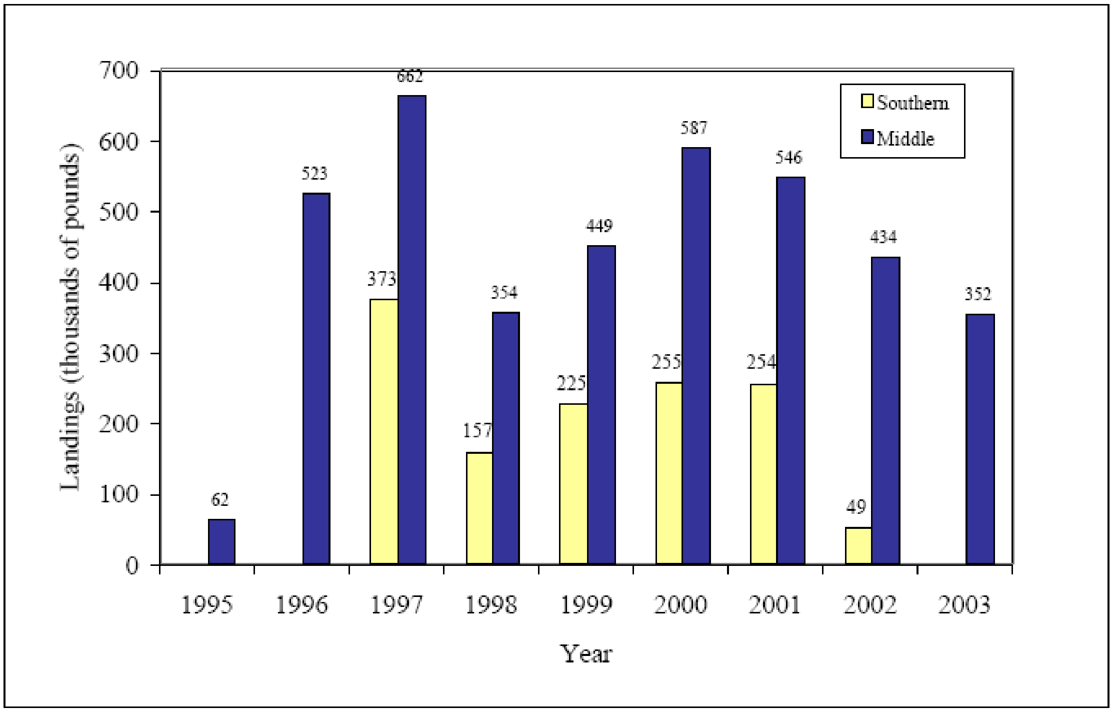


Figure 4.1-10. Total golden crab landings by year, Middle and Southern Zones.

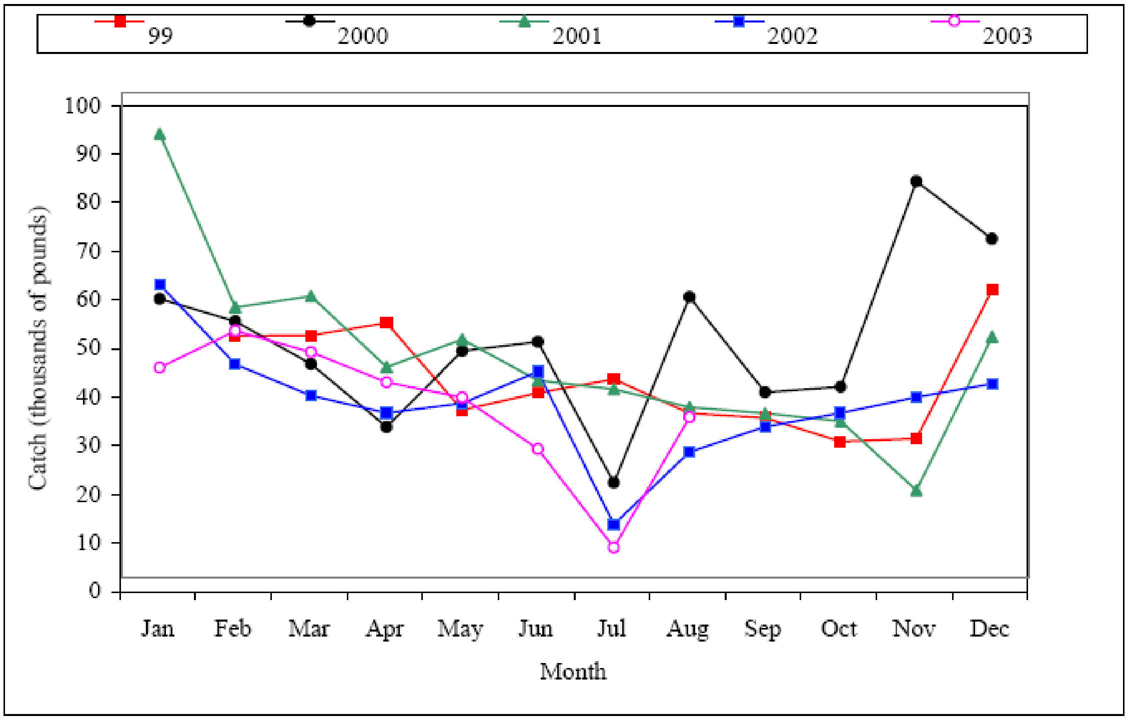


Figure 4.1-11a. Monthly catch of golden crab by year, Middle Zone.

Southern Zone

Forty-eight months of data were added (from June 1998 to May 2002), reflecting 120 additional trips (NMFS 2004, Appendix 1). No data were available from 2003. Southern Zone landings made up approximately 30% of the total across zones for the first five years (1997-2001), but only 10% of the total in 2002 (data available for January through May) (Figure 4.1-10). Southern Zone landings were relatively stable over each year at about 20,000-30,000 lbs/month, except in 1999 when no golden crab were landed until May, followed by unusually high landings greater than 40,000 lbs/month in July and August (Figure 4.1-11b).

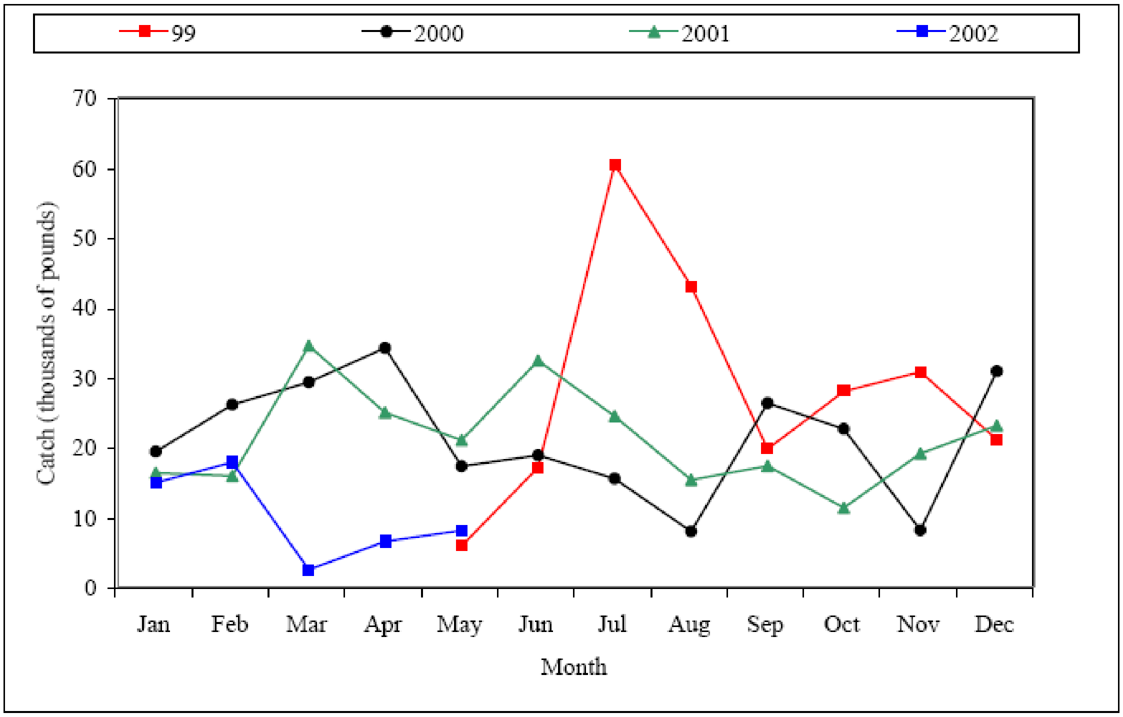


Figure 4.1-11b. Monthly catch of golden crab by year, Southern Zone.

In contrast to the Middle Zone, CPUE in the Southern Zone decreased from 1999 to 2002, stabilizing at about 22-25 lbs per trap from 2000 to 2002 (Figure 4.1-12). CPUE has been lower in the Southern compared to the Middle Zone in every year but 1999 (Figure 4.1-12). CPUE in the Southern Zone was approximately 50%-60% of CPUE in the Middle Zone from 2000 to 2002 (Figure 4.1-12).

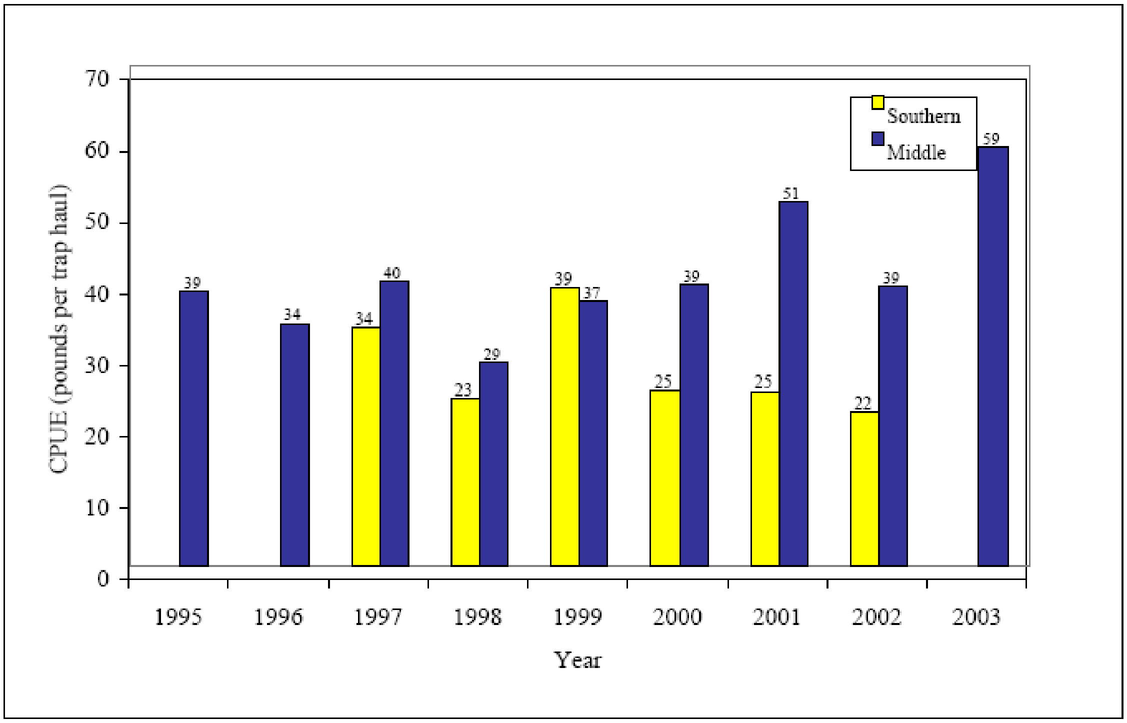


Figure 4.1-12. Golden crab CPUE by year and zone.

Southern Zone CPUE for the first five months of 2002 was at or below average for the period 1999-2002 (Figure 4.1-13b. Monthly CPUE has been more variable in this zone compared to the Middle Zone (Figure 4.1-13b).

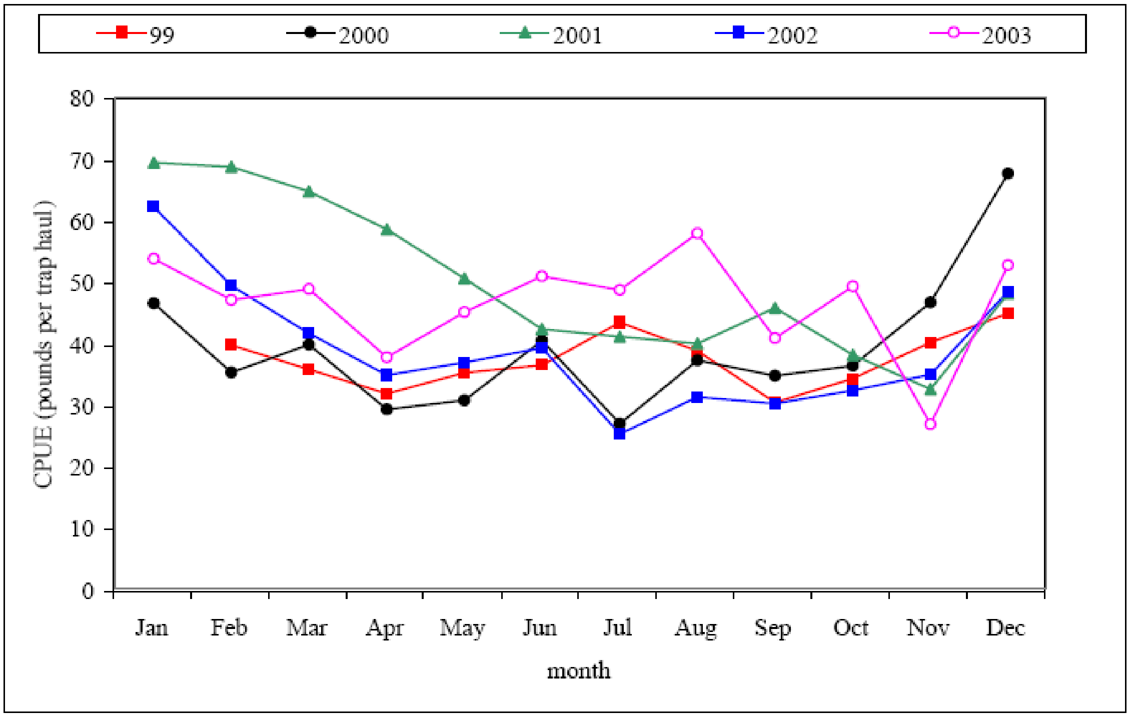


Figure 4.1-13a. Monthly CPUE of golden crab by year, Middle Zone.

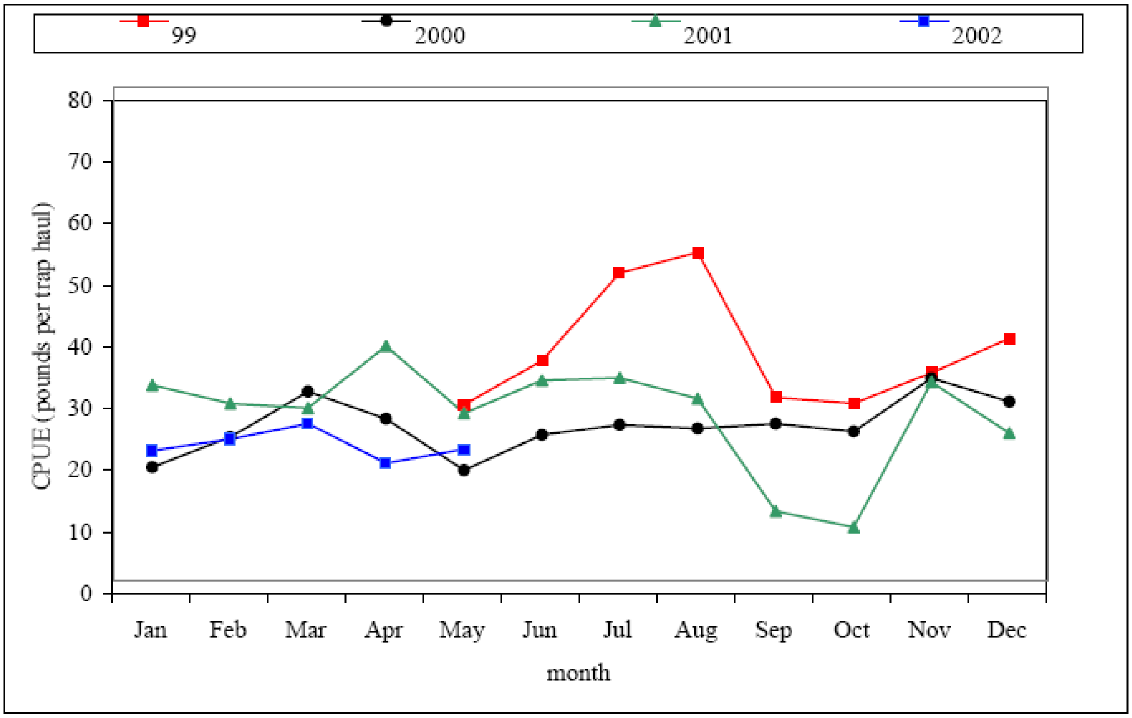


Figure 4.1-13b. Monthly CPUE of golden crab by year, Southern Zone.

TIP Sampling
The 1999 SAFE report presented size data through December 1997. This report includes samples collected through December 2003 (NMFS 2004, Appendix 2). In the interim, 12,269 crabs were measured, bringing the total measured from May 1995 to December 2003 to 17,187. Mean monthly size has been variable, and there have been no obvious trends in size by month across years (Figure 4.1-14). In addition, there has been little evidence of annual trends in mean size, although crabs were smaller in the first five months of 1999 than in other years (Figure 4.1-14, e), and in 1997, crabs were larger in most months than they were in other years (Figure 4.1-14, c).

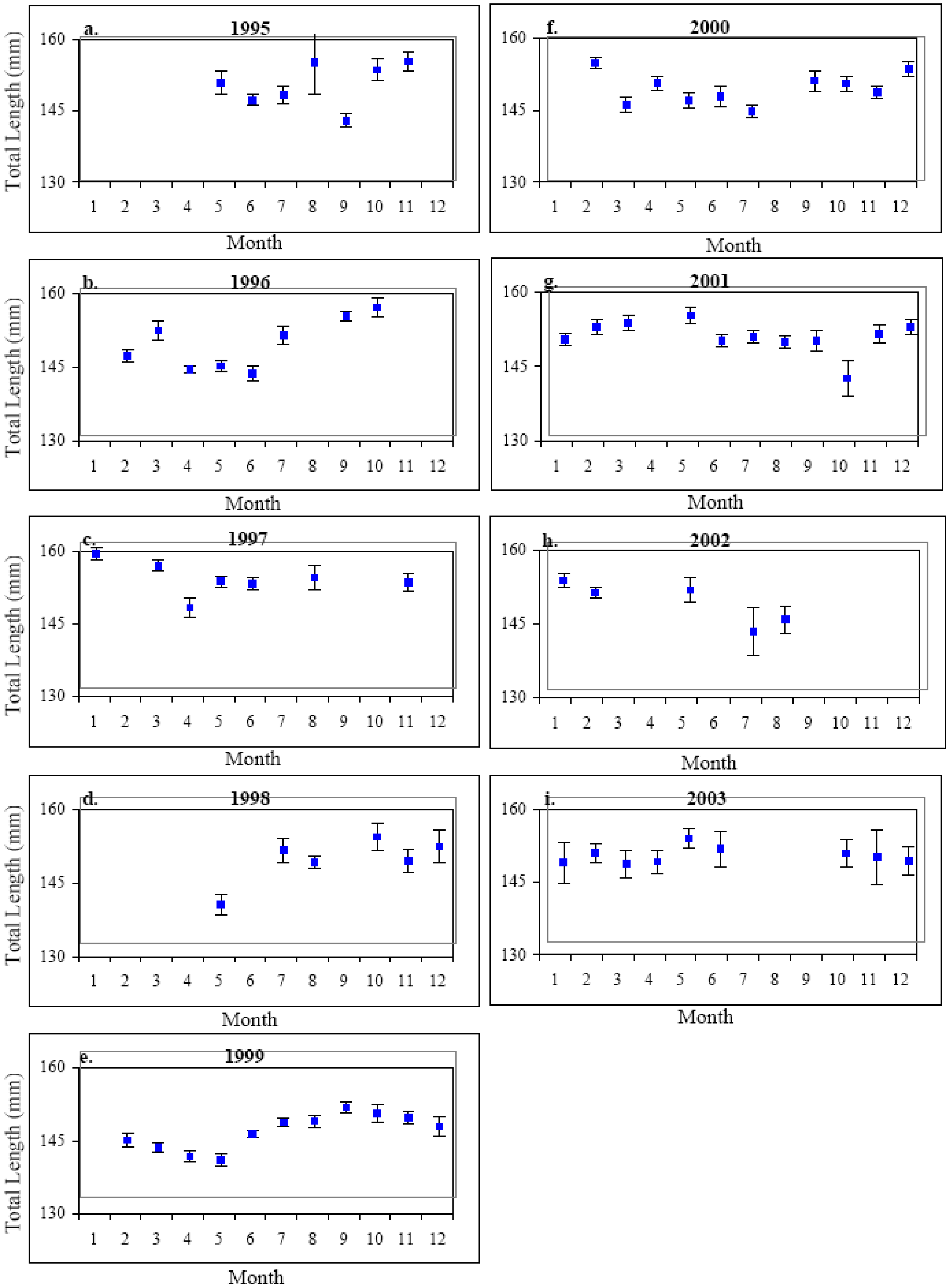


Figure 4.1-14. Mean monthly size of golden crab by year, with 95% C.I.

In contrast to mean monthly size, the length distribution of golden crabs sampled in the TIP survey has been remarkably consistent from 1995 to 2003 (Figure 4.1-15). Except for 1999 (Figure 4.1-16, e), the modal length appears to be very close to 150 mm in all years, and the breadth of sizes observed has also been similar (Figure 4.1-15, d,f-i). The modal length was notably smaller in 1999 than in other years (Figure 4.1-15, e).

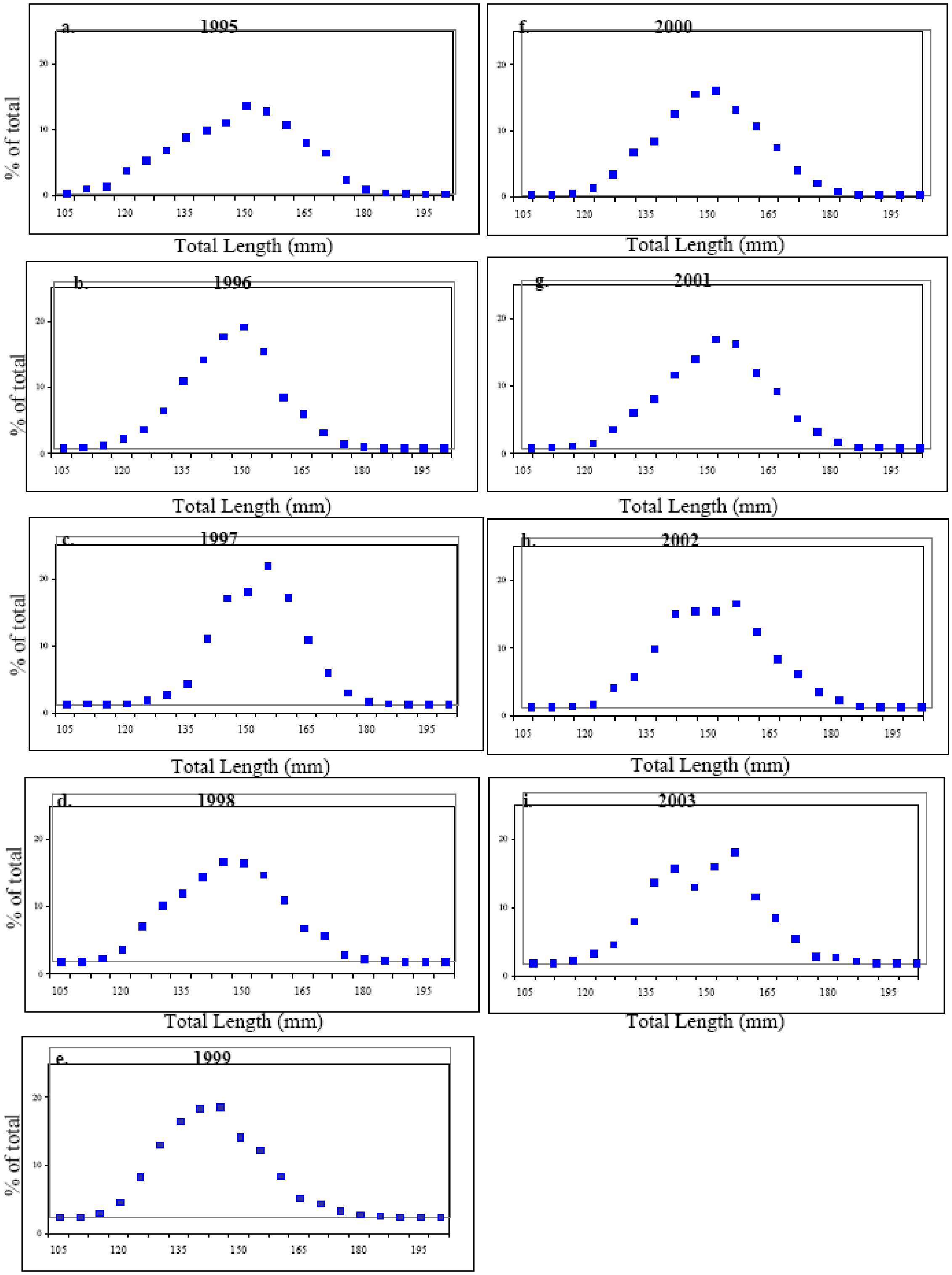
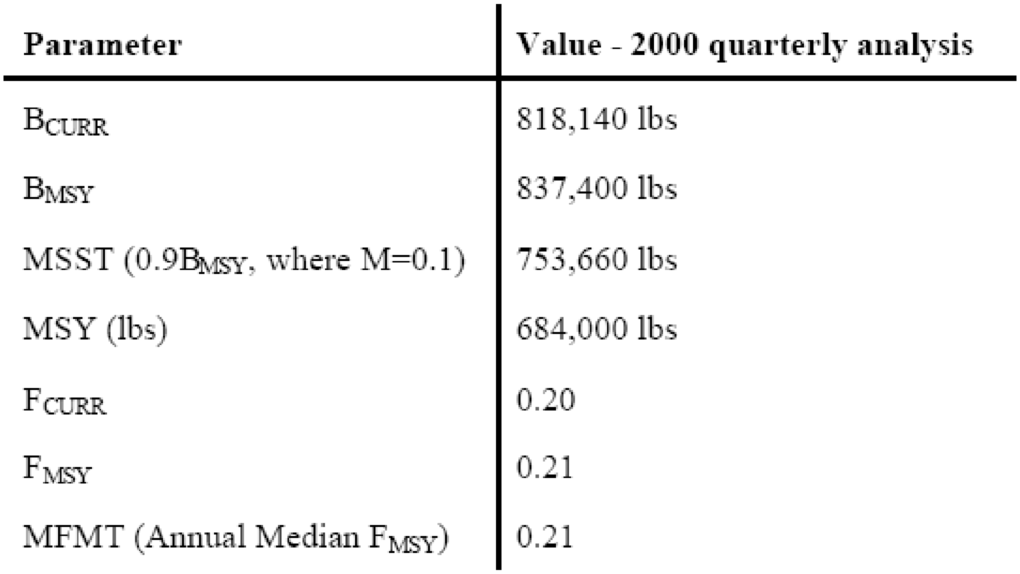


Figure 4.1-15. Length frequency of golden crabs measured in the TIP survey, 1995-2003

Production Model Analysis
Catch and estimated effort data were fit with a non-equilibrium production model to estimate stock status relative to MSY levels. The model was fit to both quarterly and annual estimates of catch and effort. Two paired annual observations of catch and effort were added to the new analysis (1999 and 2000), increasing the number of paired observations to 5 and increasing confidence in the model to some extent (Harper et al. 2000, Appendix 3). Seven quarterly estimates of catch and effort were added to the analysis (May 1998 through January 2000).

Harper et al. (2000) concluded that fitting the model with the five annual catch and effort observations resulted in less certain, although similar, estimates of stock status than did use of quarterly observations. The Harper et al. (2000) assessment concluded that, as of 2000, golden crab were neither overfished nor undergoing overfishing. Current biomass was slightly less than BMSY, but above MSST (Table 4.1-15). Current F was nearly equal to FMSY and MFMT (Table 2). The 2003 Status of Stocks report (NMFS 2004) also indicated the stock was not overfished or undergoing overfishing in 2003.

Table 4.1-15. Stock assessment parameters from the non-equilibrium production model (Harper et al. 2000 and NMFS 2004 Appendix 3).



Parameter	**Value - 2000 quarterly analysis**
B_{CURR}	818,140 lbs
B_{MSY}	837,400 lbs
MSST (0.9B_{MSY}, where M=0.1)	753,660 lbs
MSY (lbs)	684,000 lbs
F_{CURR}	0.20
F_{MSY}	0.21
MFMT (Annual Median F_{MSY})	0.21

4.1.5 Spiny Lobster

Description and Distribution

The Caribbean spiny lobster, *Panulirus argus*, is a crustacean closely related to crabs, shrimp, and crayfish. Common names for this lobster include crayfish, crawfish, langosta, and Florida lobster. There are about 12 species of lobster in Florida; Caribbean spiny lobsters are by far the most abundant. They vary from whitish to a dark red-orange. The two large, cream-colored spots on top of the second segment of the tail section are the diagnostic features for identifying this species. There are also two smaller cream-colored spots adjacent to the tail fan. Spiny lobsters lack the large, distinctive, crushing claws of their northern cousins, the American lobster.

The name "spiny" comes from the strong, forward-curving spines projecting from the hard shell that covers the body of the lobster. The spines are protection from predators and can present a definite hazard to anyone handling the animal without wearing gloves. There are two large prominent spines, sometimes called horns, above the eyes.

A spiny lobster's body has two main parts: the cephalothorax (head section) and the abdomen (tail section). The cephalothorax comprises the head, a cape-like carapace or shell, the mouthparts, antennae, antennules (smaller antennae-like structures), and ten walking legs. Spiny lobsters wave their long, spiny antennae like whips for fighting and defense. They use the shorter antennules to sense movement and detect chemicals in the water. The lobster's mouth, located on the underside of and toward the front of the cephalothorax, is surrounded by large, heavy structures called mandibles, or jaws, and by maxillipeds, or accessory jaws. Both sets of jaws are used for biting and grinding food and directing it into the mouth.

The abdomen, or tail section, is narrower than the cephalothorax. The shell covering the tail section is divided into six ring-like segments, and each segment ends in a spine on each side. Under the tail are four pairs of small leaf-like structures called pleopods (or swimmerets). The tail ends in a flat, flexible fan with a broad center section (the telson) and has two lobes on each side of the telson called uropods. This fan generates the thrust needed for the animal to "tail flip"-- a rapid backward escape mechanism that presents an armored, thorny front to any potential enemy.

To determine the sex of a spiny lobster, examine the underside of the cephalothorax and tail section. The fifth pair of the male's walking legs has sperm-duct openings at the base; these openings become greatly enlarged during the breeding season and the second walking legs of mature males are much longer relative to the other walking legs. The fifth pair of a female's walking legs has hook-like structures at the tips but her second leg does not elongate. On a male, the pleopods beneath the tail section are single and paddle-like. Each pleopod on a female has two lobes; one lobe is paddle-like, and the other lobe resembles small pincers.

The Caribbean spiny lobster occurs throughout the Caribbean Sea, along the shelf waters of the southeastern United States north to North Carolina, in Bermuda, and south to Brazil and the Gulf of Mexico. The origins of the Florida stock remain unknown as information on larval recruitment remains scarce. However, Lyons (1981) concluded that, given the constant recruitment to the fishery despite the reduction in spawning potential of the Florida stock, recruitment is probably in large part exogenous. That conclusion is supported by examination of the genome of *P. argus* populations from Venezuela to Bermuda (Silberman 1994). Restriction fragment length polymorphism analysis of mtDNA identified no differentiation between populations, suggesting a single pan-Caribbean *P. argus* stock, though populations in Brazil are genetically distinct from Caribbean populations and may represent a subspecies, *P. argus westonii* (Sarver et al., 1998).

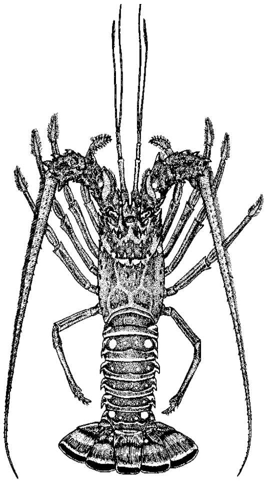


Figure 4.1-16. Spiny lobster, *Panulirus argus*

Reproduction

Mating and spawning of eggs in *P. argus* can occur throughout the range of mature adults which in the Florida Keys includes Hawk Channel, the fore reef, and deeper hardbottom regions. The release of eggs of *P. argus* in the Florida Keys occurs on the offshore reef tract and deeper hardbottom regions, principally from April through September (Bertelsen and Cox, 2001; Lyons et al., 1981; Davis, 1974). The onset of population-wide reproductive maturation of female lobsters, estimated as the size at which 50% of the population is ovigerous during the peak of the reproductive season, occurs at about 70-75 mm CL, though females as small as 57 mm CL have been observed bearing eggs (Bertelsen and Matthews, 2001). The onset of population-wide functional maturity in males, estimated by the onset of allometric growth of the second pair of walking legs, has been estimated to occur at 98 mm CL (FWC unpublished data). Mating and spawning behavior appear, in part, controlled by environmental factors. Increased day length and water temperatures have been shown to enhance courtship and the frequency of spawning (Lipcius and Herrnkind, 1987). There are generally size-specific patterns in mating and spawning. Larger females generally mate, spawn eggs, and release larvae, earlier in the reproductive season than smaller mature females (Lipcius, 1985; Bertelsen and Matthews, 2001). Smaller adult males molt early in the reproductive season, while larger males mate (Lipcius, 1985).

Size-specific differences in the onset of reproductive maturity of female *P. argus* have been noted between the lobster populations in the Florida Keys and the Dry Tortugas. The lobster population in the latter region has historically endured much lower fishing pressure and consequently, the size-structure of the lobsters there is larger than that in the Florida Keys. Females in the Dry Tortugas begin producing eggs at a much larger size than do those in the Florida Keys. It has been speculated that lobsters in both regions begin to produce eggs at the same chronological age, but fishery practices has resulted in comparatively slower growth rates in Florida Keys lobsters (Bertelsen and Matthews, 2001).

Development, growth and movement patterns

Growth rates of early-benthic-stage juveniles (i.e., 6 – 35 mm CL) in Florida Bay have been estimated to be 0.82 mm CL per week (Sharp et al., 2000). Growth rates of subadults (i.e., 50-75 mm CL) have been reported as 0.46 mm CL per week, but are lower among injured lobsters (Hunt and Lyons, 1986). Growth rates decrease dramatically between 74 mm CL (0.46 mm per week) and 76 mm CL (0.23 mm per week) as lobsters attain sexual maturity.

Panulirus argus is a highly migratory palinurid lobster species with a complex life cycle in which distinctly different habitat types are occupied during ontogeny. After spawning, the oceanic phyllosome larvae spend an estimated 9 months (Butler and Herrnkind, 1992) in the plankton, potentially dispersing thousands of kilometers. Because of the potential for *P. argus* larvae to be transported such enormous distances, understanding the factors that affect their distribution during this stage is complex and remains poorly understood. Extensive effort has been directed at understanding the recruitment dynamics of *P. argus* in south Florida, especially in Florida Bay and along the Florida Keys archipelago, which is the largest and most important expanse of nursery habitat for the species in the region (Davis and Dodrill, 1989). These studies have documented that late-stage larvae concentrate at the edge of the Florida Current, and it is there that puerulus post-larvae are first observed (Yeung and McGowan, 1991). *Panulirus argus* pueruli are nocturnally active and efficient swimmers capable of speeds of 10 cm/s (Calinski and Lyons, 1983).

Recruitment to inshore environments occurs all year round into Florida Bay and nearby regions in monthly pulses coincident with the new moon (Heatwole et al., 1991; Forcucci et al., 1994). Upon arrival nearshore, post-larvae preferentially settle into dense vegetation, especially the architecturally complex macroalgae, *Laurencia* spp. Seagrass meadows also function as settlement habitat (Acosta, 1999; Sharp et al., 2000), but the subsequent survival of lobsters settling there appears to be lower compared to those that settle within macroalgae (Herrnkind and Butler, 1986). Temperature and salinity regimes restrict *P. argus* settlement to the southernmost reaches of the Bay (Field and Butler, 1994). In other areas in the Caribbean, *P. argus* may also settle on mangrove prop roots (Acosta and Butler, 1997).

Once settled, *P. argus* pueruli metamorphose into the first benthic instar [~ 6mm carapace length (CL)] (Marx and Herrnkind, 1985; Butler and Herrnkind, 1991; Forcucci, et al., 1994). These "algal-stage" juveniles reside solitarily within vegetation until reaching 15-20mm CL, then emerge and take up refuge in crevice shelters provided by large sponges, octocorals, and solution holes. These "post-algal" juveniles occupy a relatively small home range within the nursery until they reach about 35mm CL, and then become increasingly nomadic (Herrnkind and Butler, 1986). At about 50-80 mm CL lobsters begin to move from the inshore nursery habitat to coral reefs and other offshore habitats (Hunt and Lyons, 1986).

Large juvenile and adult lobsters are very mobile and capable of moving several miles during nocturnal foraging. Lobsters have a highly developed capacity to navigate and are capable of returning to specific foraging locations or diurnal shelters like solution holes or reefs, where they often occupy communal dens or holes during daylight hours. They are nocturnal feeders and predominantly prey upon live molluscs and crustacea, including hermit crabs and conch. Although they will scavenge, they are predominately active predators and will consume up to

20% of there weight in food each night. Individual lobsters also are capable of relatively long distance migrations during spawning and groups of lobsters may also have long distance directional movement. These mass movements are well known to fishermen and have been observed to precede winter storms and hurricanes. Lobsters have been observed moving in long lines or queues during these events. Little is known about the dispersion of lobsters during these mass movements or how much of the lobster population participates in these forays.

There is no definitive research on the advection or retention of phyllosoma larvae in the Florida Keys. The hydrography of this region is dominated by the strong Florida Current, which links the Loop Current in the Gulf of Mexico with the Gulf Stream in the North Atlantic. Although the Loop Current in likely responsible for the aperiodic transport of larvae to Florida West coast on the Northern Gulf of Mexico there are insufficient surveys to resolve if the Loop current and its southern counterpart, the Tortugas Gyre, are sufficient to retain lobster in Florida. Current genetic studies have not identified region differences in lobster populations although more detailed mitochondrial DNA analysis methods that may be suitable for the identification of source populations have not been fully explored. Clarification of this biological-physical coupling will advance our understanding of spiny lobster population dynamics and promote effective management of the fishery stocks.

Ecological relationships

Caribbean spiny lobsters are primarily hard substrate dwellers. During the day, they find refuge in dens in solution holes or under sponges, corals, seagrass roots, or other structures that provide cover. At night, they leave their dens to forage in surrounding areas where prey is abundant. It has been suggested that lobsters help to maintain shelters that provide cover for other species in certain habitat. For example, lobsters may keep solution holes free of sediment, thus making them available for occupation by groupers. However, there is little known on this subject. The role of spiny lobsters in ecosystem function is unclear. Although spiny lobsters are numerically dominant predators in Florida Bay, they are likely not keystone predators there, nor are they likely to be in other systems (Nizinski, 1998).

Spiny lobsters are predatory feeders. As planktonic larvae (phyllosomes), they use their legs to spear fish larvae, which they transport and consume over long periods (Moe, 1991). All benthic stages of *P. argus* feed preferentially on molluscs, especially gastropods, and crustaceans, but will consume a wide variety of invertebrates as well as dead fish (Herrnkind et al. 1975; Cox et al. 1997; Briones 2003). Molluscs comprise up to 75% of the prey items found in lobster guts (Espinosa et al 1991; Cox et al. 1997). Larger lobsters consume larger individuals of similar prey items than do smaller lobsters. Differences in diet of juvenile and adult lobsters reflect the difference in prey assemblages between juvenile and adult habitats. Diet is apparently a reflection of the local abundance of available potential prey (Briones 2003) which lobsters locate by probing the sediment with the sensory tips of the tips of the first pair of walking legs (Herrnkind et al. 1975; Cox et al. 1997).

Spiny lobsters are food for a wide variety of predators including snappers, groupers, sharks, rays, turtles, and octopus. Algal phase juveniles are targeted by small grunts, snappers and groupers. Gray snapper have been shown to prey on small early benthic juvenile lobsters tethered in Florida Bay (Herrnkind and Butler, 1986). Smith and Herrnkind (1992) found a high proportion of early benthic juvenile lobsters in the gut contents of stingrays (*Dasyatis* spp.) and bonnethead sharks (*Sphyrna tiburo*). Nurse sharks (*Ginglyostomata ciratum*) are also known predators of *P. argus* (Cruz and Brito 1986). Eggleston et al (1990) list potential lobster predators in their study area including: gray snapper (*Lutjanus griseus*), schoolmaster snapper (*L. apodus*), mutton snapper (*L. analis*), yellowtail snapper (*Ocyurus chrysurus*), Nassau grouper (*Epinephelus striatus*), red hind (*E. guttatus*), barracuda (*Sphyraena barracuda*), green moray eel (*Gynmothorax funebris*), spotted moray eel (*G. moringa*), nurse shark (*Ginglyostomata cirratum*), southern stingray (*Dasyatis americana*), bottlenose dolphin (*Tursiops truncatus*), loggerhead turtle (*Caretta caretta*), stone crab (*Menippe mercenaria*), portunid crab (*Portunus spinimanus*), and octopus (*Octopus* spp).

Human fishers, both commercial and recreational, impact spiny lobster populations in more ways than just by direct harvest. The Florida spiny lobster trap fishery is unique in that sub-legal sized lobsters (shorts) are used as live attractants (bait) in traps. Many of these confined lobsters are injured in the process of fishing the traps. Some die from starvation while confined in traps. Others are killed by triggerfish, octopus, or other predators that are able to enter and leave traps at will. Still others die from handling or exposure. Hunt et al (1986) estimated average mortality rates of bait lobsters at 26.3% for four weeks of confinement. This estimate, however, includes death from exposure, which has presumably been reduced since 1987 as boats are now required to be equipped with live wells in order to keep shorts on board. The mortality rate for lobsters without exposure was 10.1% for four weeks (SEDAR8, 2005).

Recreational lobster divers catch or handle many lobsters for each lobster that they successfully harvest. Depending on their experience level, recreational divers may not be able to judge lobster size without capturing and physically measuring them. Some are released because they are too small, some because they are egg-bearing, and some escape after they are captured. Many of the lobsters are injured in the capture/release process. Approximately 50% of sub-legal and legal-sized spiny lobsters in Biscayne Bay, Florida, possessed injuries after the 1977 regular fishing season (compared to 31% injury immediately before that season opened in 1976; Davis 1981). Sublethal disturbances by recreational divers can increase the frequency of injured lobsters, alter shelter choice behavior, and increase predation-induced mortality of injured lobsters (Parsons and Eggleston 2005).

Abundance and status of stocks

The abundance of the stock has been recently estimated using a modified DeLury model (SEDAR 08). The estimated number of lobsters by fishing year varied from 30.4 million in 1985-86 to 39.3 million in 1999-00 and the estimate for 2003-04 was intermediate at 35.2 million lobsters. Recruitment expressed as age-1 lobsters was bimodal with an early increase in 1987-88 (17.7 million) and then a decline and another increase in 1996-97 (18.9 million) through 1998-99 then dropped reaching a low in 2000-01 (13.1 million) and then a gradual increase afterward with 15.8 million in 2003-04.

The spiny lobster fishery started in Key West in the Florida Keys in the 1800s as a bait fishery and for some local consumption. Reported landings did not exceed a million pounds until 1941 (Figure 4.1-17). These reports made to the Florida Board of Conservation did not make any explanation of the sharp increase in landings reported in 1942 and in the late 1940s. Landings made a major increase after 1965 and have varied without trend after 1970; however, landings in 2001 were the lowest in forty years. There were some landings from other states during the 1960s and early 1970s but these amounts were low and other than 1140 pounds in 1987, commercial landings of spiny lobsters have been from Florida for the last couple of decades and so we focus on Florida. Because the gear used on each trip was not recorded on trip tickets until the latter part of 1991, the proportion of landings by gear from 1978 through 1992 were taken from NOAA Fisheries' General Canvass and from the State of Florida's Marine Resources Information System thereafter. However, gear was not available on a monthly basis in the General Canvass and therefore the breakdown by gear had to be tallied on a calendar year basis even though the fishery operates on a fishing year basis. After Florida's Lobster Trap Certificate Program was implemented in 1993, divers began to produce a larger proportion of the landings as illustrated for 2003 in Figure 4.1-18. Due to the seasonal closure in the fishery, the more common way of referring to landings is by fishing year which is from August 6 through March 31 of the following year. The Florida Keys account for an average of 90% of the landings. The season with the highest landings was 1989-90 with 7.8 million pounds and the 2001-02 season had the lowest with 3.1 million pounds. If we just consider the 1993-94 and later seasons, the 1993- 97 seasons in the Florida Keys averaged 1.8 million pounds more than the five most recent seasons. The trap fishery declined an average of 2.0 million pounds per season while the diver fishery increased their harvest by 0.18 million pounds.

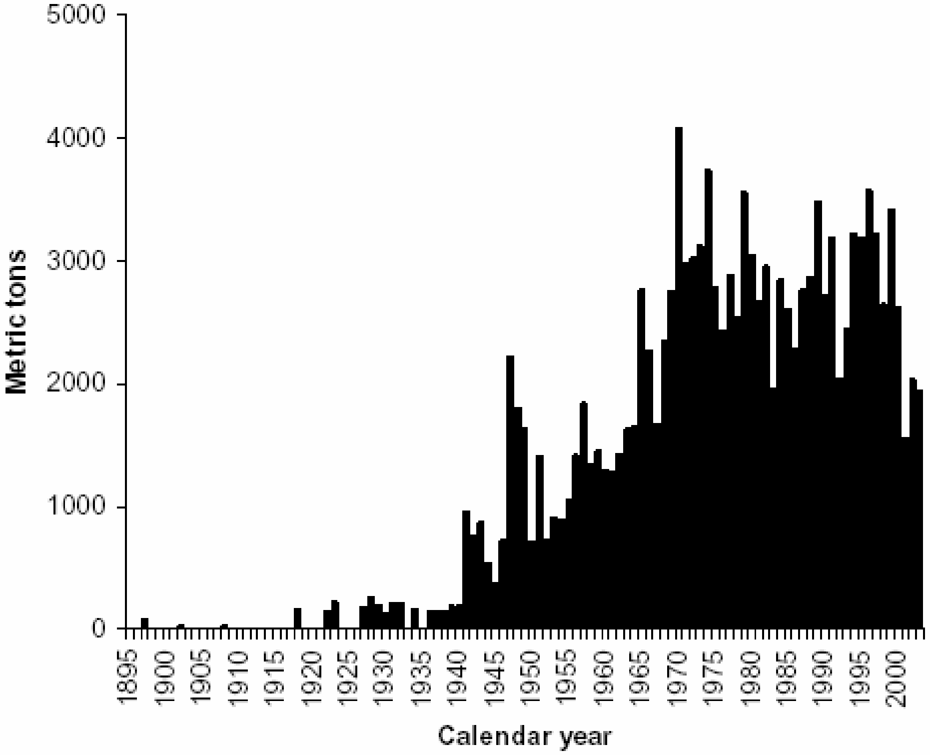


Figure 4.1-17. Commercial landings of spiny lobster in the United States by calendar year.

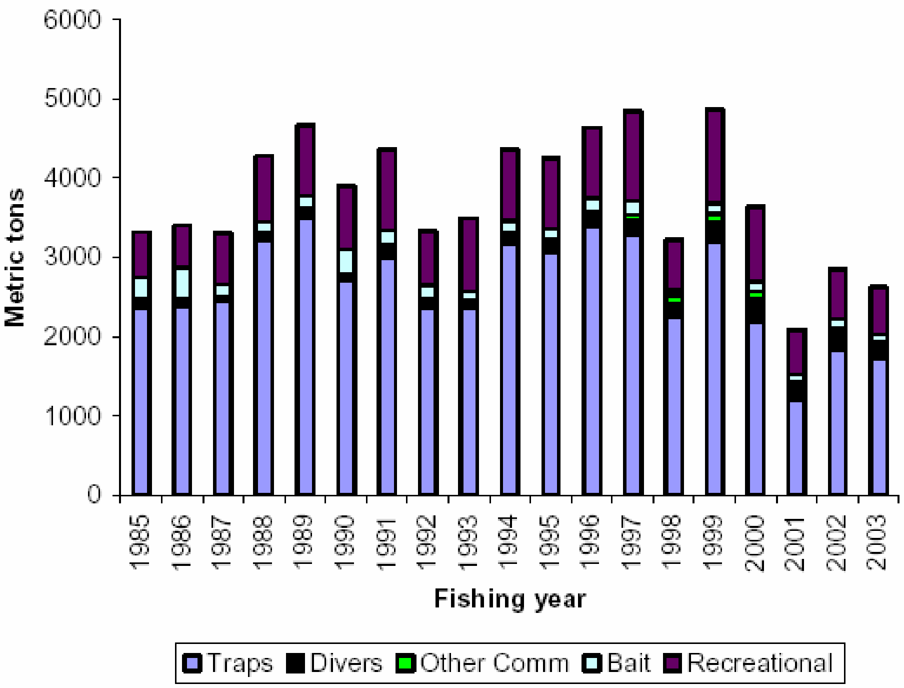


Figure 4.1-18. Allocation of spiny lobster landings in Southeastern U.S. by method or recreational and by year.

Amendment 6 of the Spiny Lobster FMP defined overfishing as fishing at a rate in excess of that associated with a static SPR value of 20% (F20%). With the current life history values and fishery practices, the fishing mortality rate on fully recruited lobsters (age-3) at a static SPR of 20% was 0.49 per year. The spiny lobster fishery in Southeast United States has fluctuated at SPR values around the 20% objective until the three most recent years (Figure 4.1-19) and was deemed to not be overfished because the fishing mortality rate on age-3 in 2003-04 (0.26 per year) was below the Council's Fmsy proxy of F20%. Even when the fishing mortality rate was adjusted for retrospective bias (0.36 per year), the fishing mortality rate in 2003-04 was still below the Council's management objective. As noted above, without a Caribbean-wide stock assessment, we were unable to determine the status of the stock with regard to the spawning biomass at MSY (Bmsy) or the Minimum Stock Size Threshold.

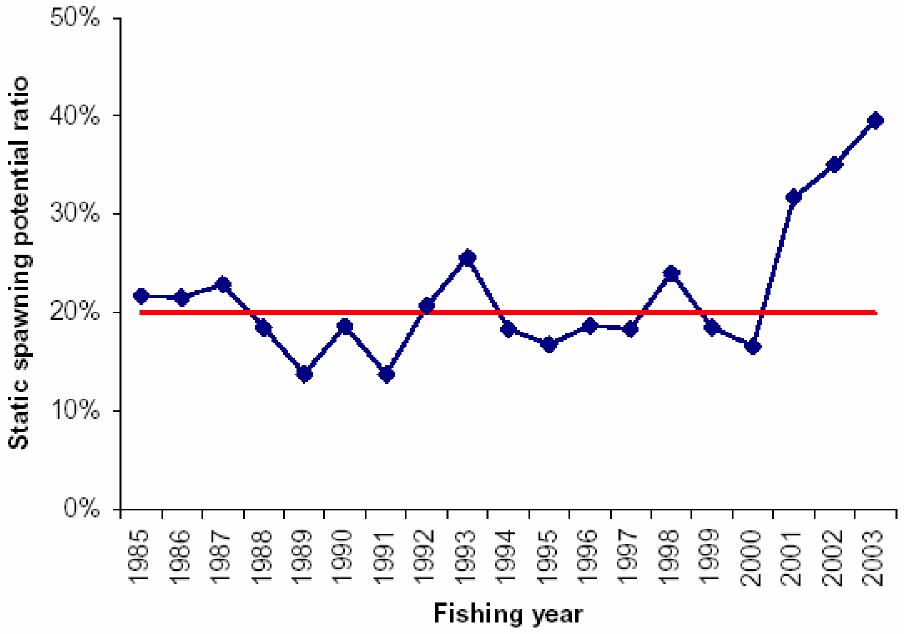


Figure 4.1-19. Spawning Potential Ratio (SPR) by fishing year and management objective of 20%.

Another factor affecting the stock abundance is the commercial trap fishing practice of placing sub-legal sized lobsters into traps to attract other lobsters. These lobsters are referred to as shorts. The question regarding stock abundance is how much additional mortality does the resource endure with this practice. The number of lobsters used for bait can be broken into how many short lobsters are used to bait traps during the season and what is the survival rate of those animals.

The estimated number of trap hauls per fishing year and the lobsters confined as bait are shown in Table 4.1-16. On average, fishers pull almost seven million traps over a typical season and they used 11.0 million sub-legal lobsters and 0.5 million legal sized lobsters as bait. Note that this model captured the effect of Hurricane Georges in 1998 when many fishers lost their traps. There is a strong seasonal pattern to bait usage because until the season has progressed a bit, there are not many sub-legal lobsters available and fishers bait with other baits, legal lobsters and whatever they can. Within a few weeks, more sub-legal lobsters are available and the use of legal lobsters declines and the traps are baited with more sub-legals.

Table 4.1-16. Bait usage and mortality for spiny lobster by fishing year 1993-2000.

Fishing		Bait usage				Bait Mortality			
Year	Landings	Trap	Shorts	Legals	Total bait	Ave	Shorts	Legals	Total

	(lb)	Hauls				bait / trap			bait
1993	5,109,464	7,178,306	9,722,203	251,608	9,973,811	1.39	413,930	8,686	422,617
1994	6,893,968	7,755,461	11,530,549	676,680	12,207,230	1.57	470,527	21,911	492,439
1995	6,676,451	7,668,209	11,939,043	554,977	12,494,020	1.63	495,107	17,928	513,035
1996	7,335,547	7,733,807	13,090,248	1,009,931	14,100,179	1.82	549,376	34,316	583,692
1997	7,097,950	7,868,428	14,370,630	427,713	14,798,343	1.88	606,392	14,749	621,140
1998	4,864,200	5,433,270	5,757,398	352,503	6,109,901	1.12	264,970	11,006	275,976
1999	6,882,285	6,563,086	12,115,455	510,228	12,625,683	1.92	482,315	15,833	498,148
2000	4,717,168	6,432,743	9,810,643	390,772	10,201,415	1.59	410,927	12,112	423,038
Average	6,197,129	7,079,164	11,042,021	521,802	11,563,823	1.62	461,693	17,068	478,761

4.1.6 Coral, Coral Reefs, and Live/Hardbottom

4.1.6.1 Shallow Water Corals

Description and distribution

Scleractinia and Milleporina (fire corals and stony corals)
Stony corals are marine invertebrates that secrete a calcium carbonate skeleton. Stony corals include members of both the Class Hydrozoa (fire corals) and true stony corals (Order Scleractinia) (Table 4.1-17). The scleractinians can be hermatypic (significant contributors to the reef-building process) or ahermatypic, and may or may not contain endosymbiotic algae (zooxanthellae) (Schumacher and Zibrowius 1985). Zooxanthellate corals, host symbiotic algae from the Genus *Symbiodinium*, which provide a phototrophic contribution to the coral's energy budget, enhance calcification, and give the coral most of its color. The largest colonial members of the Scleractinia help produce the carbonate structures known as coral reefs in shallow tropical and subtropical seas around the world. Rapid calcification rates of stony corals have been linked to the mutualistic association with single-celled dinoflagellate algae, zooxanthellae, found in the gastrodermal cells of the coral tissues (Goreau et al. 1979). The Scleractinia have diversified into multiple families which exploit the ability to form complex colonies. The individual building unit in a colony is termed a polyp: a column with mouth and tentacles on the upper side. Massive and branching stony corals are the major reef framework builders and source of sediment production. Corals provide substrata for colonization by benthic organisms, construct complex protective habitats for a myriad of other species including commercially important invertebrates and fishes, and serve as food resources for a variety of animals.

Table 4.1-17. Classification of corals included under the Council's Coral, Coral reefs and Live/ Hard Bottom Fishery Management Plan.

- Phylum Cnidaria
  - Subphylum Medusozoa
    - Class Hydrozoa
      - Order Anthoathecata
        - Suborder Capitata
          - Family Milleporidae (fire, stinging corals)
  - Subphylum Anthozoa
    - Class Anthozoa

Subclass Hexacorallia (or Zoantharia)
    Order Scleractinia (stony corals)
Subclass Octocorallia
    Order Alcyonacea (soft corals)
        Suborder Alcyoniidae (soft corals)
        Suborder Scleraxonia (gorgonians)
        Suborder Holaxonia (gorgonians)
        Suborder Calcaxonia (gorgonians)

Nearly 70 species of stony corals are known from the continental shelves of the study area, a vast majority of which have been noted from the Florida Keys and the Dry Tortugas alone (Table 4.1-18). This is a remarkably high number, considering that over 70 species are found in the Caribbean.

Corals that are limited in depth to less than 70 m are generally zooxanthellate, almost exclusively colonial, and have a strong tropical affinity (Caribbean-Bahamas, southeast Florida, Bermuda, with extreme records in Brazil and North Carolina). This group is often referred to as the shallow water reefs corals. Examples of this group include *Acropora palmata*, *Porites porites*, *Diplora labyrinthiformis*, *Mussa angulosa*, and *Eusmilia fastigiata* (Table 2).

Table 4.1-18. Common shallow water scleractinian corals identified in the management area. The distribution zones are divided as follows: (1) Atlantic Coast to NE. Florida (South Atlantic Blight); (2) SE. Florida; (3) Florida Keys and the Dry Tortugas.

Order	**Family**	**Genus species**	**Distribution**
Scleractinia			
	Acroporidae	*Acropora cervicornis*	2, 3
		Acropora palamata	2, 3
		Acropora prolifera	3
	Agariciidae	*Agaricia agaricites*	2, 3
		Agaricia fragilis	2, 3
		Agaricia humilis	2, 3
		Agaricia lamarcki	2, 3
		Leptoseris cucullata	2, 3
	Astrocoeniidae	*Stephanocoenia intersepta*	2, 3
	Caryophylliidae	*Cladocora arbuscula*	2,3
		Eusmilia fastigiata	2, 3
	Dendrophylliidae	*Tubastraea coccinea*	2, 3
	Faviidae	*Colpophyllia natans*	2, 3
		Diploria clivosa	2, 3
		Diploria labyrinthiformis	2, 3
		Diploria strigosa	2, 3
		Favia fragum	2, 3
		Manicina areolata	3
		Montastraea annularis	2, 3
		Montastraea cavernosa	2, 3
		Solenastrea bournoni	2, 3

	Solenastrea hyades	2, 3
Meandrinidae	*Dendrogyra cylindrus*	2, 3
	Dichocoenia stokesi	2, 3
	Meandrina meandrites	2, 3
Mussidae	*Isophyllia rigida*	2, 3
	Isophyllia sinuosa	2, 3
	Mussa angulosa	2, 3
	Mycetophyllia aliciae	2, 3
	Mycetophyllia danaana	3
	Mycetophyllia ferox	2, 3
	Mycetophyllia lamarckiana	2, 3
	Mycetophyllia reesi	3
	Scolymia spp.	2, 3
Oculinidae	*Oculina diffusa*	2, 3
Pocilloporidae	*Madracis decactis*	2, 3
	Madracis formosa	3
	Madracis mirabilis	2, 3
Poritidae	*Porites astreoides*	2, 3
	Porites porites	2, 3
Siderastreidae	*Siderastrea radians*	2, 3
	Siderastrea siderea	2, 3

Octocorallia (sea fans, sea whips, etc.)

For the purpose of this plan, includes species belonging to the Class Octocorallia (soft corals and gorgonians), Order Alcyonacea. Similar to stony coral corals, octocorals are colonial animals with a polyp as the individual building unit and may contain endosymbiotic algae (zooxanthellae). Unlike stony coral, octocorals do not secret a calcium carbonate skeleton but have a axial skeleton mainly composed of collagen fibers in a proteinaceous matrix. Although octocorals do not contribute to reef framework, they do contribute greatly to reef complexity and diversity.

The hardbottom, coral reef, and coral community habitats within the management area contain a considerable diversity of octocorals. Table 4.1-19 lists the distribution of the common octocorals within the management area and includes possible endemic species.

The temperate region from North Carolina to the southeast Florida coast (North of Palm Beach County, FL) contains no distinctive octocoral elements. Typical species found in this region are *Leptogorgia virgulata*, *L. setacea*, *Lophogorgia hebes*, *Muricea pendula*, and *Titanideum frauenfeldii*.

The area from Palm Beach south to the Dry Tortugas contains a tropical Atlantic fauna, which appears to be fairly homogeneous. Some faunal differences occur along the Florida reef tract in response to water temperature ranges, substrate availability, and other variables. Along this area, octocorals are very abundant component of the reef biota with benthic cover and density generally greater than the stony coral component (Jaap et al. 2004, Gilliam et al. 2007a and b).

Cairns (1977a) published a field guide to the more common gorgonians of the Gulf of Mexico, Caribbean, and Florida. Sanchez and Wirshing (2005) recently published a field guide to western tropical Atlantic octocorals. Wheaton described the octocoral fauna off southeast Florida in 20-50 meter zones (1987), off Key Largo, in 27-57 m depths (1981), at Looe Key (1988), and at Dry Tortugas (1975, 1989). DeVictor and Morton (2007) have produced a shallow water octocoral guide for the South Atlantic Blight from Cape Hatteras, NC to Cape Canaveral, FL.

Table 4.1-19. Common octocoral species from the shallow-water continental shelf regions (less than 200 m or 660 ft) of the southern United States. The distribution zones are divided as follows: (1) Atlantic Coast to NE. Florida (South Atlantic Blight); (2) SE. Florida; (3) Florida Keys; (4) Dry Tortugas. * Indicates species with principal distribution within study area (possibly endemic).

Order	Suborder	Family	Genus species	Distribution
Alcyonacea				
	Scleraxonia			
		Briareidae		
			Briarium asbestinum	2,3,4
		Anthothelidae		
			Icilogorgia schrammi	1,2,3,4
			Anthothela tropicalis	1
			Erythropodium caribaeorum	2,3,4
			**Titanideum frauenteldii*	1,2
	Holaxonia			
		Plexauridae		
			Plexaura homomalla	2,3,4
			Plexaura flexuosa	2,3,4
			Plexaura kuna	2,3,4
			Pseudoplexaura porosa	2,3,4
			Pseudoplexaura flagellosa	3,4
			Pseudoplexaura wagenaari	2,3,4
			**Eunicea palmeri*	3
			Eunicea mammosa	2,3,4
			Eunicea succinea	2,3,4
			Eunicea fusca	1,2,3,4
			Eunicea laciniata	3,4
			Eunicea tourneforti	2,3,4
			Eunicea asperula	2,3,4
			Eunicea clavigera	2,3,4
			**Eunicea knighti*	3
			Eunicea calyculata	2,3,4
			Muriceopsis flavida	2,3,4
			Muriceopsis petila	1,2,3,4
			Plexaurella dichotoma	2,3,4
			Plexaurella nutans	2,3,4
			Plexaurella fusifera	2,3,4
			Plexaurella grisea	3,4
			Muricea muricata	2,3,4
			Muricea atlantica	2,3,4
			Muricea laxa	2,3,4

		Muricea elongata	2,3,4
		**Muricea pendula*	1,2,3,4
Holaxonia			
	Gorgoniidae		
		**Leptogorgia cardinalis*	2,3,4
		Leptogorgia hebes	1
		Leptogorgia virgulata	1
		Leptogorgia setacea	1
		Leptogorgia eurale	1
		Pseudopterogorgia bipinnata	3,4
		Pseudopterogorgia acerosa	2,3,4
		Pseudopterogorgia elisabethae	3
		Pseudopterogorgia americana	2,3,4
		Pseudopterogorgia rigida	2,3,4
		Pseudopterogorgia kallos	3,4
		Gorgonia ventalina	2,3,4
		Gorgonia flabellum	3,4
		Pterogorgia citrina	2,3,4
		Pterogorgia anceps	2,3,4
		Pterogorgia guadalupensis	3,4

Protected shallow-water corals

State and Federal laws and regulations protect corals making it illegal to take any scleractinian coral in the United States. *Acropora cervicornis* and *Acropora palmata* were listed as threatened species under the Endangered Species Act in 2006. These species were once dominant on Florida reefs, but their abundance has diminished from historic levels throughout their range in the Caribbean. See section 4.3.6 of this document for a more detailed discussion of these two species.

Reproduction

Stony corals and octocorals have both sexual and asexual reproductive modes. The addition of new polyps to a colony occurs through budding of existing polyps. In this way, colonies grow in size through an asexual means of reproduction. In addition, many coral species, particularly branching ones, are also highly clonal in that they can reproduce asexually by fragmentation. That is, individual branches, when broken off from the parent colony, can re-attach to the substrate and form a new, distinct colony. These characteristics greatly complicate the population biology of corals, particularly branching species.

Corals also reproduce sexually, with sperm fertilizing egg, followed by a process of embryonic development into a planula larva. The larvae may survive long periods (i.e., one to a few weeks) floating in the water currents until they settle and metamorphose into a sessile polyp on some hard substrate. Different coral species display different sexual reproduction strategies. Some species have separate sexes while others are hermaphroditic. Some have internal fertilization and retain the developing embryos inside the mother colony to a relatively late stage of development (brooders) while others (broadcast spawners) release their gametes into the water column so that fertilization and the entire larval development phase occurs in an oceanic, highly diluting environment. Among octocorals, another reproductive strategy is surface brooding, where eggs are released passively onto the surface of the colony (Benayahu and Loya, 1983; Brazeau and Lasker, 1990; Guitiérrez-Rodríguez and Lasker, 2004). While sampling female colonies of *Pseudopterogorgia elisabethae*, Guitiérrez-Rodríguez and Lasker (2004) did not find developing embryos or planula inside the polyps, and they suggested that fertilization occurred either internally immediately before the eggs were released or externally on the surface of the maternal colony.

Brooded larvae are often able to settle shortly after release (hence higher recruitment success and lower average dispersal than broadcast spawning species). An advantage of brooding is that the eggs avoid the risk of being advected off of the reef and away from sperm of potential mates (Lasker 2006). Generally, broadcast spawning stony coral species tend to have high longevity, lower recruitment, larger maximum colony size (i.e., K-selected life history traits). Brooding stony corals are generally more weedy species which do not attain large colony size and hence have limited contribution to reef accretion (Szmant 1986). Such inter-specific differences in the mechanisms of fertilization, dispersal, recruitment, and mortality are likely important in determining the species composition of reef corals in different environments. Such differences reflect the differential allocation of energy to the basic life history functions of growth (rate and density of the skeleton), reproduction (fecundity, mode of larval dispersal, recruitment success), and colony maintenance (intra- and interspecific interactions, competitive ability, regeneration) (Connell 1973, Lang 1973, Bak and Engel 1979, Szmant 1986).

Most broadcast spawning corals release gametes only on a few nights per year. In southeast Florida, most species spawn over a few nights clustered around the full moon in late summer. Spawning synchrony is crucial in order for sessile organisms to accomplish external fertilization. Also, in the context of declining population density as is being observed for many shallow reef corals in the region, fertilization may constitute the major life-history bottleneck as dilution between colonies even few to 10s of meters distant may be prohibitive.

Brooding species often release larvae on a lunar cycle over several months or year round. *Porites astreoides*, a brooding stony coral species, releases larvae around the new moon, primarily from April to June in the Florida Keys (McGuire 1997). However, the brooding season has been reported to be from January to September farther south in Puerto Rico (Szmant 1986). *Favia fragum*, another brooding species, releases larvae monthly year-round (Szmant 1986). Surface brooding has been reported in a few octocoral species found in the management area, including *Briarium asbestinum* and *Pseudopterogorgia elisabethae* (Guitiérrez-Rodríguez and Lasker, 2004).

In either mode of larval development, planula larvae presumably experience considerable mortality (up to 90% or more) from predation or other factors prior to settlement and metamorphosis (Goreau et al. 1981). The selection of appropriate settlement substrate is not well-understood, but for several coral species, chemical cues from crustose coralline algae and microbial biofilms have been shown to induce settlement and metamorphosis (Morse et al. 1994, Morse and Morse 1996, Webster et al. 2004). Settled larvae undergo metamorphosis by generating a calcium carbonate skeleton. The mouth is situated at the upper end, and a ring of tentacles develops around the mouth. After metamorphosis onto appropriate hard substrata, metabolic energy is diverted to colony growth and maintenance. Because newly settled corals barely protrude above the substratum, juveniles need to reach a certain size to reduce damage or mortality from impacts such as grazing, sediment burial, and algal overgrowth (Bak and Elgershuizen 1976, Birkeland 1977, Sammarco 1985). Cary (1914) points out the obvious advantage of young octocorals over stony coral recruits in that their most rapid growth is perpendicular to the substratum, keeping the most active growing part of the colony in a favorable position for resource allocation. Recent studies examining early survivorship of lab cultured *A. palmata* settled onto experimental limestone plates and placed in the field indicate that survivorship is substantially higher than for *Montastraea faveolata*, another broadcast spawner, and similar to brooding species over the first 9 months after settlement (Szmant and Miller 2006). This pattern corresponds to the size of planulae; *A. palmata* eggs and larvae are much larger than those of *Montastraea* spp.

Development and growth

Most corals are colonial in that they are composed of individual units called polyps. Each polyp is an individual: it captures food, has independent digestive, nervous, respiration, and reproductive systems. A large coral colony has thousands of polyps working semi-independently to sustain the colony. Coral colonies grow via the addition (budding) of new polyps. By the same token, colonies can exhibit partial mortality whereby a subset of the polyps in a colony die, but the colony persists.

Scleractinian Density Banding and Growth

Some species of reef building corals grow into large dome-shaped colonies which can live several hundreds of years. Similar to annual growth rings in trees, these corals form annual density bands which can be revealed though radiography of skeletal slabs (Knutson et al. 1972, Dodge and Thompson 1974, Hudson et al. 1976 and others). The annual density bands result from seasonal changes in the thickness of the skeletal structures comprising the overall colony (Barnes and Devereux 1988, *Porites*; Dodge et al. 1992, *Montastraea*; Helmle et al. 2000, *Diploria*). The changes in thickness of skeletal structures are apparent as bulk-density variation over the thickness of a slab and appear as alternating period of light (high density) and dark (low density) bands on X-radiographic negatives.

Annual density bands provide a record of the linear extension rate (cm/yr) and optic density measurements of the X-radiographs can be used to determine the bulk-density of the skeleton (g/cm^3). A complete understanding of coral growth is best attained by all three parameters of growth: linear extension, bulk-density, and calcification. If two of the three parameters are measure, the third can be calculated by the follow formula:

$$\text{Extension (cm/yr)} \times \text{Density (g/cm}^3\text{)} = \text{Calcification (g/cm}^2\text{/yr)}$$

Coral growth parameter of linear extension, density, and calcification correlate with various locally specific variables including: depth, light, temperature, precipitation, salinity, nutrients. Many of these variables are interrelated, however, their impacts on coral growth can also be identified independently. Coral skeletons have also been used to assess growth responses to anthropogenic perturbations such as crude oil and oil dispersants (Lewis 1971, Knap *et al.* 1983), lead pollution (Dodge and Gilbert 1984), fallout plutonium (Benninger and Dodge 1986), turbidity and sedimentation (Loya 1976), and sediment resuspension (Dodge *et al.* 1974).

Historical skeletal growth records (extension, density, and calcification) are useful for testing hypotheses regarding variations in growth attributable to climatic changes such as rising carbon-dioxide levels and sea-surface temperature.

Growth data for some shallow-water scleractinians (brain corals and finger corals) has been summarized by Hubbard and Scaturo (1985), Bright et al. (1981) and Gladfelter et al. (1978). Most growth rates (linear extension) for *Montastraea*, *Porites*, and *Diploria* are less than 1 cm per year. Hubbard and Scaturo (1985) report average extension rates of 0.12-0.45 cm/yr for several species including *Stephanocoenia intersepta*, *Agaricia agaricites*, *Diploria labyrinthiformis*, *Colpophyllia natans*, *Montastraea cavernosa*, *Porites astreoides*, and *Siderastrea siderea*. .

Octocorallia (gorgonians)

For most gorgonian genera, the major axial skeleton component is gorgonin, which is mainly composed of collagen fibers in a proteinaceous matrix (Leversee, 1969). Gorgonin is deposited in concentric layers extracellularly around a central, hollow chambered canal, seldom exceeding a diameter of 100 µm. The axis functions as a mechanical support system facilitating the passive suspension feeding by octocorals (Lewis et al. 1992). The axis must be rigid enough to withstand the total water velocities for the particular habitat while supporting the polyps off the substratum (Muzik and Wainwright 1977). Lowenstam (1964) explains that the flexibility of the axial skeleton of gorgonians can apparently be modulated by sclerotization of the collagen within the axial skeleton. Gorgonian axes can be stiffened by the extracellular deposition of carbonates within the collagen interstitial spaces (Jeyasuria and Lewis 1987). Lewis et al. (1992) suggests that this process mat be a mechanism for dealing with different hydrodynamic forces encountered at various depths.

Many gorgonian species can be characterized by a distinct colony form and a maximum colony size, indicating determinate growth, which suggests that growth is constrained in some way (Lasker et al. 2003). In two studies on *Pseudopterogorgia elisabethae*, the developmental cycle showed a rapid growth rate after settlement which then decreased dramatically with age, suggesting an age-dependent decrease in growth rate (Lasker et al. 2003; Goffredo and Lasker 2006). This size- or age-dependent decrease in growth rates may be due to interactions between the gorgonian colony and its environment (i.e. the balance between nutrient uptake and metabolic rates) instead of a genetically determined developmental plan (Lasker et al. 2003). A common method to determine growth rates of octocorals is by taking linear height measurements of a tagged colony over a period of time, the results usually varying between species. The most accurate method of estimating the age of a colony is counting growth rings seen within the axial skeleton rather than basing it on growth rates. However, counting growth rings usually requires the collection of the colony. Using both methods, height-age equations can be derived for a species (Grigg 1974).

Growth rates can vary dramatically within a species and between different species. Lasker et al. (2003) studied determinate growth in *Pseudopterogorgia elisabethae*. The resulting branch growth rates varied, ranging from negative values (branch loss) to 17.8 cm per year. A later study on this species performed by Goffredo and Lasker (2006) showed growth rates that decreased as a function of height. Colonies that were 0-10 cm in height had a growth rate of 3.5

cm per year; 20-30 cm colonies had a growth rate of 2.6cm per year; and 40-50cm colonies had a growth rate of 0.5 cm per year. Yoshioka (1979) studied the ecology of *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa*, calculating their linear growth rates to be about 5 cm per year for *P. americana* and 6 cm per year for *P. acerosa*. Growth rates were higher for colonies exposed to higher light levels, showing that environmental factors affect the growth of a colony. Reproduction was delayed for 3–5 years until colonies were mature, ranging 15-30 cm respectively. Growth rates of *Pseudoplexaura porosa* branches can exceed 15cm per year (Lasker unpublished data). Due to these variations in growth rates, calculations determining the accurate age of a given colony should be based on growth rings and colony height (not solely on height).

Ecological relationships

Stony corals and octocorals derive energy from several sources including from sunlight through their photosynthetic, symbiotic zooxanthellae (algae living in the coral tissue), from consumption of zooplankton, from bacteria (which act as biochemical recycling agents), from consumption of detritus, and perhaps even directly from dissolved organics.

Corals are subject to the ecological pressures of predation (by fish and invertebrates), competition for space, and other interactions with associated organisms. In some instances, such as the symbiotic relationship of corals to zooxanthellae, the association is mutually beneficial. At the other end of the spectrum, however, are predatory pressures such as those applied by certain reef fishes and invertebrates that eat corals.

The importance of coral ecosystems and associated habitats has been well documented by numerous studies, reviews, and symposia (e.g., Jones and Endean, 1973, 1976; Bright and Pequegnat, 1974; Taylor, 1977; Bright, Jaap and Cashman, 1981, Jaap, 1984, Jaap and Hallock, 1990, Chiappone, 1996). Many of those documents emphasize the complex structure of coral ecosystems, the importance of coral for habitat, the sedentary lifestyle and its implications, the wide geographic and bathymetric distributions, and the many behavioral, physiological, ecological, and physical associations that combine to yield an exceedingly complex biological community. The Magnuson-Stevens Act recognizes these values and lists several corals as continental shelf fishery resources subject to exclusive U.S. use beyond the EEZ.

Ecosystems which include coral (hardbottoms, coral reefs, and coral communities) often represent unique arrays of plants and animals in an integrated ecosystem. The key too many of these systems, if there can be one most important link, is often coral itself, since the corals provide habitat and/or food for most of the other members of the ecosystem. Connell (1973) and Grassle (1973) have studied aspects of population ecology and diversity within coral reefs. Individual biotic components have also been studied -among them, microbes (DiSalvo, 1973), algae (Cribb, 1973), holothurians (Bakus, 1973), shrimps and prawns (Bruce, 1976), echinoderms (Clark, 1976), fishes (Goldman and Talbot, 1976), and others. The resultant coral community is exceedingly complex and productive. Helfrich and Townsley (1965), Odum (1971), DiSalvo (1973), Sorokin (1973c), and others have attempted to quantify and qualify the productivity of corals and their associated biota (e.g., microorganisms) compared to other marine and terrestrial communities.

Because of their vast species diversity, trophic complexity, and productivity, mature coral communities possess numerous mechanisms that past researchers believed may enable them to resist normal disturbances, especially those biological in nature (Endean, 1976). However, coral reefs have declined throughout the Caribbean including off the Florida coast over the past several decades. Numerous factors play major roles in coral health and may potentially threaten the continued viability of domestic corals. These factors include water quality, algal blooms, increased water temperatures, physical impacts from ship groundings and marine construction activities, sedimentation, pollution, nutrient enrichment, diver/snorkeler damage, disease, and over-fishing. Most of the coral reefs and coral communites in the management area may be degraded to such a degree that self-regulating mechanisms are no longer functional.

Massive decline of *Acropora* spp. has occurred over the last several decades throughout the Caribbean, including the Florida Keys. Exact cause of the decline is unknown, but it is likely due in part to the spread of disease, particularly white band and white pox. Several other diseases, including white plague and black band have also affected many coral species throughout the region. The etiology is not well-known for many of these diseases. However, their onset often occurs in the summer months indicating that warmer temperatures may promote their spread (Ward et al. 2007).

In addition, bleaching events associated with high sea temperatures have resulted in coral mortality. Bleaching occurs when the symbiotic zooxanthellae (algae) living within coral tissues are expelled or broken down. Because much of the nutrition of corals is derived from the zooxanthellae, the result can be starvation of the corals if the contribution from zooxanthellae is lost. Corals are often able to recover from bleaching depending on the extent, duration, and severity. Unfortunately, rising sea temperatures associated with predicted climate change may lead to more numerous and/or severe bleaching events in the future (Donner et al. 2007).

The special nature of corals as a fishery is further highlighted by their sedentary attached (not mobile) existence, which separates them from the subjects of many other fishery plans. Protection via escape or camouflage is limited by the design of coral skeletons and polyps. Although some protection is afforded by polyp withdrawl, strict energy budgets restrict the use of such behavior. Hence, in the midst of persistent adversity, (e.g., water pollution, extreme temperatures, sedimentation), corals appear precariously susceptible. The life history of the octocorallian and scleractinian corals is similar to the other invertebrate species. The fruits of coral sexual reproduction are planulae larvae; the larvae are free living (planktonic or benthic). The larvae select settlement sites through chemoreceptors, settle, and undergo metamorphosis to juvenile, sessile corals. Because of their vulnerability to environmental conditions, continued survival of corals will be dependent on management strategies that incorporate more of an ecosystem approach and tackle large scale issues such as water quality.

Abundance and status of stocks

Since the early 1980s, most Caribbean reefs including those of the Florida reef tract have undergone dramatic changes from the classic descriptions of structure and zonation. At this point in history, a sequence of large disturbances seems to have precipitated these dramatic changes in Caribbean reef structure. These disturbances in the early 1980s included a series of bad hurricanes, the Caribbean-wide die-off of the important herbivorous urchin, *Diadema* *antillarum*, and the widespread mortality of the important reef-building coral species, *A. palmata* and *A . cervicornis,* due to disease. The result of these disturbances was an overall decline in coral cover coinciding with a dramatic increase in the cover of macroalgae (seaweeds). Aronson and Precht (2001) argue that the *Acropora* spp. die-off was the primary cause of this shift in benthic community structure, while Hughes (1994) and other authors maintain that changes in herbivory regime (overfishing and *Diadema* die-off) are primarily responsible. It is clear that this shift was a result of multiple disturbances, much of whose effects have not been abated on a region-wide scale. That is, *Diadema antillarum*, *A. palmata*, and *A. cervicornis* have not shown major recovery, though the Florida reef tract generally retains high herbivorous fish abundances. Simultaneously, macroalgae still dominate many Florida coral-reef substrates. Hence, the classic reef zonation patterns described above do not reflect Caribbean reef structure today, nor in the foreseeable future.

For purposes of discussing relative abundance and status of stocks of shallow-water corals, the management unit may be subdivided into four regions based on general species compositions. Each of these regions is discussed individually below.

North Carolina to Central Florida (Cape Canaveral)

NOAA's Office of Coastal Zone Management (l979d) cited reports that three to 30 percent of the shelf region is covered by live bottom habitats. The coral fauna along the edge of the continental shelf from Cape Hatteras, North Carolina, to Cape Canaveral, Florida, is sparse, in low diversity and is thus not characterized as a coral community. These are hardbottom habitats in which few corals are present. Studies by Menzies, et al. (l966) and Macintyre and Milliman (l970) indicate that Pleistocene algal accumulations account for the ledges, small terraces, and slight rises of the continental margin off North and South Carolina, while oolitic deposits predominate in the more southerly sector. *O. varicosa* is present on the inner and mid-shelf (3 to 40 m) as small discrete colonies (<30 cm diameter, usually <15 cm), and on the outer shelf and upper slope to depths of 152 m either as individual colonies (l to 2 m diameter), thickets, or banks. While *O. varicosa* has been found in water as deep as 128 m (off Cape Lookout, North Carolina) and as far north as Cape Hatteras, North Carolina, the majority of the thickest growth occurs off the east coast of Florida, from Cape Canaveral to Ft. Pierce, in the area of the Oculina Bank Habitat Area of Particular Concern.

Corals on the outer continental shelf proper are characterized by patches of low relief hardbottom also referred to as live bottom (Struhsaker, 1969). Hardbottom communities throughout this shelf area have been reviewed by Continental Shelf Associates (1979).

These areas are inhabited by tropical and subtropical fishes, coralline algae, sponges, hydroids, and various species of other invertebrates and coral. They have been described at depths of 20 to 40 m (66 to 132 ft) from Onslow Bay, North Carolina, by MacIntyre and Pilkey (l969) and Huntsman and MacIntyre (1971). Four other species of scleractinians were noted: *Balanophyllia floridana* Pourtales; *Phyllangia americana* Milne-Edwards & Haime; *Astrangia danae* Agassiz (= *A. astreiformis* M.-E. & H.); and the ivory brush coral, *Oculina arbuscula* Verrill. Additional scleractinian records for the North Carolina continental shelf include a number of small, mostly solitary species: *Rhizosmilia maculata* (reported as *Bathycyathus maculatus*), *Dasmosmilia* *lymani*; *Rhizatrochus fragilis* (reported as *Monomyces fragilis*); *Paracyathus defilipii*; and *Cladocora* sp. (Cerame-Vivas and Gray, 1966).

Reports from South Carolina and Georgia waters (Powles and Barans, 1979; Reed, 1978, personal communication, respectively) indicate that the coral fauna is largely the same as off North Carolina, except that coral patches are even more sparsely distributed (Barans, 1978, personal communication). Gray's Reef occurs in this region, approximately 33 km (18 nm) east of Sapelo Island, Georgia. This complex rises from a depth of 22 m (72 ft) to a crest at 18 m (59 ft). It is approximately 6 km (3.2 nm) long and 2 km (1 nm) wide. The geology of Gray's Reef has been studied by Hunt (1974). Although the area is not a true coral reef, a number of corals and their associates are found there. Porter (1978, personal communication) noted that the biomass is dominated primarily by a large pink ascidian (probably *Eudistoma* sp.), secondly by the gorgonian *Leptogorqia* sp. (probably *L. virgulata*), and thirdly by scleractinians, *Oculina varicosa* identified by J. K. Reed and eye coral, *Oculina arbuscula*. If confirmed, this identification extends the range of *O. arbuscula* from Charleston to Savannah (McCloskey 1970). Other species noted by Porter include stump coral (*Solenastrea hyades*), star coral (*Montastraea annularis*, uncommon), *Cladocora arbuscula*, *Astrangia poculata*, and *Phyllangia americana*.

Bayer (1961) stated that the shelf octocoral fauna from the East Coast of Florida north of Cape Canaveral is indistinguishable from the fauna from Georgia and the Carolinas. Reports from North Carolina (Menzies et al. 1966, Cerame-Vlvas and Gray 1966), South Carolina (Powles and Barans 1979), and Georgia (Reed 1978, personal communication) appear to confirm this conclusion for both octocorals and scleractinians.

Central Florida to South Florida (Cape Canaveral to Palm Beach)

This shelf region represents a transitional zone for coral fauna and deserves special consideration. The shelf edge contains a conspicuous band of pinnacles, benches, mounds, and troughs (here collectively referred to as hardbottoms) which are often capped by the Ivory Tree Coral, *Oculina varicosa* Lesueur. Although the species occurs at least as far north as Cape Hatteras, North Carolina (Reed 1980b), its structural development is greatest in this region; thickets 1-2 m (3-6 ft) high are found on pinnacles with up to 25 m relief (Avent et al. 1977, Reed 1980). A major portion of the shelf edge is littered with *Oculina* debris (MacIntyre and Milliman 1970).

The *Oculina* community harbors a rich vertebrate and invertebrate fauna which includes other scleractinians (*Astrangia poculata* (Peters et al. 1988), *Balanophyllia floridana*, *Cladocora debilis*, *Paracyanthus pulchellus*, and *Coenocyathus* species) and octocorals (*Telesto nelleae*, and *Tltanideum frauenfeldii*) (Avent et al. 1977). Two hundred species of mollusks, 47 species of amphipod crustaceans, 21 species of echinoderms, and 50 species of decapod crustaceans have been found directly associated with *Oculina varicosa* (Reed et al. 1982).

Although shelf-edge *Oculina* communities seem not to persist south of Jupiter, Florida, the species is found on coquinoid rock ledges scattered over the shallow shelf south to St. Lucie Inlet and Stuart, Florida (27° 10'N latitude) where *Oculina* is associated with decidedly Carolinian octocorals such as *Lophogorgia* and *Leptogorgia* spp. In spite of the Antillean ecological character of other groups which persist north to Cape Canaveral (Avent et al. 1977, Briggs 1974), the scleractinian and octocorallian fauna became Antillean only south of St. Lucie Inlet (in a similar fashion to the Mollusca studied by Work 1969). The coquinoid ledges here possess the same species noted above, but mixed with tropical genera such as the *Diploria* (brain coral), *Isophyllia* (cactus coral), *Montastraea* (star coral), and the octocorals *Eunicea*, *Pseudopterogorgia*, and *Gorgonia* (Reed 1979, personal communication).

Southeast Florida Coast (Palm Beach to Fowey Rocks)

South of 27° North latitude to near Miami, the continental shelf narrows to 3 to 5 km (1.6 to 2.7 nm) and the warm waters of the Florida current become the most dominant hydrographic feature (Lee and McGuire 1972). Thus, in the vicinity of Palm Beach, Florida, a diverse reef community develops. The coral communities in the southeast Florida region are tropical in character, zoogeographically similar to that of the Florida Keys but less well developed than the majority of the Florida reef tract. Section 3.3.1.1 discusses three coral habitat categories: coral communities patch reefs, and outer bank reefs. Much of the underlying substrate is a Holocene elkhorn coral, *Acropora palmata*, and staghorn coral, *A. cervicornis*, relic reef which lies 15 to 30 m (50 to 100 ft.) below present sea level. The reef has not been actively accreting for the last 8,000 years (Lighty et al. 1977; Banks et al. 2007). The system of coral communities from Palm Beach County to Miami-Dade County can be characterized as a series of discontinuous reef lines that parallel the shoreline. As an example, in Broward County there are generally three lines of reef (terraces); inner reef crests in 3 to 5 m, middle reef crests in 7 to 9 m, and the outer reef in16 to 23 m water depths (Banks et al. 2007, Walker et al. 2007). Nearshore of the Inner Reef is a series of nearshore ridges (Moyer 2003, Banks et al. 2007, Walker et al. 2007).

The coral community found within this region is generally dominated by gorgonian corals (Order Alcyonacea). A number of earlier studies have provided limited descriptions of the reef community in this region. Goldberg (1973a and b) has characterized the deeper zones of this community (20 to 30 m; 66 to 100 ft) by the presence of the gorgonian *Iciligorgia schrammi*. Wheaton and Jaap (1976) and Courtenay et al. (1975) discussed reef zonation off Palm Beach and Miami Beach, respectively. Wheaton described the octocoral fauna on the offshore reef terrace from Palm Beach County to Looe Key (Wheaton 1987). Blair and Flynn (1989) observed coral community structure off Miami. Goldberg (1973) reported an average octocoral density off Palm Beach County of 25.1 colonies/m^2.

Coral, coral reefs, and coral community habitat status is mostly recorded as part of monitoring efforts (Gilliam et al. 2007a and b) originated as impact and mitigation studies from adverse environmental impacts to specific sites (dredge insults, ship groundings, pipeline and cable deployments, and beach renourishment). Beginning in 1997, in response to beach renourishment efforts in Broward County, annual collection of environmental data (sedimentation quantities and rates and limited temperature measurements), and coral (stony corals and gorgonians), sponge, and fish abundance/cover data was conducted at 18 sites. In 2000 five new sites were added and in 2003 two additional sites were added for a total 25 sites (Gilliam et al., 2007a). In 2003, the Florida Department of Environmental Protection (FDEP) was awarded funding for a coral reef monitoring along the southeast Florida coast. Florida DEP contracted this work en toto to the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWC-FWRI) who is working with Nova Southeastern University's National Coral Reef

Institute. Ten sites were installed: three in Miami-Dade County, four in Broward County, and three in Palm Beach County (Gilliam et al. 2007b). Three additional sites were installed in Martin County in 2006. The Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP) is an extension of the Florida Keys Coral Reef Evaluation and Monitoring Project (CREMP) which utilizes the same methods (Beaver et al. 2005).

Stony coral density is generally 2-3 colonies/m^2 and coverage generally 2-3%. Much of stony coral cover in this region is less than 1% but several nearshore areas have coverage greater than 10%. The south Florida region (especially offshore Broward County) has a number of unique staghorn coral, *Acropora cervicornis*, patches. These patches appear to be healthy with measured coverage greater than 30% (Gilliam et al. 2007a and b). Over 30 stony coral species have been identified in this region with common stony corals including *Montastrea cavernosa*, *Siderastrea siderea*, *Porites astreoides*, and *Stephanocoenia intersepta* (Gilliam et al. 2007a).

Octocorals are more abundant that stony corals in this region. Density can approach 20 colonies/m^2 (Gilliam et al. 2007a) with coverage of 20% (Gilliam et al. 2007b). Much less data exist on the species richness due to the difficulty of field identification, but common species include several *Eunicea* species, *Plexaura flexuosa*, *Pseudopterogorgia americana*, and *Muricea muricata*.

Monitoring data has shown that, although some differences were determined between years at some sites, in general stony coral cover on the reefs off Broward County (Gilliam et al. 2007a) has been stable. Regional data collected by the SECREMP project has also shown stability in stony coral and octocoral cover (Gilliam et al. 2007b). SECREMP and CREMP data indicate that southeast Florida reefs generally have reduced stony coral species richness and stony coral cover than the Dry Tortugas or Florida Keys coral reefs. Benthic cover by octocorals is, interestingly, very similar throughout the Florida reef system while southeast Florida reefs appear to have reduced macroalgae cover compared to reefs in the Dry Tortugas and the Florida Keys (Beaver et al. 2005, Gilliam et al. 2007b).

The southeast Florida coral communities lie within three km of the coast offshore a highly urbanized area comprising a population of over 5 million people (the population of Broward County alone exceeds 1.8 million). These reefs are important economic assets: a 2001 economic assessment estimated the annual reef input for Miami-Dade, Broward, and Palm Beach Counties at 5.8 billion dollars (Johns et al. 2003). Potential impacts to the system include those from commercial and recreational fishing and diving, sewer outfalls, marine construction activities (fiber optic cables, channel dredging, gas pipe lines), and major shipping ports and ship groundings. Southeast Florida has three major shipping ports; Port of West Palm Beach, Port Everglades (Broward County), and the Port of Miami. At Port Everglades alone, over 5,300 ships call on an annual basis. This heavy ship traffic very near and within a coral reef system has resulted in nearly one ship grounding per year offshore Broward County since the early 1990’s. The overuse and misuse of the coral community resources is currently a major issue affecting the status of these resources and as south Florida continues to grow impacts to the resources will increase.

Florida Keys (Fowey Rocks to the Dry Tortugas)

Coral reefs and coral communities are common within the south Florida coastal ecosystem. Well developed coral reefs similar to those found in the Bahamas and Caribbean occur from Fowey Rocks to Tortugas Banks: 25° 40' – 24° 30'N latitude, 80° 30' – 82° 40'W longitude (Jaap 1984, Jaap and Hallock 1990). High profile bank reefs parallel the island arc in a band four to six miles from shore. Outer bank reefs are characterized by spur and groove formations (Shinn 1963), elkhorn coral (*Acropora palmata*), and *Millepora complanata* (encrusting fire coral) at the reef crest. Patch reefs are found between the coast and the offshore bank reefs and typically are characterized by an irregular ring of large boulder corals (*Montastraea annularis*, *M. cavernosa* (star corals), *Colpophyllia natans*, *Diploria labyrinthiformis*, and *D. strigosa* (brain corals). Between the different habitat types in the Florida Keys, the patch reefs tend to have the highest mean percent coral cover (Beaver et al. 2005). The diversity of corals is quite variable, upwards of 60 stony coral species have been documented on an individual bank reef (Jaap et al. 1989). The diversity and abundance of octocorals tends to be greatest in patch reefs and offshore deep reefs. Functionally, coral reefs enhance the abundance and variety of life, provide a living breakwater that protects the coast from storm waves, provide economic benefit from fisheries and tourism, and are important education and research resources.

The Coral Reef Evaluation and Monitoring Project (CREMP), constitutes the first successful, long-term monitoring project that has documented status and trends of coral reefs throughout the 2,800 square nautical miles Florida Keys National Marine Sanctuary. Between 1996 and 2004, the project reported a 44% reduction in stony coral cover. A significant decline in percent cover of stony corals was documented between 1997 and 1999. From 1999 to 2004, the percent cover of stony corals has remained essentially unchanged. The significant declines in mean percent stony coral cover between 1997 and 1999 were largely due to losses in *M. annularis*, *A. palmata*, and *M. complanata*. The large decline in mean stony coral cover was evident in all three regions in the Florida Keys (Lower, Middle, and Upper Keys) (Beaver et al. 2005).

Many well developed patch and outer bank reefs, such as Carysfort Reef and Key Largo Dry Rocks, occur shoreward of the 18-m (60 ft) isobath and were historically dominated by *Acropora palmata* (elkhorn) and *Millepora complanata* (encrusting fire coral) at the crest, followed by *A. cervicornis* (staghorn), *Montastraea annularis* (small star coral), and *M. cavernosa* (large star coral), in successively deeper zones (Shinn, 1963). Prior to the 1990's, specific information on the distribution and abundance of corals on these reefs was available in individual works at localized sites (in spite of their position as the northernmost *Acropora* reefs in the western Atlantic). The Caribbean-wide decline of *Acropora* spp. dating from the mid 1980's has yielded *A. palmata* and *A. cervicornis* rare to absent in most Florida Keys sites. The outer bank reefs of Biscayne National Park to the north have been described by Voss et al. (l969) but quantitative data on distribution and abundance of corals on a single reef were not included. Wheaton (unpublished) surveyed reefs in Biscayne National Park from 1978 to 1981.

Looe Key Reef (12.9 km, 200° off the SW tip of Big Pine Key, 24° 37'N, 81° 24'W) is a representative outer bank reef. The reef was subdivided into reef flat, spur and groove, forereef, and deep reef habitats to characterize these habitats (Wheaton and Jaap, 1988). Inshore of the reef there is a fan-like mosaic of seagrass and sediments. The reef crest at Looe Key is dominated by *Millepora complanata* (encrusting fire coral), *Porites astreoides* (mustard hill coral), and *Palythoa caribaeorum* (golden sea mat). A spur and groove system extends seaward of the reef crest and is 5 to 9 m (16 to 30 ft) deep at the seaward spur terminus. *Acropora palmata* (elkhorn coral) skeletal material is the principal construction component of the spur formations (Shinn 1963). The numerically abundant corals in spur and grooves include: *Porites astreoides*, *Millepora complanata*, *Agaricia agaricites, Montastraea cavernosa*, and *Acropora cervicornis*. Colonies of very large, living *Montastraea annularis* (small star coral), *Diploria strigosa* (brain coral), and *Colpophyllia natans* (boulder brain coral) are also present.

Generally, patch reefs found in the lagoon between the outer reefs and the Florida Keys may include star corals *Montastraea* spp., fire corals *Millepora* spp., regular finger coral *Porites porites* (*P. furcata* or *P. divaricata*), mustard hill coral *P. astreoides*, starlet coral *Siderastrea* spp., brain coral *Diploria clivosa*, and staghorn *Acropora cervicornis*. *Acropora palmata* (elkhorn) is less common on patch reefs than fore-reef crests. Antonius et al. (1978) found that five species composed 50 percent of the stony corals found on the patch reefs at Looe Key; *Millepora complanata*, the star corals *Dichocoenia stokesi*, *Siderastrea siderea*, and *Montastraea annularis* accounted for eight to ten percent each, while staghorn coral *Acropora cervicornis* dominated with 15 percent of the total. However, *A. cervicornis* no longer dominates anywhere in the Florida Keys.

Quantitative information dealing with distribution and abundance of gorgonians is available for several back reef areas in the Florida Keys. Opresko (1973) has analyzed gorgonian data for Boca Chita Pass, Soldier Key, and Red Reef. Bagby (1978) studied three sites off Key Largo, Florida, chosen to provide a view of the influence of increasing oceanic conditions. Bagby (1978) found that *Pseudopterogorgia americana* and *P. acerosa* were the most widespread species. In agreement with the conclusions of Opresko (1973), *P. acerosa* was most common inshore, while *P. americana* was more dominant at offshore patch reefs. Equally widespread, but numerically less dominant, were the species *Plexaurella dichotoma* (double-forked *Plexaurella*) and *Plexaura flexuosa*. Two species, *Eunicea succinea* and *Pterogorgia citrina*, were distributed in abundance at both Soldier Key and Nine Kilometer Reef, but not in intermediate areas. *Pseudoplexaura porosa* was dominant on Five Kilometer Reef and *Plexaura homomalla* (black sea rod) was of considerable importance on Red Reef, but neither was prominent elsewhere in the areas studied. *Plexaura flexuosa* and *Pseudopterogorgia americana* dominated the shallow reefs at Long Key, Dry Tortugas (Wheaton, unpublished). Thus, any or all of these species can be found prominently on inshore or offshore reefs, in shallow water or on outer reefs at depths up to 20 m (66 ft). Their relative abundance on a given reef must therefore be interpreted with caution. Shallow patch reefs near the outer reef tract display a number of clear-water indicator species. *Gorgonia ventalina*, *Muriceopsis flavida*, *Briareum asbestinum*, and *Pseudopterogorgia bipinnata* all fall in this category, in decreasing order of consistency (Opresko, 1973; Bagby, 1978).

At four pairs of reefs in Biscayne National Park Wheaton (unpublished) surveyed octocoral abundance and density by transect, species count, and photographic analysts. Octocoral colonies usually comprised more than half of the total coral colonies. The five most abundant species (53.9 percent of total octocorals) were *Plexaura flexuosa*, *P. homomalla*, *Gorgonia ventalina*, *Eunicea succinea*, and *Pseudopterogorgia americana*. Mean numbers of octocoral colonies counted along a 20 m (66 ft) transect of the eight reefs were 102.81 and 155.17 (Wheaton unpublished).

4.1.6.2 Live/hardbottom species

Refer to section 3.3.1.2

4.1.6.3 Deepwater Corals

Description and distribution

Refer to section 3.3.1.3

Reproduction

(From SAFMC DWC Research and Monitoring Plan)
Lophelia pertusa has been studied more extensively than other species, using samples from Norway, the Gulf of Mexico and the Florida Straits. Seasonality of gametogenesis appears to vary with location. The gametogenic cycle of samples collected from the Norwegian Fjords began in April and terminated with spawning in March the following year (Brooke and Jarnegren in prep.). In the Gulf of Mexico, however, gametogenesis begins in November and spawning probably occurs in late September/October (S. Brooke unpubl.). Fecundity of both sets of samples is high but quantified data have not yet been compiled. Research into reproduction of octocorals from Alaska and New England is also underway (Simpson unpubl), and some work has been done on reproduction in Alaskan stylasterines, which are all brooders and produce short-lived planulae (Brooke and Stone in review). Larval biology has been described for *O. varicosa* (Brooke and Young 2005) but not for any of the other deepwater corals.

Development and growth

(from SAFMC DWC Research and Monitoring Plan)
The growth of *L. pertusa* has been measured using various methods (Duncan 1877; Dons 1944; Freiwald 1998; Gass and Roberts 2006), which have estimated growth rates between 4-26 mm per year, with the most likely estimates at approximately 5mm per year (Mortensen and Rapp 1998). These methods have measured linear extension rather than calcification rates, but the latter could potentially be calculated from growth rates and skeletal density. Growth rates of some gorgonians and antipatharians have also been measured using rings in the gorgonian skeleton and isotopic analysis (e.g., Sherwood et al. 2005, Andrews et al. 2002, Risk et al. 2002; Williams et al. 2006) and in some cases the colonies are extremely old (hundreds to thousands of years) and have very slow growth rates (e.g., Druffel et al. 1995; C. Holmes et al. unpubl. data).

Field observations on distribution of *L. pertusa* indicate that the upper thermal limit for survival is approximately 12°C, and laboratory studies on *L. pertusa* tolerance to temperature extremes corroborate these observations (S. Brooke unpubl. data). Preliminary experiments with heat shock proteins show expression of HSP-70 in response to exposure of temperature greater than 10°C (S. Brooke unpubl. data). Experiments on tolerance to sediment load indicate that samples of *L. pertusa* from the Gulf of Mexico show >50% survival in sediment loads of 103 mgL-1 for 14 days, and can survive complete burial for up to 2 days (Continental Shelf Associates in review). Given the proximity of some coral habitats to oil and gas extraction sites, tolerance to drilling fluids and fossil fuels should also be investigated.

Further laboratory and field experiments are needed to examine the individual and interactive effects of environmental conditions such as temperature, sedimentation, and toxins. A range of responses or endpoints should be examined including more modern techniques such as cellular diagnostics. These include examination of levels of stress proteins produced by cells in response to external conditions such as heat shock proteins, ubiquitin, etc. There are general classes of cellular products that are known to be indicative of specific stressors such as nutritional stress, xenobiotics, metals, temperature. These techniques are being increasingly used in shallow coral systems as a more sensitive organismal response to stress (i.e. more sensitive than mortality). These responses should be measured in combination with more standard parameters such as growth, respiration, and fecundity.

Coral growth rates provide information on the rates of habitat production in deepwater coral ecosystems while coral mortality and bioerosion counterbalance this production with destruction. Understanding the positive and negative sides of this balance, particularly under the changes in environmental conditions that are anticipated in the coming decade or two, is crucial to the management and conservation of deepwater coral habitat and habitat function (e.g. fishery production).

Ecological relationships

Refer to section 3.3.1.3

Abundance and status of stocks

Refer to section 3.3.1.3

4.1.7 Sargassum

Refer to section 3.3.2.

4.1.8 Dolphin and Wahoo

Description and Distribution

(from DW FMP)

Dolphin

The common dolphin, *Coryphaena hippurus*, is an oceanic pelagic fish found worldwide in tropical and subtropical waters. The range for dolphin in the western Atlantic is from George's Bank, Nova Scotia to Rio de Janeiro, Brazil. They are also found seasonally throughout the Caribbean Sea and the Gulf of Mexico, and they are generally restricted to waters warmer than 20°C (Oxenford, 1997). They support economically important fisheries from North Carolina through the Gulf of Mexico and within the Caribbean Sea, including the northeast coast of Brazil.

Pompano dolphin, *Coryphaena equiselis*, a more pelagic species, has been recorded off North Carolina, Florida, Bermuda, and in the central Atlantic, Gulf of Mexico, and Caribbean including off Puerto Rico. Pompano dolphin were found in waters which exceed 24°C (Mather and Day, 1954).The common dolphin and pompano dolphin will subsequently be referred to as dolphin because they are not often distinguished in data collection systems.

There is pronounced seasonal variation in abundance. Dolphin are caught off North and South Carolina from May through July. Dolphin caught off Florida's East Coast are caught mainly between April and June. February and March are the peak months off Puerto Rico's coast. Dolphin are caught in the Gulf of Mexico from April to September with peak catches in May through August (SAFMC, 1998a).

Wahoo

The wahoo, *Acanthocybium solandri*, is an oceanic pelagic fish found worldwide in tropical and subtropical waters. In the western Atlantic wahoo are found from New York through Colombia including Bermuda, the Bahamas, the Gulf of Mexico, and the Caribbean. Wahoo are present throughout the Caribbean area, especially along the north coast of western Cuba where it is abundant during the winter (from FAO species guide; FAO, 1978).

There is pronounced seasonal variation in abundance. They are caught off North and South Carolina primarily during the spring and summer (April-June and July-September), off Florida's east coast year-round, off Puerto Rico and the U.S. Virgin Islands year-round with peak catches between September and March, in the Gulf of Mexico year-round, in the eastern Caribbean between December and June, and in Bermuda between April and September (SAFMC, 1998a).

Reproduction

Dolphin

Common dolphin are batch spawners and have a protracted spawning season. Evidence for a continuous spawning season is attributed to the presence of several size classes of eggs found in the ovaries (Beardsley, 1967; Oxenford, 1985; Perez and Sadovy, 1991. Size at first maturity ranges from 350 mm fork length (FL) (Florida) to 530 mm FL (Gulf of Mexico) for sexes combined. Males first mature at a larger size than females. Size at full maturity ranges from 550 mm FL (Florida) to 600 mm FL (Puerto Rico) for females (Table 4). Ripe pompano dolphin have been collected in the Atlantic as small as 205 mm standard length (SL) (Gibbs and Collette, 1959).

Table 4.1-20. Summary of reproductive characteristics reported for dolphin (Coryphaena hippurus) from the western central Atlantic (Source: Oxenford, 1997; references found in Oxenford, 1997).

The sex ratios in the catch tend to be female-biased although they vary with size of fish captured. The batch-fecundity-length relationship is strongly exponential ranging from 85,000 (approximately 400-600 mm FL) to 1.5 million (approximately 1300-1400 mm FL) eggs per batch.

Wahoo

Estimates of size at first maturity from North Carolina are 86 cm FL for males and 101 cm FL for females (Hogarth, 1976). Preliminary estimates from Bermuda are similar (males = 102 cm FL; females = 95 cm FL) (Murray, 1998). Fecundity estimates from North Carolina range from 560,000 eggs (for a 6.13 kg or 13.52 lb wahoo) to 45 million eggs (for a 39.5 kg or 87.10 lb wahoo) (Hogarth, 1976).

Hogarth (1976) examined wahoo reproductive tissues and determined that the spawning season extends from June through August with peak spawning in June and July. In addition, wahoo caught off North Carolina in September and October were determined to be post-spawners.

Development, growth and movement patterns

Dolphin

Development

Eggs - The eggs of dolphinfish have been described as buoyant, colorless, spherical, and having 1.2~1.6 mm diameter (Mito, 1960). Melanophores and xanthophores appear on embryo, yolk and oil globule during later stages of development (Ditty et al., 1994). The yolk is described as a single pale yellow oil globule, approximately 0.3-0.4 mm diameter with coarse segmentation that fades after preservation (Mito, 1960). Local studies on the mean mature egg size in the wider Caribbean include estimates of 0.97 mm in Barbados (Oxenford, 1986), 1.3 mm diameter off the North Carolina coast (Hassler and Rainville, 1975), 1.4 mm diameter (eggs collected in the plankton, not the ovaries) in the Gulf of Mexico (Ditty et al., 1994). Larval length at hatching is reported to be 3.95 mm, and consumption of yolk and oil globule at 5.7 mm (Mito, 1960). Ditty et al. (1994) concluded that in water temperatures between 25º and 30º C, dolphin eggs would hatch in 26 to 38 hours. Ditty et al. (1994) believed that all spawning occurred in oceanic waters over or beyond the continental shelf. The average station depth for capture in their study was 1,198 m.

Larvae - Ditty et al. (1994) found larvae abundant throughout the year in the Gulf of Mexico, but small larvae were found primarily during warm months. Peak abundances were from April to November. They found larvae primarily in water temperatures greater than 24º C and salinities greater than 33 ppt. Few larvae were collected at salinities less than 25 ppt. They also found that the catch of dolphin larvae increased with the increasing concentration of Sargassum. In the Florida Current peak abundance of dolphinfish larvae was noted in early summer (Gibbs and Collette, 1959) and from November to May and in August (Beardsley, 1967). Several studies of larval collections made off of North Carolina determined that they are present July to September (Beardsley, 1967), March and May (Anderson et al., 1957a, b), October (Anderson and Heumann, 1956), and late summer (La Monte, 1952). In the South Atlantic Bight from May to February—young common dolphinfish were harder to obtain than adults or juveniles of pompano dolphinfish (Gibbs and Collette, 1959). No significant diel differences in catch of larvae for either species; overall more common dolphinfish caught than pompano dolphinfish (Fahay, 1975). Off of Maine larvae of common and pompano dolphinfish were significantly more abundant at night and catch of larval common dolphinfish increased with concentration of Sargassum (Eldridge et al., 1977). In the Gulf of Mexico dolphinfish were collected from the sargassum off of Texas in July (Pew, 1957). In this SEAMAP study, differences in numbers of common and pompano dolphinfish were not significantly different among seasons or between night and day, but overall numbers of common dolphinfish were significantly more abundant than numbers of pompano dolphinfish. Shcherbachev (1973) found larvae to feed on crustaceans, mainly copepods. He noted that larval dolphin start feeding on larval fish when they reach 20 mm standard length.

Juveniles - Juvenile dolphin inhabit the entire Atlantic. Juvenile dolphin are closely associated with floating objects and Sargassum (Gibbs and Collette, 1959; Beardsley, 1967; and Rose and Hassler, 1974). Manooch et al. (1984) found fish to make up the largest portion of juvenile dolphin's diet, but invertebrates also were an important part.

Adults - Beardsley (1967) found that female dolphin mature between 350 mm and 550 mm FL. Males begin to mature at a larger size around 400 to 450 mm (Beardsley, 1967). Both sexes reach sexual maturity in their first year of life (Beardsley, 1967). Beardsley (1967) found increased numbers of adults in late spring and summer when water temperatures were 26° to 28°C. Adults generally prefer oceanic salinities, although captive dolphins tolerated salinities ranging from 16 to 26 ppt and temperatures from 15° to 29.4° C (Hassler and Hogarth, 1977). The diet of adult dolphin mainly includes fish (Gibbs and Collette, 1959; Shcherbachev, 1973; Rose and Hassler, 1974; Manooch et al., 1984; Massuti et al., 1998), although squid and crustaceans are also taken. Rose and Hassler (1974) found that five fish families accounted for 74% of the prey weight. These were Exocoetidae (26%), Scombridae (22%), Carangidae (12%), Balistidae (9%), and Coryphaenidae (5%). *Sargassum* was also present in 28% of the stomachs examined and occurred most frequently in the stomachs of small female dolphin. *Sargassum* was found in stomach contents by Rose and Hassler (1974) and Manooch et al. (1984) but was likely ingested incidentally while dolphin were feeding on the fish residing in *Sargassum* mats. Larger males seem to prefer open ocean habitat while females and smaller males remain associated with *Sargassum* and floating debris. Rose and Hassler (1974) postulated that males were more active feeders than females of similar length. They further theorized that since males are substantially heavier than females of similar age, a greater amount of food is required to sustain their metabolism and this requirement for additional food causes more voracious feeding. The open ocean habitat provides larger prey for the larger male dolphin. Rose and Hassler (1974) used catch records from charter boats as the basis for this hypothesis.

Spawning - Adults reach sexual maturity within their first year of life and spawning take place year-round in waters warmer than 24°C in the Atlantic (Beardsley, 1967). Peak spawning seems to take place in the spring and early fall (Beardsley, 1967). Like most fish, fecundity in dolphins increases with increasing size (Beardsley, 1967). Beardsley (1967) estimated that female dolphins produce 240,000 to 3 million eggs annually. In Barbados the spawning season was reported to be extended (Oxenford, 1986). In Bermuda, there was peak spawning in September and October (Migalski, 1958). In the Florida Current spawning occurred from November to July with a peak in March (Beardsley, 1967). In this work, Beardsley also noted a sudden appearance of Stage V fish in July (3 months after peak spawning) that may be attributed to the migration of the spawning population north, and the arrival of a new population from the south that had already completed spawning. From size data of 78 juvenile dolphinfish of *Coryphaena equiselis*, it was inferred that the species most likely spawned in January and February in the tropical mid-Atlantic (Potthoff, 1971). A study off the coast of Maryland estimated peak spawning in July and August (Gibbs and Collette, 1959). In Puerto Rico, spawning was at a peak in February (Erdman, 1956). In June in the Gulf Stream specimens were caught that were ripe or very close to ripe, and peak spawning was determined to be in June and July (Rose, 1965) and May and June (Schuck, 1951). Work by Arocha et al. (1999) in Venezuela found spawning to be biannual in May and October-November. This estimate was based on incidence of mature gonads from 21 females with advanced vitellogenic oocytes collected during four observer-covered longline trips in 1995 (Arocha et al., 1999).

Age and growth

Dolphin grow rapidly and show average first year daily growth rates ranging 1.6 mm FL (North Carolina) to 4.2 mm FL (Gulf of Mexico). The relationship between fork length and weight is presented in Figure 4.1-20. There are a number of estimates of L∞ from the northern area and a value of 1,400 to 1,500 mm FL appears appropriate for this stock (SAFMC, 1998a). A summary of available length-weight relationships for dolphin from the western central Atlantic is presented in Oxenford, 1997.

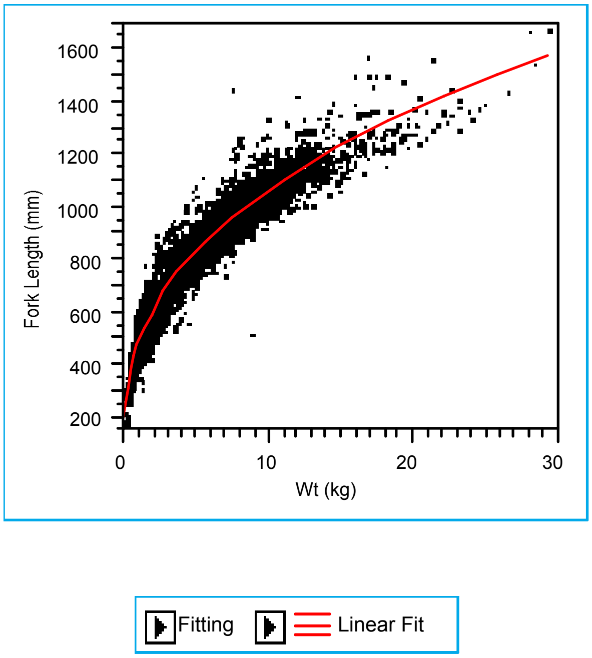


Figure 4.1-20. Dolphin, *Coryphaena hippurus*, length-weight relationship (Source: Goodyear, 1999).

Thompson (1999) examined the relationship between dolphin weight and length based on recreational data from MRFSS, the Texas Creel Survey, and the Headboat Survey (N=32,215). The length weight relationship was found to be similar for the Atlantic and Gulf of Mexico and pooling the data provided the resulting relationship: the natural log of the whole weight equals the natural log of the fork length in centimeters minus 10.42 ($\ln weight = 2.71 \ln FL - 10.42$).

Beardsley (1967) examined 511 dolphin from waters off south Florida ranging in size from 475 to 1,525 mm fork length (FL). Of the 1-year olds, the size range was 475 to 1,175 mm FL. Prager (2000) to provide values for use in empirical estimates of mortality rates for the first stock assessment for dolphin, took a von Bertalanffy growth function and fit it to the grouped length-at-age data of Beardsley (1967). Prager (2000) indicates the following growth function resulting from the analyses describes sizes at age reasonably well:

$Lt = L\infty(1 - \exp(-K(t - t0)))$ $\quad$ $Lt = 1710 (1 - \exp(-0.583[t - 0.7]))$

Table 4.1-21. Summary of length-weight relationships for dolphin (*Coryphaena hippurus*) from the western central Atlantic (Source: Oxenford, 1997; references found in Oxenford, 1997).

Location	Sex	Range in length (mmFL)	Sample size (no.fish)	a	b	kg at 1000 mmFL	Data source
North Carolina	All	672-966	18	2.00x10^{-9}	3.22	9.21	Schuck (1951)*[1]
North Carolina	Males	275-1350	176	0.50x10^{-7}	2.75	8.89	Rose & Hassler (1968)
	Females	310-1275	325	1.27x10^{-7}	2.59	7.76	
Florida	Males	550-1300	19	1.45x10^{-7}	2.58	7.97	Beardsley (1967)*[2]
	Females	500-1225	40	5.75x10^{-8}	2.71	7.60	
Puerto Rico	All	381-1479	852	3.80x10^{-8}	3.49	891?	Perez *et al.*(1992)*[3]
	Males	490-1479	261	1.78x10^{-8}	3.62	1289?	
	Females	445-1310	591	5.75x10^{-8}	3.36	691?	
	All	358-1323	332	1.41x10^{-8}	2.92	8.11	Perez & Sadovy (1991)
	All	381-1479	170	3.80x10^{-8}	2.78	8.31	Rivera Betancourt (1994)
Cuba	All	500-1200	56	3.21x10^{-5}	2.67	7.02	Garcia-Arteaga *et al.* (1997)*[4]
Barbados	All	160-1365	365	1.45x10^{-8}	2.91	7.85	Oxenford (1985)
	Males	239-1365	123	1.24x10^{-8}	2.94	8.31	
	Females	160-1240	207	2.22x10^{-8}	2.84	7.58	

*1 Relationship given in original text appears to be in error. Relationship given here was recalculated with data extrapolated from length-weight graph.
*2 Relationships given in original text were wrong (confirmed by pers. comm. with author on 11.5.84.). Relationships given here are recalculated from extrapolation of data shown in the length-weight graph.
*3 Relationships given in original text appear to be in error. Authors have been contacted on 9.10.97.
*4 Relationship is for length in cm.

Mortality rates and longevity

Prager (2000) estimated natural mortality (M) for dolphin to be between 0.68 and 0.80. Prior to the exploratory stock assessment one study reported total instantaneous mortality estimates derived from a Robsen-Chapman estimator of approximately 8.2 for dolphin from the Gulf of Mexico (Bentivolglio, 1988). Prager (2000) indicated that the estimate did not seem feasible for the Atlantic where Beardsley (1967) found one 4 year old dolphin in a sample of 511. If one assumes random sampling, then the probability of finding a fish that old in such a small sample was close to zero. Therefore, it is almost certain that the estimate is imprecise or inaccurate, that the vital rates in the Gulf differ greatly from the Atlantic or the vital rates have changed dramatically over time (Prager, 2000).

Absent direct estimates of mortality, two empirical methods of Hoenig (1983) and Pauly (1979) were applied to approximate mortality rates of dolphin in the Atlantic. Tables 4.1-22a and 4.1-22b present the estimates of total and natural mortality based on these methodologies. For the range of maximum ages reported in the three studies of 3 to 4 years, the Hoenig method provides estimates of total mortality rate Z from 1.42/yr declining to 1.06/yr (Table 4.1-22b). Estimates of M by Pauly's method are specific to growth parameters and water temperatures. Over the range of mean water temperatures from 20°C to 28°C, M is estimated to be between 0.68/year and 0.80/year (Table 4.1-22c).

Table 4.1-22a. Estimates of instantaneous rate of total mortality and corresponding annual survival fraction; method Hoenig (1983) (Source: Prager, 2000).

Maximum age (years)	Total Mortality rate (Z)	Survival Fraction (S)
2.50	1.71	0.18
2.75	1.55	0.21
3.00	1.42	0.24
3.25	1.31	0.27
3.50	1.21	0.30
3.75	1.13	0.32
4.00	1.06	0.35
4.25	1.00	0.37
4.50	0.94	0.39
4.75	0.89	0.43
5.00	0.85	0.43

Table 4.1-22b. Estimates of instantaneous rate of annual natural mortality M as a function of growth parameters and mean water temperature; method of Pauly (1979) (Source: Prager, 2000).

Mean water temp (C°)	Natural Mortality (M) from Oxenford and Hunte (1983)	M from Beardsley (1967)	M from Rose and Hassler (1968)
20	2.254	0.681	0.262
22	2.355	0.712	0.273
24	2.452	0.741	0.285
26	2.545	0.769	0.295
28	2.634	0.796	0.306
30	2.719	0.822	0.316

Table 4.1-22c. Estimates of instantaneors rate of annual natural mortality from the Western Central Atlantic (Oxenford, 1999).

Location	Mortality Parameter	Mortality Model	Fish Group	Instantaneous Mortality (annual)	Percentage actual mortality (annual)	Reference
Gulf of Mexico	Total (Z)	Robson and Chapman (1961)	All	8.18	99.97	Bentivoglio (1988)
				8.23	99.97	
				8.67	99.98	
Barbados	Total (Z)	Ricker (1975)	All	3.93	98.03	Oxenford (1985)
		Beverton and Holt (1956)		5.84	99.71	
		Hoenig (1983)		4.22	98.53	
	Natural (M)	Pauly (1980)	All	2.56	92.23	Oxenford (1985)
			Males	3.3	96.29	
			Females	2.52	91.94	

St. Lucia	Total (Z)	Ziegler (1979)	All	3.53	97.07	Murray (1985)
	Natural (M)	Pauly (1983)	All	0.66	48.28	Murray (1985)

Movement Patterns and Stock Structure

Though there is a healthy ongoing debate about stock structure for dolphinfish in the Western Central Atlantic, the best available scientific information indicates that the U.S. portion of this range consists of a single stock. Oxenford (1997) conducted a preliminary investigation of the common dolphin stock structure within the western central Atlantic and suggested that there are at least two separate unit stocks located in the northeast and southeast regions of the western central Atlantic. This hypothesis was based on: observed seasonality, months of peak abundance, and mean size of dolphin from commercial and sport fisheries, which suggested two different migratory circuits; a comparison of life history characteristics of dolphin from North Carolina, Florida, and Barbados, which showed marked differences in average first year growth rates, fecundity-length relationships, size and age at first maturity, and mean mature egg size; and on observed differences in allelic frequencies at the IDH-2 locus determined through electrophoresis.

One conclusion from the Dolphin Wahoo workshop was that the working hypothesis should be a two stock model for the Western Central Atlantic and that the northern stock should include dolphin from the Gulf of Mexico, the U.S. South Atlantic including Puerto Rico, the U.S. Virgin Islands, the Mid-Atlantic, and the New England coasts (SAFMC, 1998a).

A genetic study by Robyn S. Wingrove (2000) at the University of Charleston was conducted to test the hypothesis of Oxenford (1997) and investigate the possible presence of additional stocks in the Gulf of Mexico and western central Atlantic using Restriction Fragment Length Polymorphism (RFLP) analysis of the ND-1 region of the Mitochondrial DNA (mtDNA). Dolphin DNA samples collected in the western central Atlantic originated from the Carolinas, Georgia, Florida, the Gulf of Mexico, Puerto Rico, Bermuda, the Azores, Martinique, Barbados, Tobago, and Brazil. The ND-1 region of each specimen was amplified by Polymerase Chain Reaction (PCR) and digested with five different restriction endonucleases. The results from the analysis of the frequency distribution of composite mtDNA haplotypes and Analysis of Molecular Variance (AMOVA) found no significant differences between samples collected in the western central Atlantic. These analyses support the hypothesis of a single unit stock and a management unit including common dolphin from the Gulf of Mexico, the U.S. South Atlantic including Puerto Rico, the U.S. Virgin Islands, the Mid-Atlantic, and the New England coasts would be appropriate. However, given the extremely limited amount of intermixing necessary to maintain genetic homogeneity between separate stocks, these results should not be taken as proof of a lack of stock structure.

Wahoo

Development

Eggs - No data currently exist on the distribution of wahoo eggs in the Atlantic. Adult wahoo spawn near Cuba in the Straits of Florida and Straits of Yucatan (Wollam, 1969). Wollam

(1969) also found larvae in these same areas. It is therefore postulated that wahoo eggs are similarly distributed.

Larvae - Wollam (1969) captured twelve larvae ranging from 4.5 to 10.0 mm standard length in the Straits of Yucatan and Florida. All of these larvae were taken in water depths greater than 400 m, except one larvae which was captured in 32 m of water. All larvae were captured between May and October, and none of the larvae were captured in surface waters. The larvae were caught in obliquely towed nets and Wollam (1969) stated that the larvae have a preference for waters below 100 m.

Juveniles - No data exist on the habitat of juvenile wahoo. It is assumed that juveniles inhabit waters with temperatures of 22° to 30° C and are associated with Sargassum. Juvenile wahoo are reported to travel in small schools (Hogarth, 1976).

Adults - Adult wahoo in the Atlantic are pelagic in nature and generally associated with Sargassum (Manooch and Hogarth, 1983). Rathjen and Squire (1960) recorded wahoo in similar temperature ranges of 22° to 28° C and from May to October off the coast of North Carolina. Adults feed mainly (over 95%) on fish (Hogarth, 1976; Manooch and Hogarth, 1983). Squids and crustaceans make up the remaining portion of their diet. Representative prey species found by Manooch and Hogarth (1983) were round herring (*Etrumeus teres*), Atlantic flyingfish (*Cypselurus melanurus*), frigate mackerel (*Auxis thazard*), butterfish (*Peprilus triacanthus*), porcupinefish (*Diodon hystrix*), juvenile carangids, and balistids. Round herring, Atlantic flyingfish, and frigate mackerel belong to the fast swimming pelagic community. The others belong to families that are associated with *Sargassum*. Manooch and Hogarth (1983) found that wahoo do not usually eat small food items, nor do they feed readily at the surface. They also found no apparent relationship between size of the wahoo and the size of the prey. They theorized that the wahoo is able to use its sharp teeth to render large fish into consumable sizes.

Spawning - Both females and males mature within the first year of life (Hogarth, 1976). Males spawn when reaching a size of 860 mm total length and females when they reach 1,000 mm total length (Hogarth, 1976). Wollam (1969) stated that wahoo have a long spawning season that lasts from May to October with a peak in June and occurs near Cuba in the Straits of Florida and Straits of Yucatan. Fecundity is size dependent in wahoo and was found by Hogarth (1976) to be 8.7 million eggs in a 1,365 mm total length female. He further estimated that a 1,550 mm female would produce 12.8 million eggs, a 1,645 mm female would produce 33.2 million eggs, and a 1,753 mm female would produce 45.3 million eggs.

Age and growth

Wahoo appear to be very fast growing in their first year attaining a size of over 39 inches (Hogarth, 1976). The relationship between fork length and weight is presented in Figure 4.1-21. Estimates of L_∞ range from 2,210 mm FL (North Carolina) (Hogarth, 1976) to 1,560 mm FL (St. Lucia) (Murray, 1998). Estimates of k (annual) range from 0.152 (North Carolina) to 0.37 (St. Lucia).

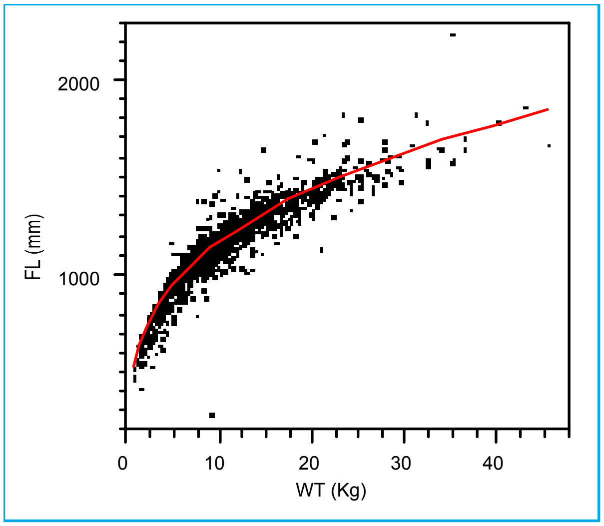


Figure 4.1-21. Wahoo, *Acanthocybium solandri*, length-weight relationship (Source: Goodyear, 1999).

Mortality Rates and Longevity

The only mortality estimates available are from a study conducted in St. Lucia (Murray, 1998). The values are listed below (Table 4.1-23) for five different years.

Table 4.1-23. Estimates of total and annual mortality for wahoo (Source: Murray, 1998).

Mortality Model Used	Total Mortality (Z)	Annual Mortality (A)
Length based catch curve	1.17	68.96%
	1.52	78.13%
	1.45	76.54%
	1.75	82.62%
	2.34	90.37%

Longevity is believed to be at least 5 years based on work from North Carolina (Hogarth, 1976).

Movement Patterns and Stock Structure

There have been no investigations of wahoo stock structure. Given this, a working hypothesis could be a single stock model for the western central Atlantic, including the Gulf of Mexico, the U.S. South Atlantic including Puerto Rico, the U.S. Virgin Islands, the Mid-Atlantic, and the New England coasts.

Ecological relationships

Dolphin

Dolphin are voracious, surface water, daytime predators. They eat a wide variety of fish species including: small oceanic pelagic species (e.g., flying fish, halfbeaks, man-o-war fish, Sargassum fish, and rough triggerfish); juveniles of large oceanic pelagic species (e.g., tunas, billfish, jacks, and dolphin); and pelagic larvae of neritic, benthic species (e.g., flying gurnards, triggerfish, pufferfish, and grunts). They also eat invertebrates (e.g., cephalopods, mysids, and scyphozoans) suggesting that they are essentially non-selective, opportunistic foragers. Rose (1966) examined the stomach contents of 373 dolphin off North Carolina and found the following food items by relative weight: Exocoetidae - 24%, Scombridae - 22%, Carangidae - 12%, Invertebrates - 12%, Miscellaneous Fish Families - 11%, Monacanthidae - 7%, Coryphaenidae - 5%, Unidentified Fish - 4%, and Balistidae - 3%. An analysis of prey ranked as to importance in dolphin diets is presented in Table 4.1-24

Predators (from Oxenford, 1997; references included in Oxenford, 1997):
The diets of other oceanic pelagic species indicate that dolphin, particularly juveniles, serve as prey for many oceanic fish. Their predators include large tuna (Parin, 1968; *Thunnus alalunga*: Murphy, 1914; *T. albacares*: Penrith, 1963, Dragovich and Potthoff, 1972, Takahashi and Mori, 1973, Matthews et al., 1977), sharks (Parin, 1968; *Hexanchus griseus*: Bigelow and Schroeder, 1948), marlin (Sund and Girigorie, 1966, Parin, 1968: *Makaira nigircans*: Farrington, 1949, Takahashi and Mori, 1942; *Tetrapturus albidus*: Wallace and Wallace, 1942, Nakamura, 1971, Nakamura and Rivas, 1972; *T. audax*: Abitia-Cardenas et al., 1997), sailfish (I*stiophorus platypturus*: Beardsley et al., 1972, Takahashi and Mori, 1973) and swordfish (*Xiphias gladius*: Gorbunova, 1969).

Table 4.1-24. Dietary importance (by rank) of the five main prey categories of dolphin (*Coryphaena hippurus*) from the western central Atlantic assessed by numerical abundance (Source: Oxenford, 1997; references found in Oxenford, 1997).

Location		**Southeastern & Gulf states of USA**	**North Carolina**		**Barbados**	
Data source		**Manooch et al. (1984)**	**Gibbs & Collette (1959)**	**Rose & Hassler (1974)**	**Lewis & Axelsen (1967)**	**Oxenford & Hunte**
No. dolphin		2219	46	396	70	397
Fish	Ammodytidae	.	3	.	.	.
	Balistidae	1	5	3	4	4
	Carangidae	5	.	2	.	.
	Coryphaenidae	.	.	4	.	.
	Dactylopteridae	.	.	.	1	1
	Exocoetidae	.	.	.	3	3
	Gempylidae	.	1	.	.	.
	Monacanthidae	.	.	.	2	.
	Nomeidae	.	.	.	5	.
	Ostraciidae	.	.	5	.	.
	Scombridae	.	2	.	.	.
	Syngnathidae	3	.	.	.	.
	Tetraodontidae	.	4	.	.	.
Invertebrates	Cephalopoda	.	.	.	.	5
	Decapoda	4	.	1	.	.
	Mysidacea	.	.	.	.	2
	Stomatopoda	2	.	.	.	.

Wahoo

Wahoo are essentially piscivorous. Based on work in North Carolina (Hogarth, 1976), fish accounted for 97.4% of all food organisms. These fish included mackerels, butterfishes, porcupine fishes, round herrings, scads, jacks, pompanos, and flying fishes. Invertebrates, squid, and the paper nautilus comprised 2.6% of the total food.

Abundance and status of stocks

Dolphin

Time-series data seems to indicate neither decline in stock abundance nor a decrease in mean size of individual fish (SAFMC, 1998a). Some stock analysis was provided by the Mackerel Stock Assessment Panel (MSAP, 1992). Prager (2000) conducted the first comprehensive exploratory stock assessment for dolphin based on landings from the U.S. Atlantic and Gulf of Mexico. This assessment was conducted exclusively from U.S. pelagic longline data for 1986-1997. In the assessment, he estimated that dolphinfish was not overfished in 1998 because biomass was 150 percent of BMSY. Similarly, Prager determined that fishing mortality in 1997 was 50 percent less than FMSY and therefore dolphinfish were not overfished. The estimated MSY for this stock is 12,200 tonnes with an 80 percent confidence interval of 8,500~21,100. No decline in abundance was suggested by the CPUE indices. In fact, the biomass seems to increase significantly from the late 1980s to the early 1990s. The estimates generated by Prager (2000) suggest the species may be able to withstand a relatively high rate of exploitation. The abundance index developed for the assessment indicates an increasing trend in stock size, and the surplus production model based on the index, estimates the recent stock status to be above the biomass at MSY. However, Prager (2000) indicates that the positive indications are balanced by the uncertainty and numerous reasons for caution including: under excessive mortality rates, even a species resistant to exploitation may undergo geographically or temporally localized depletion or be exploited at suboptimal yield per recruit; the current stock structure is only based on limited evidence; and the estimates of vital rates are several decades old. This assessment did not evaluate the impact of the recreational fishery on the dolphinfish population, and according to this research, the mean size of dolphinfish caught has not declined historically although anecdotal evidence from local Miami anglers is to the contrary. The assumption of this assessment is also that the US longline catch is representative of all of the removals of the northern stock of western Atlantic dolphinfish. This is obviously not the case as removals by U.S. and Caribbean recreational anglers, Caribbean commercial fisheries and fisheries of countries such as Venezuela represent a large portion of the removals.

A preliminary stock assessment (Mahon and Oxenford, 1999) conducted for dolphin from Barbados has key implications for taking a precautionary approach in the management of dolphin and wahoo resources (SAFMC, 1998a):

A. There is a high risk of stock depletion with little warning given that the fishery may remain feasible at low stock levels because of the tendency of the fish to aggregate and the current trends for increasing fishing effort.
B. There is a potential for recruitment overfishing given that fish are economically valuable before size at first maturity and the high interannual variability in abundance apparently driven by environmental factors.
C. That a yield-per-recruit (YPR) approach to selecting a management target is probably inappropriate since even the more conservative F0.1 values are likely to lead to a significant reduction in spawning stock biomass.
D. A precautionary approach to management which in the first instance attempts to maintain the status quo of the fishery is recommended. This will require that current catch levels not be exceeded and that recent conflict between sectors of the fishery (commercial longliners and

recreational anglers) be resolved. Status quo might reflect trends (average catch and effort levels) in the fishery over the last five years (through 1997).

Parker et al. (2000) assessed the dolphinfish stock in the eastern Caribbean using two types of length-based models (length-based catch curve and length-based virtual population analysis (VPA)). The results of this analysis suggested that fishing mortality is much greater than the fishing effort at MSY and as a result, catches from the stock are below MSY. These results were deemed to be highly uncertain and dependent on growth parameters that were not well estimated (Die, 2004). The results of this research may also be skewed due to the fact that a separate northern and a southern stock is not well supported, and again, the assumption is that the analysis was on a representative portion of the removals for the stock. Therefore, the high mortality may be attributed to a migration from the eastern Caribbean to other regions.

Most recently, Parker and colleagues (2006) compiled catch statistics and a selection of abundance indices from around the Western Central Atlantic and analyzed these data using a non-equlibrium surplus production model called A Stock-Production model Incorporating Covariance (ASPIC) (Prager 1994). Ultimately, they concluded that existing data were insufficient to determine stock status. As is often the case with surplus production models, the dolphinfish model did not converge because of the lack of a clear best-fitting solution. The problem was that a simple explanation of stock dynamics would have been required to explain highly variable and generally increasing catch data with no clear signal of depletion in the abundance indices. Simple surplus production models are highly structured and so unable to provide complex explanations for such data. Yet, adequate data were lacking to support a more complex model. Any interpretation of these data must also take into account their generally poor quality.

Wahoo

To date there has been no attempt at a comprehensive stock assessment for wahoo. Therefore, the status of the stocks is unknown at this time. Proxy MSY estimates were provided by the NMFS SEFSC and were used to specify the status determination criteria in the Dolphin Wahoo FMP.

4.1.9 Calico Scallops

Description and Distribution

Calico scallops, *Argopecten gibbus* (Linnaeus 1758), are part of the bivalve mollusc family Pectinidae that contains all commercial species of scallops (Waller 1991). They are unified by series of minute denticles formed in the notch of the right valve, most visible in early juvenile stages. Waller (2006) indicates there are four major groupings or subfamilies, three of which are monophyletic (Camptonectinae, Palliolinae and Pectininae) and one of which is paraphyletic (Chlamydinae). At least six species in the subfamily Pectininae are commercially exploited: *Aequipecten operularis* (queen scallop), *Argopecten irradians* (bay scallops) and *A. gibbus* in the North Atlantic, *Aequipecten tehuelchus* (Tehuleche scallop) in the South Atlantic, and *Argopecten purpuratus* (Chilean scallop) and *A. ventricosus* (Catarina scallop) in the eastern Pacific.

Identification of calico scallops can be made from shell color and morphology. The upper (left) valve has red or maroon calico markings over a white or yellow base; the lower (right valve) is more lightly pigmented. The calico markings on the shell distinguish this scallop from the solid gray or brown upper valve of the bay scallop, which resembles the calico scallop in size. Calico scallop shell morphology varies with locality (Krause et al. 1994), but generally the species reaches 40 to 60 mm (1.6-2.4 in) in shell height (a straight line measurement of the greatest distance between the umbo and the ventral margin), with a maximum size reported to be about 80 mm (3.2 in) in shell diameter (a straight line measurement of the greatest distance between the anterior and posterior margin) (Roe et al. 1971). The shells are almost equally convex, deeply ridged, with 17 to 23 ribs on the right valve (Waller 1969).

The calico scallop occurs most often at moderate depths of 18-73 m (59-240 ft) and restricted generally to the continental shelf of the western North Atlantic and Gulf of Mexico between about 35° N and 20° N latitude (Broom 1976). The range includes the northern side of the Greater Antilles, throughout the Gulf of Mexico, to Bermuda and slightly north of Cape Hatteras (possibly Delaware Bay) in waters varying from 2 m (6.6 ft) at Bermuda to 370 m (1,214 ft) on the northern side of the Greater Antilles (Allen and Costello 1972). Off the Florida east coast, depth of occurrence was 9 to 74 m (30-243 ft) while off North Carolina, south of Cape Hatteras, calico scallops were reported at depths of 13 to 94 m (43-308 ft) (Allen and Costello 1972). Adults are generally restricted to open marine waters but juveniles do recruit to estuarine areas (Waller 1969). The closely related species *Argopecten irradians* and *A. nucleus* have overlapping ranges but are more common in estuarine waters, especially seagrass beds.

Calico scallop beds are generally distributed on the continental shelf parallel to the coastline. These beds are most abundant off Cape Lookout, North Carolina; Cape Canaveral, Florida; and Cape San Blas, Florida, in the northeastern Gulf of Mexico (Allen and Costello 1972). Scallop abundance fluctuates at each area, with good years followed by years when none are available. On the Cape Canaveral grounds, scallops occur in long narrow bands, or beds, more than 800 m (2,625 ft) long and several hundred meters wide. A calico scallop bed near Cape Lookout, North Carolina, was elliptical and 15 km (9.3 mi) long. Off Cape San Blas, in 1957, a bed 16 km (9.9 mi) long by 8-16 km (5.0-9.9 mi) wide was located (Bullis and Ingle 1959). The greatest concentrations of these scallops appeared to be near coastal prominences (Allen and Costello 1972). A population of calico scallops was located in 1977 offshore of the South Carolina/Georgia border in 37-45 m (121-148 ft) (Anderson and Lacey 1979). The scallop bed was also elliptically shaped and oriented perpendicular to the coast. Concentrations have also been reported from the eastern Gulf of Mexico between Sanibel Island and Dry Tortugas.

The Cape Canaveral scallop grounds are among the largest in the world, extending over 321.8 km (200 mi) from St. Augustine to near Stuart, Florida. Depths of the heaviest concentrations of calico scallops off Cape Canaveral from 1960-1967 ranged from 26-49 m (85-161 ft), as recorded by exploratory fishing cruises (Miller and Richards 1980). Roe et al. (1971) reported depth distributional differences off Florida, noting scallops south of Cape Canaveral were generally found in shallower water than north of the Cape. However, Sutherland (unpublished report) reported that scallop beds located north of Cape Canaveral were not always found in deeper water than beds south of the Cape. Estimates of the calico stock distribution and abundance from data obtained with RUFAS (Remote Underwater Fishery Assessment System) were used to visually capture the scallop resource (c.f. May et al., 1971). Tumbler dredges were used to obtain ground-truth samples to enable comparison with historic survey and fishery data (Figure 4.1-22). They found the bed width was highly variable and ranged from 6.7 to 2,633.5 m (22 to 8,640 feet). Juvenile calico scallop beds in 1970 surveys accounted for almost 4 percent of scallop distribution. Scallop occurrence was uniformly less than 4 percent of completed transect miles.

Calico scallops occur off North Carolina at water depths of 13-94 m (Schwartz and Porter 1977). In April of 1949, a survey cruise by the Institute of Fisheries Research located calico scallops off New River Inlet (Chestnut 1951). Other beds located by the U.S. Bureau of Commercial Fisheries (now National Marine Fisheries Service) have existed intermittently since 1959. Cummins et al. (1962) reported that the principal calico scallop grounds located near Cape Lookout were described as elliptical in shape and were approximately 16 km long. Other lesser beds were located in 19-37 m depths northeast and southeast of the Cape. Schwartz and Porter (1977) reported that the fishery concentrated in an area located southeast of Cape Lookout in 1971. A bed located 16 to 24 km south of Beaufort, NC in depths of 20-25 m and inside the 28 m contour produced approximately 1 million pounds of meats in 1972 (Schwartz and Porter 1977). The R/V *Dan Moore*, a North Carolina Division of Marine Fisheries (NCDMF) exploratory research vessel, surveyed beds southwest of New River and northeast of Cape Lookout but failed to locate commercial quantities of calico scallops. Exploration by the R/V *Dan Moore* in February and April 1975 in an area 20 nautical miles south of Bogue Inlet produced no scallops. This area only had shell material, sponge, coral and starfish (Powell et al. 1975a; Powell et al. 1975b). In 1978, the R/V *Dan Moore* surveyed a calico scallop bed off the coast of South Carolina. This trip was arranged after South Carolina biologists captured small sub-adult scallops incidental to rock shrimp during May of 1977. Trawlers taking rock shrimp were also catching large quantities of small scallops. In January of 1978, scallops were landed in Mount Pleasant, SC. This bed was located 77 km (48 mi) south of Charleston Sea Buoy and was determined to be 11.3 km (7 mi) in width and 8 km (5 mi) in length running perpendicular to the shore (Holland et al. 1978).

Government sponsored surveys in the South Atlantic Bight have been describing calico scallop distribution, along with other important benthic resources like the many species of shrimps, since at least the late 1950s (Bullis and Ingle 1959; Bullis and Cummins 1961). This program used a variety of trawls and dredges because of the large variety of targeted species, and often calico scallops were collected as by-catch of another targeted species. The program continued through at least the mid 1960s (Figure 4.1-22). Additional cruises in the 1970s utilized both dredge and video survey methods (May et al. 1971). During the peak of the fishery in the 1980s, there was some survey activity in Florida (Blake and Moyer 1989; Figure 4.1-23). Much more information was probably gathered by fishermen themselves (Figures 4.1-24 and 4.1-25). Recent Florida surveys are being conducted under NOAA's MARFIN program (Figure 4.1-26). Figures 4.1-24 and 4.1-25 were provided by representatives of the calico scallop industry during scoping meetings and public hearings on calico scallop management and present recent calico scallop harvest areas/distribution, spawning locations, and shell distribution off southeast Florida.

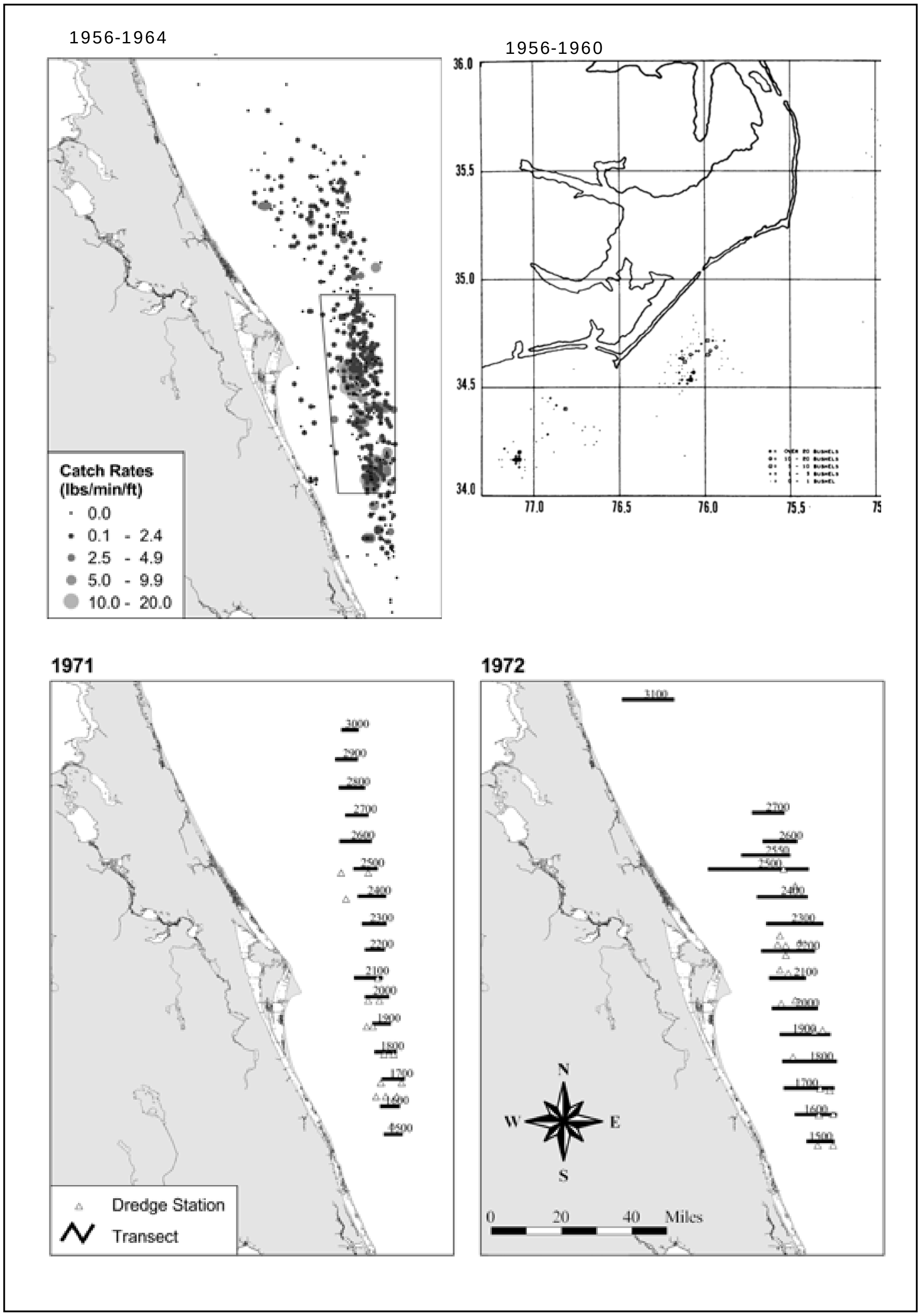


Figure 4.1-22. Historic NOAA calico scallop surveys. Top left, data compiled from the R/V *Silver Bay*. Top right, North Carolina surveys. Bottom, two "RUFAS" cruises.

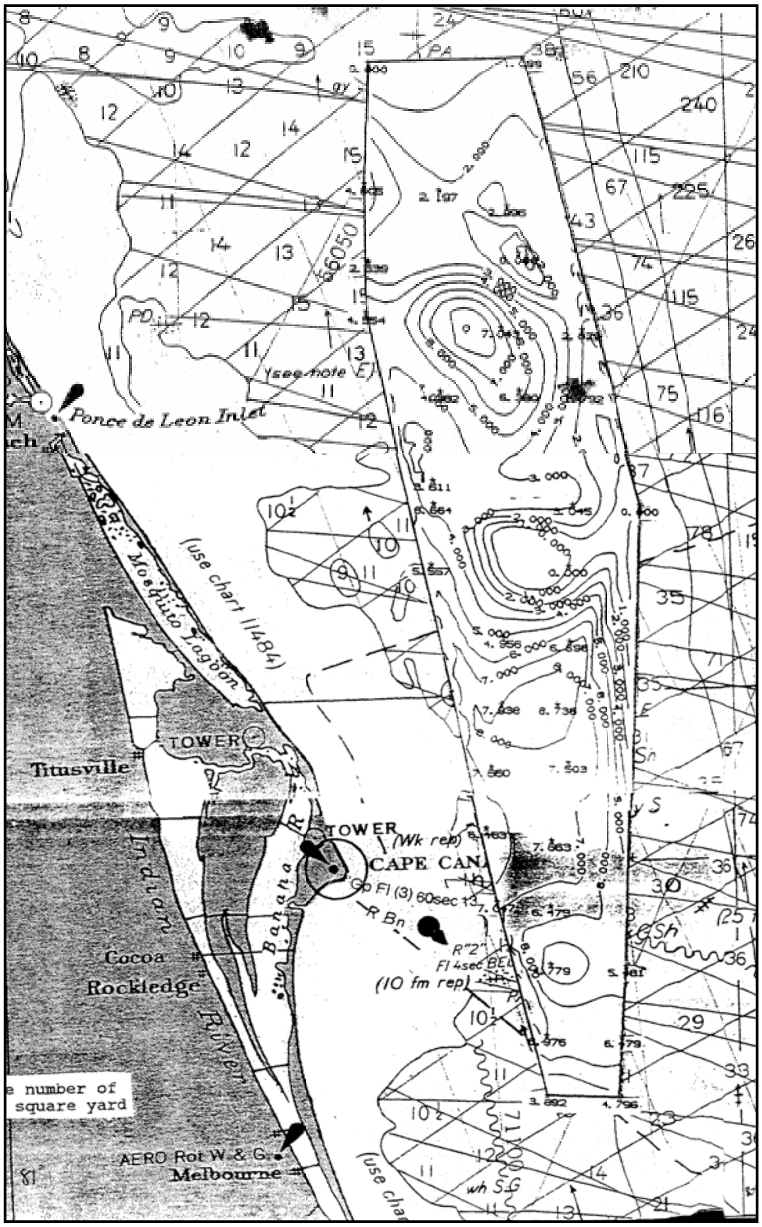


Figure 4.1-23. 1980s survey by Blake and Moyer, contours of estimated scallops per square yard.

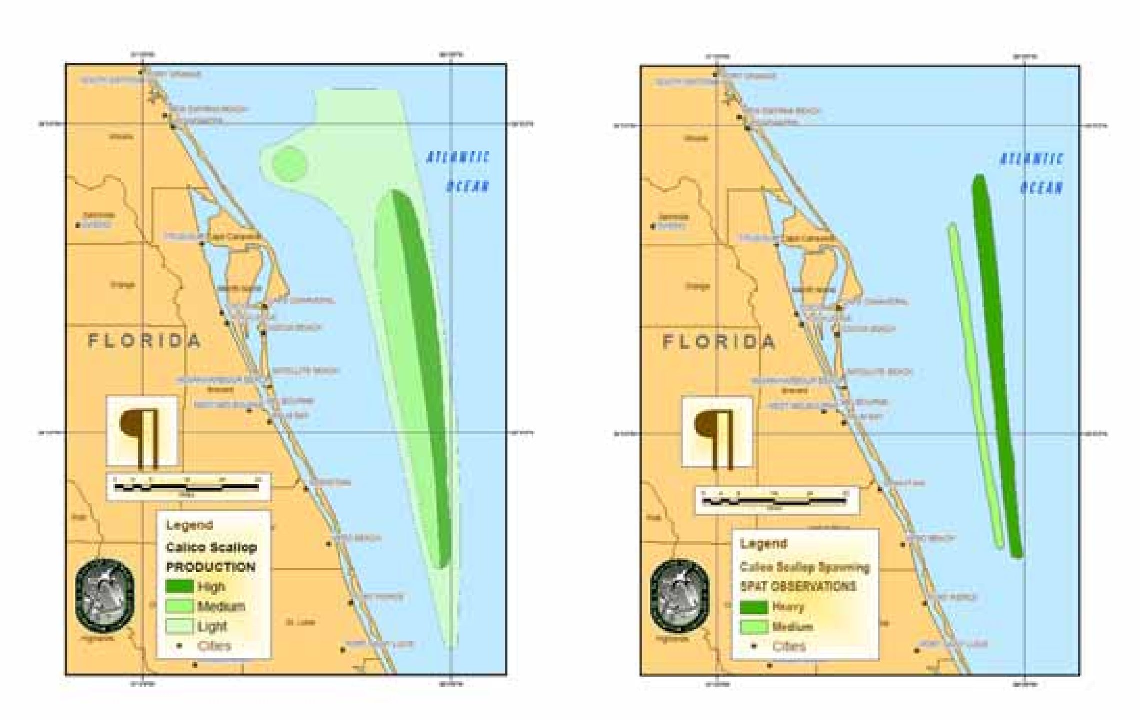


Figure 4.1-24. Calico scallop spawning areas and fishing grounds (Source: William Burkhardt, Calico Scallop Advisory Panel). Reproduced from SAFMC 1998 (Draft Calico Scallop FMP).

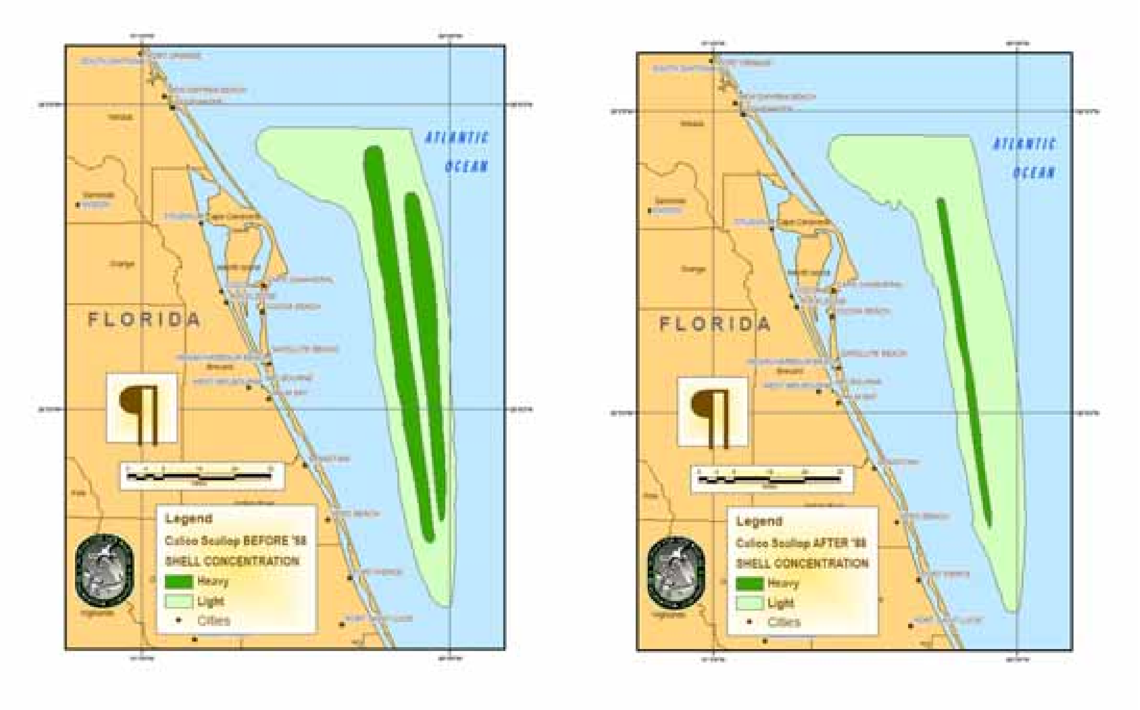


Figure 4.1-25. Calico Scallop shell distribution (Source: William Burkhardt, Calico Scallop Advisory Panel). Reproduced from SAFMC 1998 (Draft Calico Scallop FMP).

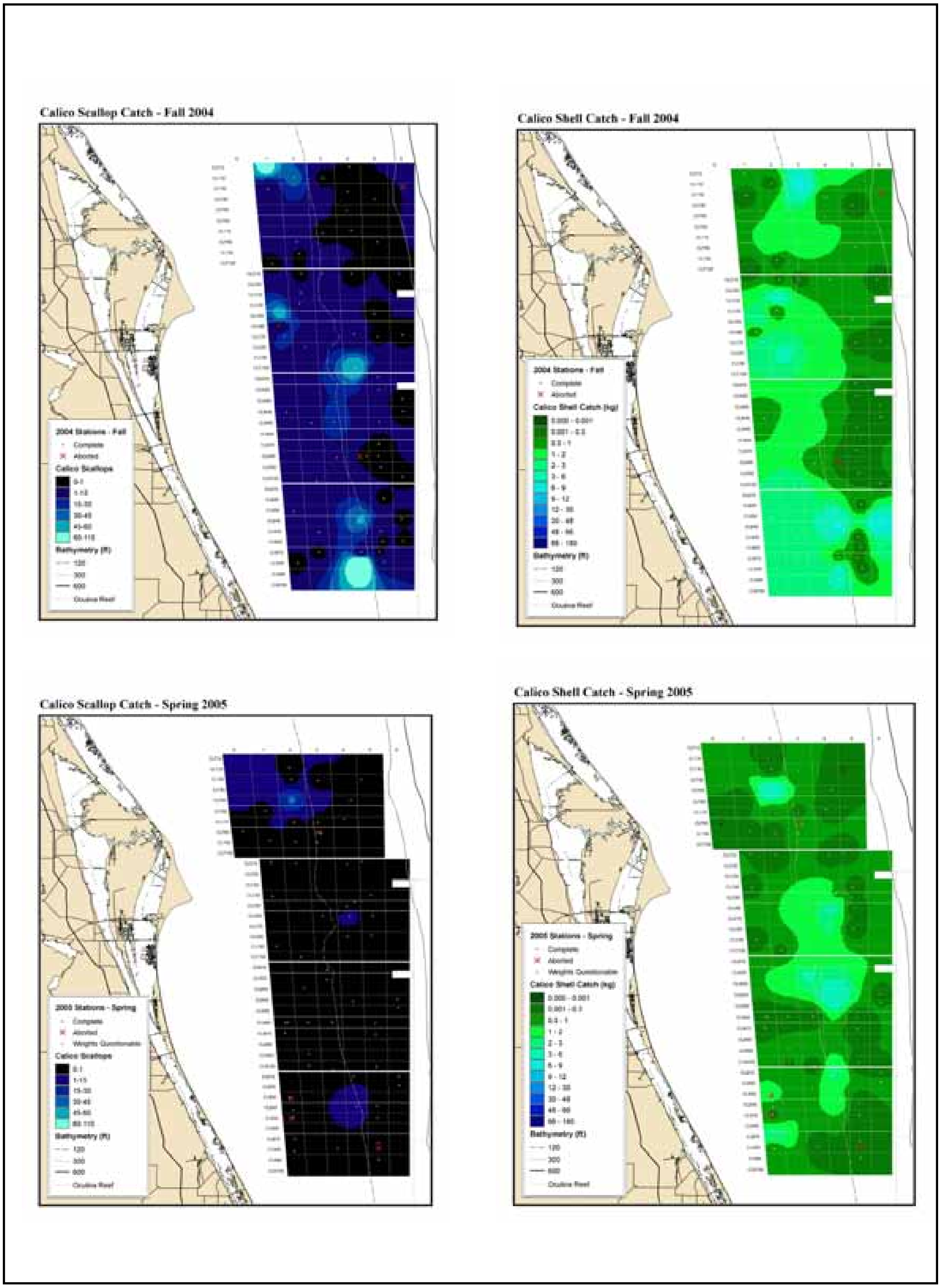


Figure 4.1-26. Current calico scallop distribution (left) and calico scallop shell distribution (right) for two seasons of sampling (FWRI) in the vicinity of Cape Canaveral, FL.

Reproduction

Maturity in Atlantic calico scallops is correlated with age rather than size (Roe et al. 1971). Change in ovarian color was found to correlate with reproductive stage (Miller et al. 1979). Scallops as small as 23.0 mm have been observed with developed gonads, and scallops as small as 20 mm, estimated to be as young as 71 days old, can probably begin spawning (Miller et al. 1979). Atlantic calico scallops are hermaphroditic, ejecting first sperm and then eggs into the water where fertilization occurs. Laboratory spawned calico scallops produced eggs with a diameter of 60 microns (Costello et al. 1973).

Changes in water temperature may stimulate spawning. Peak spawning is thought to occur at temperatures around 18°C (Allen 1979) in both spring and fall but scallops may spawn intermittently many times during the spawning season, and spat have been observed throughout the year. The fall peak is secondary to the spring peak, and does not occur in all years. No data on fecundity of Atlantic calico scallops was located. The closely related bay scallop (*Argopecten irradians*) can produce 12.6 to 18.6 million eggs at age 1 year, and some individuals will produce a second, smaller spawn at an age of 18 months (Bricelj et al. 1987). Based on an age at first reproduction of about 6 months, and a maximum age of 24 months, the oldest calico scallops may survive for up to four spawning seasons. It is difficult to determine if any individual scallop actually spawns more than once, because scallops often suffer increased mortality after a spawn, but multiple, smaller batches of eggs seems likely for this species.

Development, growth and movement patterns

In the laboratory at 23°C and 35 ppt, trochophore larvae were observed at 24 hr and larvae settled at 235-270 micron on day 16 (Costello et al. 1973). Larvae settle as spat in 14 to 16 days and attach to substrates with byssal threads from the foot. Juveniles can reach 10 mm by an age of two months, and thereafter grow at about 0.65 mm per week. Calico scallops reach commercial shell height of 4 to 4.5 cm (1.6 to 1.8 in) in 6 to 8 months, and have a life span averaging only 18 to 20 months, with a maximum age of 24 months (Allen and Costello 1972). The maximum shell height attained is at least 68.9 mm (Waller 1991).

Part of the North Carolina stock may result from larvae transported northward from the Cape Canaveral grounds by the Gulf Stream. Krause et al. (1994) found that the North Carolina stock and Cape Canaveral stocks were more similar morphometrically and genetically than two stocks within Florida waters. However, oceanographic data suggest that most larvae would be retained at Cape Canaveral (Leming 1979). Cyclic movement of bottom waters on and off the continental shelf ranged in period from 2-23 days during the summer (mean around 11.5 days) to 3-6 days in winter. Both were related to fluctuations in wind stress. The results also suggest that the net transport of most larvae would result in displacement from the spawning ground of only 7 - 40 km over the two week larval phase. The author also said that the predicted pattern of dispersal could explain the long, oval shaped beds which have been observed; elongate elipses roughly parallel to the bathymetry. These same patterns of water movement probably generate a high flux of both nutrient rich and food rich water across the shelf edge at depths around 40 m, which are optimal for the rich benthic abundance and diversity present.

Ecological relationships

Most scallops are primarily filter feeders on phytoplankton, benthic microalgae, and to varying degrees suspended particulate organic matter and detritus (Bricelj and Shumway 1991). Although no studies are available for calico scallops, the genus *Argopecten* has been studied extensively. Clearance rates vary from less than 1 liter/hr/g dry tissue weight at very high algal concentrations to over 10 liters/hr/g dry tissue weight at low algal concentrations (MacDonald et al. 2006). Using our rough estimates of 1 billion individuals, with an average dry tissue weight of 2 mg, the calico scallop population could then be estimated to clear 10 billion liter/hr (1 million m^3/hr) or 8.8 billion m^3/yr. In terms of biomass, these rates translate to about 8 mg/hr/g dry tissue weight or 140 million kg of phytoplankton per yr removed from the east Florida shelf waters.

Calico scallops can be among the most abundant members of the benthic community near the shelf edge and thus a large potential prey source for other species. Predators on juvenile and adult scallops include seastars, gastropods, squid, octopus, crabs, sharks, rays, and bony fishes. Schwartz and Porter (1977) found that at least 24 of the 33 most common fishes examined in North Carolina preyed on scallops. Nine species did so commonly: *Spheroides maculatus, Stenotomus aculeatus, Diplectrum formosum, Orthopristes chrysopterus, Monacanthus hispidus, Balistes capriscus, Centropristis striata, Mustelus canis*, and *Synodus foetens*. Two invertebrates, *Luidia clathrata* and *Astropecten articulatus*, were found to be common predators and at least 19 other invertebrates were implicated in scallop predation. One fear is that at-sea shucking of scallops may result in increased abundance of these predators on the scallop beds by attracting them to the discarded viscera. An additional survey in North Carolina waters in the 1980s found a similar collection of incidental species (Table 2). Economically important species include *Paralichthys albigutta*, *P. lethostigma*, and *P. dentatus*, as well as the penaeid shrimp *Farfantepenaeus duorarum* (Stephan 1989).

Table 4.1-25. List of incidental species captured from scallop trawl November 1988 (From Stephan 1989).

Species	Common Name
Finfish	
Bellator militaris	Horned searobin
Centropristis ocyurus	Bank sea bass
C. philadelphica	Rock sea bass
Citharichthyes macrops	Spotted whiff
C. spilopterus	Bay whiff
Diplectrum formosum	Sand perch
Etropus crossotus	Fringed flounder
Gymnachirus melas	Naked sole
Hippocampus erectus	Lined sea horse
Lagodon rhomboides	Pinfish
Monacanthus hispidus	Planehead filefish
Orthopristis chrysoptera	Pigfish
Paralichthys albigutta	Gulf flounder
P. dentatus	Summer flounder

P. lethostigma	Southern flounder
Prionotus evolans	Striped searobin
P. roseus	Bluespotted searobin
P. salmonicolor	Blackwing searobin
P. scitulus	Leopard searobin
Scophthalmus aquosus	Windowpane
Scorpaena sp.	Scorpionfish
Sphoeroides maculates	Northern puffer
Stenotomus chrysops	Scup
Syacium papillosum	Dusky flounder
Symphurus plagiusa	Blackcheek tonguefish
Synotus foetens	Lizardfish
Trachinocephalus myops	Snakefish
Invertebrates	
Aequipecten muscosus	Rough scallop
Arbacia punctulata	Purple urchin
Arcinella cornuta	Florida spiny jewelbox
Astropecten articulatus	Margined sea star
Calappa flamea	Shame-fase crab
Chione latilirata	Imperial venus
Cnidaria	Sea nettles
Glatheidea	Hermit crab
Hepatus epheliticus	Dolly Varden crab
Laevicardium laevigatum	Egg cockle
Ludia clathrata	Slender sea star
Lytechinus variegatus	Short-spined sea urchin
Murex sp.	Murex
Ophiothricidae	Short spined brittle star
Pecten raveneli	Ravenel's scallop
Farfantepenaeus duorarum	Pink shrimp
Portunus gibbessi	Portunid crab
P. spiymanus	Spiny-handed crab
Scyllaridae	Slipper lobster
Sicyonia sp.	Rock shrimp
Xenophora conchyliophora	Atlantic carrier shell

Wells et al. (1964) identified 112 species of benthic invertebrates from the North Carolina scallop beds, most of which were found as fouling organ isms on scallops shells. The most abundant was *Balanus amphitrite* (up to 200 per shell) and the polycheates *Pomatoceros caeruleus* (up to 65 per shell) and *Sabellaria floridensis* (up to 28 per shell). All three species were present on essentially every scallop. The dry weight of the associated epifauna weighed 40-50 percent of the dry weight of the shell itself. A similar amount of fouling occurred on the inside surface of the shells of dead scallops.

A protistan parasite of the genus *Marteilia* was first recorded from the east Florida calico scallop beds in samples collected during 1991 (Moyer et al. 1993). There is no direct evidence that this parasite caused mortality in the scallop population, but the samples from which the parasite was identified were collected during a major scallop mortality event that occurred in February 1991. Moreover, species of *Marteilia* have been implicated in mass mortalities of oysters in Europe and Asia (Moyer et al. 1993), so this organism certainly has the capability of instigating a mass mortality event in calico scallops. The history of *Marteilia* on the east Florida shelf, and its occurrence in calico scallop populations in the Gulf of Mexico or off North Carolina, is presently unknown.

Several other parasites have been linked to calico scallops but no mortalities have been directly attributed to them: *Echeneibothrium* (cestode) (Singhas et al. 1993), *Pontonia margarita* and *Pinnotheres maculatus* (decapod crustaceans), *Boonea seminude* (gastropod), *Ceratoneries tridentate* and *Polydora websteri* (polychaetes), and *Pinnotheres maculates* (crab) (Wells et al. 1964). The decapod crustaceans which inhabit the mantle cavity are likely commensal, causing little impact on host scallops. Worms that cause blisters (*Polydora* sp., *Pontonia* sp. and *Pinnotheres* sp.) weaken the shell and may increase the incidence of predation or at least cause the host to spend resources repairing injuries to the shell (Wells et al. 1964). *Odostomia seminuda* (ectoparasitic gastropod) will similarly drain resources by attaching to the shell and draining body fluids from the mantle edge (Wells et al. 1964). Eggs and developing larvae of the nematode *Sulcascaris sulcata*, the loggerhead stomach worm, may be found in muscles of calico scallops. This nematode in scallops has also been incorrectly identified as *Paranisakis pectinis* and possibly as a species of *Porrocaecum* (Cheng 1978). Eggs released in turtle feces can be ingested by scallops, and developed larvae can later re-infect turtles that consume scallops (Berry and Cannon 1981). The encysted larvae appear as a 2 - 2.5 mm blemish on the meat. They do not pose any threat to humans because it will be killed during freezing, cooking or even human body temperatures (Otwell and Koburger 1985). Another parasite, the encysted nematode larvae, *Echeneibothrium* sp., has been found in calico scallop gonads. Alteration of intestinal epithelium is the most serious tissue damage observed, but, failure of a local population in North Carolina coincided with the appearance of this parasite (Singhas et al. 1993).

Abundance and status of stocks

Most individuals of this species are probably located in the Cape Canaveral population. The maximum harvest, 42.7 million pounds in 1984, would equate to about 8.54 billion adult scallops, based on an average of 200 meats per pound (assuming 1 pint = 1 pound), assuming all of the scallops present were harvested. Other populations would add significantly to the potential overall abundance. The Florida Gulf of Mexico populations may reach abundances of around 1 billion or more, based on a harvest approaching 5 million pounds of meat 1993, and the North Carolina population might achieve abundances of 0.5 billion based on catches approaching 2 million pounds of meat in 1978. It is unknown if any of the populations are present at those levels today. Based on a 30 year average harvest of 5 million pounds per year, the Florida population would average around 1 billion individuals. The abundance in local populations can change by 50 fold between successive years (Anonymous 1981).

Disappearance of Atlantic calico scallops from a particular area commonly occurs, and the size of the stock shows considerable annual fluctuations. Monthly mortality on the Cape Canaveral bed was estimated at 12% during recruitment periods and 23 % during post-spawn periods, and ranged from 1-31% (Roe et al. 1971). Declines and mass mortalities have occurred on the grounds off North Carolina and Florida. Possible causes include migration, poor larval transport from elsewhere, and increased fishing pressure following introduction of shucking and eviscerating machines. Spawning stock is maintained because (1) not all beds are harvested each year; (2) the spawning stock includes scallops too small to market; and (3) individuals at densities too low to harvest.

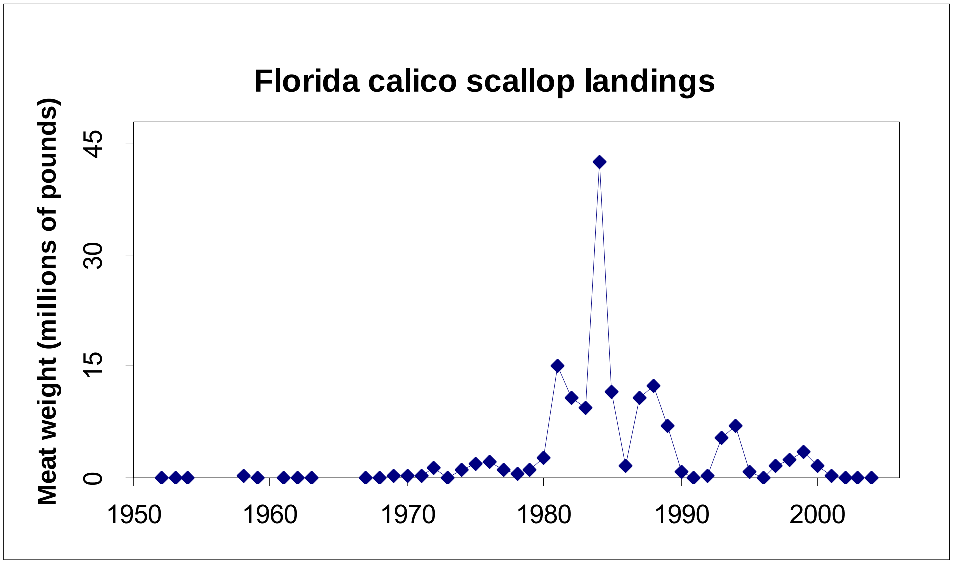
The oceanography of the east Florida shelf is highly variable and strongly influenced by the Gulf Stream. Gulf Stream meanders and other topographic and meteorological events can induce upwelling of cold, nutrient rich water onto the continental shelf (Leming 1979). This water may have positive effects on scallop biology by increasing food supply (Atkinson et al. 1984). Negative impacts also are possible, particularly the dispersal of larvae away from the natal habitat as the upwelled water mass is swept northward off the shelf (Leming 1979). The implications of upwelling to calico scallops inhabiting the east Florida shelf are not well known, but such upwelling events are an historic feature of the continental shelf in this area and in other areas where abundant calico scallop populations have been recorded (e.g., Atkinson et al. 1984; Muller-Karger 2000). To the degree that upwelling events on the east Florida shelf reflect larger scale oceanographic events such as the El Niño Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO), which may cycle on a decadal or even longer time scale, these upwelling events may induce relatively long-term cycles in calico scallop abundance.

Reliable information on the geographic extent of current fishable stocks, if any, is unavailable. The most reliable data comes from fishery dependant monitoring in Florida and North Carolina (Table 4.1-26; Figure 4.1-27). These sources show that the fishery in NC peaked in 1972 and in Florida in 1984. Despite having annual harvests in Florida averaging 9.6 million pounds of meat per year for over a decade, and harvests that exceeded one million pounds in North Carolina there are no current harvests. Concentrations of scallops have been observed in the Cape Canaveral beds and off Cape San Blas in recent years, but not harvested.

Table 4.1-26. Commercial landings and ex-vessel value from North Carolina (NCDMF Trip Ticket Program) and Florida calico scallop fishery.

YEAR	Pounds of Meat	Value $	Pounds of Meat	Value $
1952			275	
1953			3,742	861
1954			184	
1958			248,000	
1959	6,572	$2,629	15,400	
1960	111,726	$44,691		
1961	22,427	$8,971	3,648	1,459
1962			16,453	5,169
1963			176	39
1965	871,100	$244,709		
1966	1,856,760	$368,685		
1967	1,388,606	$308,843	20,736	7,672
1968			29,916	12.787
1969			196,724	179,473
1970	1,574,087	$498,570	195,764	195,764

1971	1,285,304	$432,025	288,575	370,299
1972	1,050,320	$492,899	302,767	407,030
1973	556,315	$353,757	1,624	2,055
1974			1,074,354	587,799
1975			1,882,239	1,249,510
1976			2,268,802	1,621,977
1977			113,244	837,170
1978			477,813	751,912
1979	43,301	$80,973	1,257,292	1,710,469
1980			2,582,471	3,619,497
1981	244,324	$307,215	15,170,881	14,277,460
1982			10,841,988	11,276,834
1983	101,977	$178,476	9,351,781	11,666,133
1984	1,184	$888	42,700,000	23,485,000
1985			11,500,000	18,170,000
1986			1,565,784	2,974,990
1987			10,936,384	21,982,131
1988	668,064	$702,134	12,410,456	22,338,820
1989	335,521	$469,164	6,981,704	11,938,713
1990	384,783	$530,590	874,376	820,165
1991			39,000	38,220
1992			205,111	174,906
1993	2,912	$3,640	5,306,545	4,439,34
1994			6,879,061	3,898,733
1995			949,805	625,912
1997			1,714,849	1,749,365
1998			2,396,511	2,065,041
1999			3,593,596	3,448,072
2000			1,740,000	482,069
2001			314,372	387,802
2002			42,232	63,020
2003			61,704	80,215
2004			0	0
2005			0	0



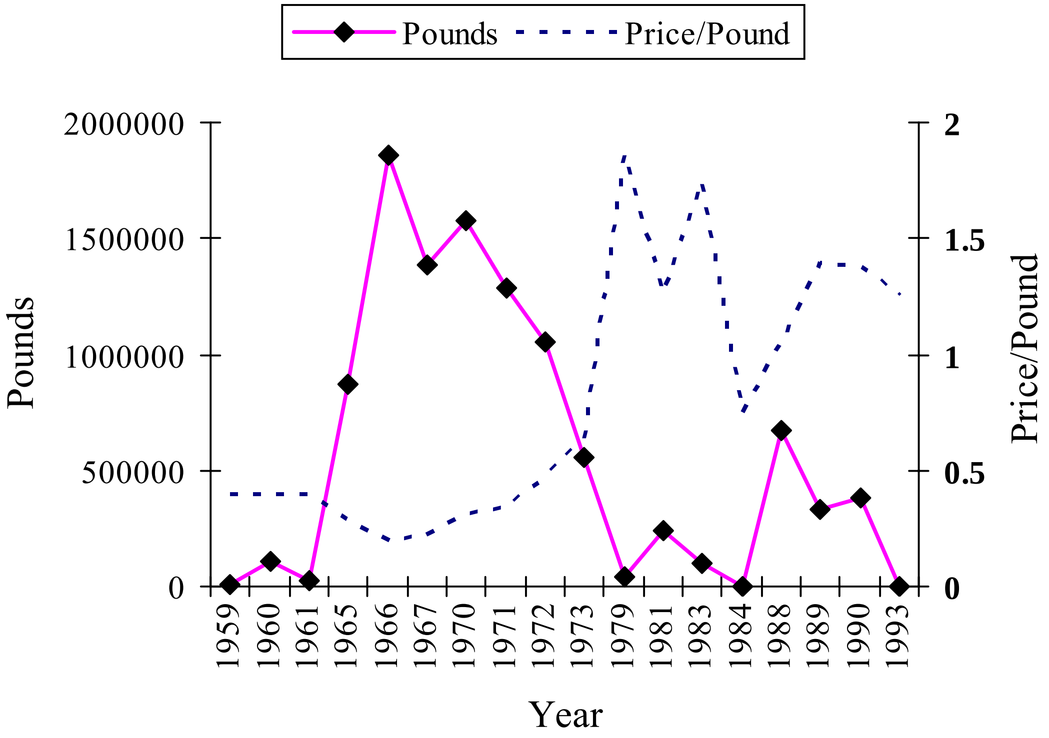


Figure 4.1-27. Ex-vessel value and price per pound for calico scallops (Schwartz and Porter 1977; NCDMF Trip Ticket Program).

The NCDMF has managed the calico scallop fishery by proclamation since 1974. North Carolina Fisheries Rules state that it is unlawful to land or possess aboard a vessel, calico scallops except at such times as designated by the Fisheries Director by proclamation (15A NCAC 3K .0504). The seasons varied through time based on the availability of calico scallops. Generally, calico scallop season opened in early spring and closed when catches became low. The last opening in North Carolina was in February of 2001 because of some scattered reports of available calicos. However, no landings were made in 2001. Presently, trawlers heading north out of Beaufort Inlet to participate in the summer flounder fishery will sometimes make a tow over the traditional beds to ascertain if commercial quantities of calico scallops exist (David Taylor, NCDMF, personal communication).

The intermittent fishery for calico scallops results from the unpredictable nature of scallop stocks. Naturally occurring fluctuations in stocks are attributed to natural mortality, migration, and poor larval recruitment. In addition, stocks may have been depleted by overfishing which stemmed from the introduction of the scallop shucking and eviscerating machines (Schwartz and Porter 1977; NCDMF 1989)

The NCDMF has been involved in calico scallop monitoring since 1968 when monitoring was carried out on the R/V *Dan Moore* from 1968-1981. The last survey made by NCDMF was in

November of 1988 on the scallop grounds east and west of Cape Lookout Shoals using a 3.7 m scallop trawl (Stephan 1989). Scallops consisting of two cohorts were found on the eastern side of the Cape only. The smaller size cohort consisted of shell heights of less than 46 mm and made up 43% of the total number of scallops. The larger cohort consisted of scallops whose shell height ranged from 48 mm to 64 mm (Figure 7).

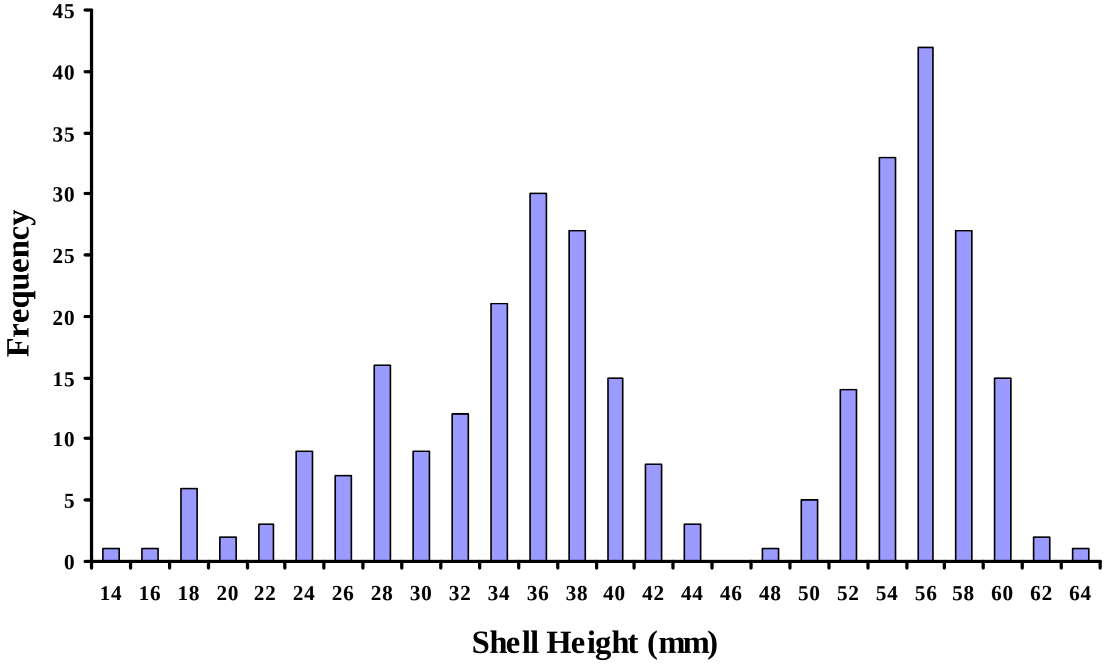


Figure 4.1-28. Shell height frequency for calico scallops collected November 1988 (From Stephan 1989).

4.2 Other Managed Species in the South Atlantic

4.2.1 Atlantic Menhaden

Description and Distribution

Atlantic menhaden are members of the worldwide family Clupeidae, one of the most important families of fishes both economically and ecologically (Ahrenholz 1991). Clupeids are characteristically very numerous and form large, dense schools. Many of the species are filter feeders, being either primary consumers, feeding on phytoplankton, or secondary consumers, feeding on zooplankton, or both. Many clupeids are in turn, prey for various piscivorous predators through virtually their entire life.

Atlantic menhaden are euryhaline species that inhabit nearshore and inland tidal waters from Florida to Nova Scotia, Canada (Ahrenholz 1991). Spawning occurs principally at sea with some activity in bays and sounds in the northern portion of its range. Eggs hatch at sea and the larvae are transported to estuaries by ocean currents where they metamorphose and develop as juveniles. Adults stratify by size during the summer, with older, larger individuals found farther north. During the fall, Atlantic menhaden migrate south and disperse from nearshore surface waters off North Carolina by late January or early February. Schools of adult menhaden reassemble in late March or early April and migrate northward. By June the population is redistributed from Florida to Maine (Ahrenholz 1991).

Atlantic menhaden are abundant in the estuarine and nearshore ocean waters of North America from Nova Scotia to central Florida. They have been taken in commercial quantities from northern Florida to southern Maine. A few individuals have been taken as far north as St. John, New Brunswick, and St. Mary Bay, Nova Scotia. The southern limit seems to be Indian River City, Florida (Hildebrand 1963). Spawning occurs in the ocean, while larvae and juveniles utilize coastal estuaries. The adult population stratifies by age and size, with the older and larger individuals farther northward, and the younger and smaller fish in the southern half of the species' range (Ahrenholz 1991).

Reproduction

Most Atlantic menhaden reach sexual maturity during their third year of life (late age 2) at lengths of 180 - 230 mm fork length (FL). Spawning occurs year-round throughout much of the species' range, with maximum spawning off the North Carolina coast during late fall and winter. Adults then move inshore and northward in spring and stratify by age and size along the Atlantic coast (Rogers and Van Den Avyle 1989). During this northern migration, spawning occurs progressively closer inshore and by late spring, some spawning occurs within coastal embayments. There are definite spring and fall spawning peaks in the Middle and North Atlantic Regions, with some spawning occurring during the winter in the shelf waters of the Mid-Atlantic Region. Larval menhaden have been collected as far as 64km inland in the Santee River channel and backwater sloughs, South Carolina (Meador 1982), suggesting spawning may occur in inland waters.

Atlantic menhaden are relatively prolific spawners. Predicted fecundities range from 38,000 eggs for a small female (180 mm FL) to 362,000 for a large female (330 mm FL) according to an equation derived by Lewis et al. (1987):

$$\text{Number of eggs} = 2563 * e^{0.015*FL}$$

This equation was derived by fitting an exponential model to length-specific fecundity data for fish collected in 1978, 1979 and 1981, as well as data reported in two earlier studies (Higham and Nicholson 1964; Dietrich 1979) for fish collected during 1956-1959 and in 1970. Fish in all three studies were collected from the North Carolina fall fishery, which harvests fish of all ages.

Analysis of eggs and larvae collected at various locations along the Atlantic coast during 1953-75 (e.g., Judy and Lewis 1983) generally confirmed earlier knowledge of spawning times and locations based on observations of adults with maturing or spent ovaries (e.g., Reintjes and Pacheco 1966). During December-March, most spawning-age fish congregate in offshore waters south of Cape Hatteras.

Maximum spawning probably occurs at this time. Checkley et al. (1988) reported maximum spawning off North Carolina in January 1986 during periods of strong northeast winds in up-welled water near the western edge of the Gulf Stream. Spawning continues at a decreasing rate closer inshore as fish migrate north in late March. By May, most spawning is restricted to coastal waters north of Cape Hatteras.

Spawning reaches a minimum in June, but continues at a low level until September north of Long Island. As mature fish migrate south in October, spawning increases from Long Island to Virginia. The capture of a 138 mm juvenile Atlantic menhaden in an estuary on the Maine coast in October 1990 (T. Creaser, Maine DMR, pers. comm.; as cited in ASMFC 1992) suggests that a limited amount of spawning may occur as far north as the Gulf of Maine. Some ripening female menhaden were offloaded on to the Soviet processing ship near Portland, Maine in August and September 1991 (S. Young, Maine DMR observer on the M/V *Riga*, pers. comm.; as cited in ASMFC 1992). Egg and larval surveys have been restricted to waters south of Cape Cod (Judy and Lewis 1983) and, thus, would not have produced any evidence for spawning in the Gulf of Maine.

Development, growth and movement patterns

Atlantic menhaden produce pelagic eggs about 1.5 mm in diameter which hatch within 2.5-2.9 days at an average temperature of 15.5°C (Hettler 1981). Embryonic development is completed in <36 hr at 20- 25°C, but takes about 200 hr at 10°C (Ferraro 1980). Egg mortalities observed in the laboratory were >90% at 10°C, and 48-92% at 15, 20 and 25°C (Ferraro 1980).

A full morphological description of Atlantic menhaden eggs and larvae was provided by Jones et al. (1978). Hettler (1984) compared Atlantic menhaden (*Brevoortia tyrannus*) larvae with gulf and yellowfin menhaden (*B. patronus* and *B. smithi*) larvae. Atlantic menhaden larvae co-occur with yellowfin menhaden larvae along the east coast of Florida to North Carolina, but not with gulf menhaden.

A fourth species (*B. gunteri*) occurs exclusively in the Gulf of Mexico. Powell and Phonlor (1986) also compared early life history characteristics of Atlantic and gulf menhaden.

Yolk-sac larvae hatched at 3-4 mm standard length (SL) and maintained at 16° and 24°C began to feed at 4.5-5 mm SL (Powell and Phonlor 1986). First feeding was a function of size, not age. Larvae raised at 16°C began feeding after 5 days, while larvae raised at 24°C began feeding after only 2 days. Larvae reached 10.7 mm SL after 21 days at 20°C. Caudal and dorsal fins developed at 9 mm, and all fin rays were developed by 23 mm (Reintjes 1969). The swimbladder and acoustico-lateralis system become functional in larvae measuring approximately 20 mm (Hoss and Blaxter 1982).

Low temperatures (<3°C for >2 days) killed most larvae held in laboratory experiments (Lewis 1965, 1966), although mortality depended on acclimation temperature and the rate of thermal change. Best survival occurred at temperatures >4°C and salinities of 10-20 ppt.

Larvae which hatch offshore are transported shoreward and enter estuaries in the south Atlantic region after 1-3 months at sea (Reintjes 1961) at a size of 14-34 mm FL (Reintjes and Pacheco 1966). Larval migration into estuaries occurs during May-October in the north Atlantic region, October-June in the mid- Atlantic, and December-May in the south Atlantic (Reintjes and

Pacheco 1966). Larval condition improved rapidly after fish entered two North Carolina inlets (Lewis and Mann 1971).

Metamorphosis to the juvenile stage occurs at about 38 mm total length (TL) during late April-May in North Carolina estuaries and later in the year farther north. Most larvae entered the White Oak estuary (North Carolina) in March and moved upstream to a fresh water-low salinity zone where they transformed into "pre-juveniles" in late March-April and then into juveniles in late April-May (Wilkens and Lewis 1971). Other studies (Weinstein 1979; Weinstein et al. 1980; Rogers et al. 1984) also show young menhaden are more abundant in shallow, low salinity (< 5 ppt) estuarine zones. Metamorphosis to the "pre-juvenile" stage occurs at lengths >30 mm TL and to the juvenile stage beyond 38 mm TL (Lewis et al. 1972). Metamorphosis is rarely successful outside of the low-salinity estuarine zone (Kroger et al. 1974), although Atlantic menhaden have been successfully reared from eggs to juveniles in high salinity water (Hettler 1981).

The morphological changes that occur at metamorphosis are associated with a change in feeding behavior. Larvae feed on individual zooplankters, whereas juveniles rely more heavily on filter feeding (June and Carlson 1971; Durbin and Durbin 1975). This shift in feeding behavior is associated with a loss of teeth and an increase in the number and complexity of the gill rakers through which sea water is filtered as it passes through the gills. Older larvae (25-32 mm) feed on large copepods, but only rarely on small zooplanktonic organisms (Kjelson et al. 1975). Fish larger than 40 mm FL feed primarily on phytoplankton (June and Carlson 1971), but zooplankton has also been reported as an equally important food source in juvenile Atlantic menhaden (Richards 1963; Jeffries 1975). Juveniles are capable of filtering particles as small as 7-9 microns (Friedland et al. 1984) and, thus, directly utilize the abundant small photosynthetic organisms that are not consumed by most other species of fish. Detritus derived from saltmarsh cordgrass (*Spartina alterniflora*) has also been reported as a primary food source for juveniles in North Carolina saltmarshes (Lewis and Peters 1984). Based on calculations incorporating feeding rates and population estimates from eight east coast estuaries, Peters and Schaaf (1981) concluded that juveniles must consume more food during estuarine residency than is available from a strictly phytoplankton-based food chain.

Young-of-the-year menhaden congregate in dense schools as they leave shallow, estuarine waters for the ocean, principally during August to November (earliest in the north Atlantic region) at lengths of 75-110 mm TL (Nicholson 1978). Many of these juveniles migrate south along the North Carolina coast as far as Florida in late fall and early winter and then redistribute northward by size as age-1 fish during the following spring and summer (Kroger and Guthrie 1973; Nicholson 1978). Larvae which enter the estuaries late in the season may remain there for an additional year and emigrate to the ocean at age 1.

Age-1 menhaden migrate north and south along the coast over a greater distance than young-of-the-year juveniles (Nicholson 1978). Abundance and distribution of juvenile Atlantic menhaden is monitored by the marine resource agencies of most Atlantic coast states under a variety of estuarine surveys using trawls and seines. According to a survey conducted by AMAC in February 1990, juvenile menhaden have been taken from Massachusetts to Georgia (there is no survey on the Atlantic coast of Florida). Juvenile menhaden were observed in Gulf of Maine estuaries during 1998 and 1999.

Juveniles collected at 2-3 day intervals have shown growth rates of nearly 1 mm/day (Reintjes 1969). Water temperatures >33°C caused death in young-of-the-year and age-1 Atlantic menhaden (Lewis and Hettler 1968), although the time until death depended, in part, on acclimation factors. Sudden exposure to lethal temperatures, for example, caused greater mortality. Juvenile Atlantic menhaden can adjust rapidly to abrupt changes (increase or decrease) in salinity from 3.5 to 35 ppt and vice-versa (Engel et al. 1987). Juveniles raised in low salinity water (5-10 ppt) were more active, ate more, had higher metabolic rates, and grew faster than juveniles raised in high salinity water (28-34‰) (Hettler 1976).

Adult Atlantic menhaden are strictly filter feeders, grazing on planktonic organisms. They can be observed swimming slowly in circles, in tightly packed schools, with their mouths wide open and their opercula (gill flaps) flaring. In lab experiments (Durbin and Durbin 1975), they fed on small adult copepods as well as phytoplankton. Organisms smaller than 13-16 microns (slightly larger than the minimum size reported by Friedland et al. (1984) for juveniles) were not retained in the gills. Menhaden did not feed on large zooplankton (10 mm brine shrimp) in these experiments. The filtering process is purely mechanical; particles are not selected by size (Durbin and Durbin 1975). These experiments showed that the filtering rate depended on mouth size, swimming speed, food particle concentration, and the mechanical efficiency of the gill rakers. The structure of the "branchial basket," the area underneath the opercula where the extremely fine and closely-spaced gill filaments and gill rakers are located, was described in detail by Friedland (1985).

Growth occurs primarily during the warmer months. Fish as old as age 8 were fairly common during the 1950s and early 1960s, but in more recent years, fish older than age 6 have been rare. Older (age-6) fish reach an average length of 330 mm FL and a weight of 630 g, although growth varies from year to year and is inversely density-dependent. Growth rates appear to be accelerated during the first year when juvenile population size is low and are reduced when juvenile population size is high.

Adults migrate extensively along the entire United States East Coast. Following winter dispersal along the south Atlantic coast, adults begin migrating north in early spring, reaching as far north as the Gulf of Maine in June. Older and larger fish migrate farther than younger, smaller fish. The return southern migration occurs in late fall and early winter.

Stock Structure and Migration

The Atlantic menhaden resource is believed to consist of a single unit stock or population, based on tagging studies (Dryfoos et al. 1973; Nicholson 1978). Adult Atlantic menhaden undergo extensive seasonal migrations north and south along the United States East Coast. Early reports of this migratory behavior were made by Roithmayr (1963) based on the decrease in the number of purse seine sets north of Cape Cod in September. Also, Reintjes (1969) observed the disappearance of fish in October north of Chesapeake Bay and their appearance off the coast of North Carolina in November. Nicholson (1971) examined latitudinal differences in length-frequency distributions of individual age groups at different times of year and described a cyclic north-south movement with the largest and oldest fish proceeding farthest north such that the population stratifies itself by age and size along the coast during summer. A study of length frequencies at the time of first annulus formation on scales (Nicholson 1972) supported the concept of a north-south migratory movement and also indicated that a great deal of mixing of fish from all areas occurs off the North Carolina coast before fish move northward in spring.

Returns of tagged Atlantic menhaden (Dryfoos et al. 1973; Nicholson 1978) have generally confirmed what was already concluded from earlier work and added some important details. Adults begin migrating inshore and north in early spring following the end of the major spawning season off the North Carolina coast during December-February. The oldest and largest fish migrate farthest, reaching the Gulf of Maine in May and June. Adults that remain in the south Atlantic region for the spring and summer migrate south later in the year, reaching northern Florida by fall. Fish begin migrating south from northern areas to the Carolinas in late fall. During November, most of the adult population that summered north of Chesapeake Bay moves south around Cape Hatteras.

Mortality

The Atlantic menhaden population is subject to a high natural mortality rate. There is a somewhat reduced probability of death from natural causes when the population is being harvested. Natural mortality is also higher during the first two years of life than during subsequent years. Ahrenholz et al. (1987a) reported an annual instantaneous natural mortality rate (M) of 0.45 in the absence of fishing; this rate is equivalent to an annual reduction in population numbers of 36%. This rate is quite high compared to other pelagic marine species. Atlantic herring, for example, is characterized by an 18% annual natural mortality rate (Fogarty et al. 1989). During the 1955-1987 period, under exploitation, the annual natural mortality rate for age-1 Atlantic menhaden was 30% and, for ages 2 and older, it was 20% (see Vaughan 1990). Natural mortality removes an estimated 30% of the exploited population at age 1 and 20% each year thereafter.

Menhaden natural mortality is probably due primarily to predation, since the fish are so abundant in coastal waters during the warmer months of the year. All large piscivorous sea mammals, birds, and fish are potential predators on Atlantic menhaden. Menhaden are preyed upon by species such as bluefish, striped bass, king mackerel, Spanish mackerel, pollock, cod, weakfish, silver hake, tunas, swordfish, bonito, tarpon, and a variety of sharks.

Coastal pollution and habitat degradation threaten marine fish species, such as Atlantic menhaden, which spend their first year of life in estuarine waters and the rest of their life in both ocean and estuarine waters.

Other poorly understood sources of natural mortality for Atlantic menhaden are diseases and parasites. A partial list of parasites was given in Reintjes (1969), but there is no information available concerning the extent of parasitism or its possible effect on survival. Ahrenholz et al. (1987b) described the incidence of ulcerative mycosis (UM), a fungal infestation which was observed in menhaden over much of their range in 1984 and 1985 and in a more restricted area in 1986. A large fish kill in Pamlico Sound, North Carolina in November, 1984 was associated with UM, but its primary effect may be to weaken fish, making them more susceptible to other causes of mortality, such as predation, parasites, other diseases, and low dissolved oxygen concentrations. The overall impact of UM on the 1984 and 1985 year classes could not be assessed, but it was not believed to be significant (Ahrenholz et al. 1987b). However, Vaughan et al. (1986b) believed that the mortality effects of a disease or other event must be “truly catastrophic” to be detectable.

Another source of natural mortality for Atlantic menhaden (and many other species) may be “red tide.” The term refers to the color of water caused by the rapid multiplication (a “bloom”) of single-celled planktonic organisms called dinoflagellates, which produce a toxic compound. The toxin accumulates in the tissues of filter-feeding animals which ingest the dinoflagellate. An outbreak of red tide occurred along the coast of the Carolinas during November, 1987 - April, 1988 when Gulf Stream water containing the dinoflagellates was transported into coastal waters. Menhaden recruitment in Beaufort Inlet during this period was severely reduced (S. Warlen, NMFS, Beaufort N.C., pers. comm.; as cited in ASMFC 1992). A new species of toxic dinoflagellate was identified as the causative agent in a major menhaden kill in the Pamlico River, North Carolina, in May, 1991. Problems with toxic phytoplankton organisms may increase in the future since their appearance has been correlated with increasing nutrient enrichment in estuarine and coastal waters which are subject to increasing organic pollution (Smayda 1989).

An additional source of mortality are fish "kills" which occur when schools of menhaden enter enclosed inshore bodies of water in such large numbers that they consume all available oxygen and suffocate. The mean lethal dissolved oxygen concentration for menhaden has been reported to be 0.4 mg/l (Burton et al. 1980). Bluefish are known to follow (or even chase) schools of menhaden inshore, feeding on them, and may contribute to their mortality by preventing them from leaving an area before the oxygen supply is depleted. Oxygen depletion is accelerated by high water temperatures which increase the metabolic rate of the fish; at the same time, oxygen is less soluble in warm water. Menhaden which die from low oxygen stress can immediately be recognized by the red coloration on their heads caused by bursting blood capillaries. Just before death, the fish can be seen swimming very slowly in a disoriented manner just below the surface of the water. This is a common phenomenon which has been observed throughout the range of the species. Menhaden spotter pilots have reported menhaden "boiling up" from the middle of dense schools, and washing up on the beach, apparently from oxygen depletion within the school. This phenomenon was observed during December, 1979 in the ocean off Atlantic Beach, North Carolina (M. Street, NC DMF, pers. comm.; as cited in ASMFC 1992). Smith (1999a) reported a similar event off Core Banks, North Carolina, in December 1997. Other species are not nearly as susceptible simply because they do not enter enclosed inshore waters in such large numbers.

Ecological relationships

Menhaden are extremely abundant in nearshore coastal waters because of their ability to directly utilize phytoplankton, which is the basic food resource in aquatic systems. Other species of marine fish are not equipped to filter such small organisms from the water. Consequently, such large populations of other species cannot be supported. Because menhaden are so abundant in nearshore coastal and estuarine waters, they are an important forage fish for a variety of larger piscivorous fishes, birds, and marine mammals. In ecological terms, menhaden occupy a very important link in the coastal marine food chain, transferring planktonic material into animal biomass. As a result of this, menhaden influence the conversion and exchange of energy and organic matter within the coastal ecosystem throughout their range (Peters and Schaaf 1981; Lewis and Peters 1984; Peters and Lewis 1984).

Because menhaden only remove planktonic organisms larger than 13-16 microns (7 microns for juveniles) from the water, the presence of large numbers of fish in a localized area could alter the composition of plankton assemblages (Durbin and Durbin 1975). Peters and Schaaf (1981) estimated that juvenile menhaden consumed 6-9% of the annual phytoplankton production in eight estuaries on the east coast, and up to 100% of the daily production in some instances. A large school of menhaden can also deplete oxygen supplies and increase nutrient levels in the vicinity of the school. Enrichment of coastal waters by large numbers of menhaden can be expected to stimulate phytoplankton production. Oviatt et al. (1972) measured ammonia concentrations (from excretion) inside menhaden schools that were five times higher than ambient levels 4.5 km away. At the same time, chlorophyll values increased by a factor of five over the same distance, indicating the grazing effect of the fish on the phytoplankton standing crop. Oxygen values were not significantly reduced by the fish, but were much more variable inside the schools than outside them.

Also, in a study of energy and nitrogen budgets (Durbin and Durbin 1981), food consumption rates, energy expenditures, and growth efficiency were examined. Results indicated that swimming speed, the duration of the daily feeding period, and the concentration of plankton in the water controlled the energy and nitrogen budgets for this species.

Predator/Prey Relationships

Atlantic menhaden are a major forage species for a wide number of important predatory fish species including, but not limited to, bluefish, striped bass, weakfish, king mackerel, bluefin tuna and sharks (Grant 1962; Reintjes and Pacheco 1966; Manooch 1973; DeVane 1978; Saloman and Naughton 1983; Juanes et al. 1993; Hartman and Brandt 1995a, 1995b). Marine mammals, including whales and porpoises, also have been reported to feed on menhaden (Bigelow and Schroeder 1953). Since Atlantic menhaden are eaten by predators in several ecosystems, they serve as a direct pelagic link in the food web between detritus and plankton and top predators (Rogers and Van Den Avyle 1989).

Ecological Role

Atlantic menhaden occupy two distinct types of feeding niches during their lifetime. They are sizeselective plankton feeders as larvae and filter feeders as juveniles and adults. Data on the food of larvae before they enter the estuary is currently unavailable. After entering the estuary, menhaden larvae appear to be extremely selective for prey of certain sizes and species. Larvae from the Newport River estuary, North Carolina, ranging in size from 26-31 mm TL (mean = 29 mm TL), consumed copepods and copepodites of only four taxa, which composed 99% by number and volume of their gut contents (Kjelson et al. 1975). These prey items, ranging from 300 to 1200 microns in length (mean = 750 microns), were eaten despite an abundance of copepod nauplii, barnacle larvae, and small adult copepods in plankton tows. Larvae that were offered copepods in the laboratory ignored all other food items, including *Artemia* and *Balanus* nauplii (June and Carlson 1971). Larval menhaden in the Newport River estuary, North

Carolina, fed primarily during daylight (Kjelson et al. 1975).

Juvenile and adult Atlantic menhaden strain particulates from the water column with a complex set of gill rakers. The rakers can sieve particles down to 7-9 microns (Friedland et al. 1984), including zooplankton, larger phytoplankton, and chain-forming diatoms. Biochemical analyses indicated that the gut contents of juveniles vary with prey availability; reliance on zooplankton decreases as the fish move from open waters to marshes (Jeffries 1975). Atlantic menhaden may also be capable of eating epibenthic materials (Edgar and Hoff 1976). Peters and Schaaf (1981) speculated that the annual phytoplankton and phytoplanktonbased production in east coast estuaries is not sufficient to support the juvenile Atlantic menhaden population during its residency and that the abundant organic detritus may be eaten in addition to copepods, etc. Lewis and Peters (1984) reported that juvenile Atlantic menhaden in North Carolina salt marshes primarily ate detritus.

The role of Atlantic menhaden in systems function and community dynamics has received little attention. Larvae and juveniles are seasonally important components of estuarine fish assemblages (Tagatz and Dudley 1961; Cain and Dean 1976; Bozeman and Dean 1980). Estimates of the mean daily ration for larvae range from 4.9% (Kjelson et al. 1975) to 20% (Peters and Schaaf 1981) of wet body weight.

Assimilation of ingested energy exceeded 80% for plant and animal material (Durbin and Durbin 1981). Because of their tremendous numbers, individual growth rates, and seasonal movements, these fish annually consume and redistribute large amounts of energy and materials, including exchanges between estuarine and shelf waters. Kjelson et al. (1975) noted that the copepod taxa preferred by larval menhaden and other species decreased from a mean value (2 years) of 81% to 48% of the total zooplankton biomass during the period of larval residence. They speculated that this decrease may be partly explained by larval feeding. Durbin and Durbin (1975) suggested that Atlantic menhaden in coastal waters may also alter the composition of plankton assemblages by grazing on certain size ranges.

Related Species and Hybrids

There are two species of menhadens that occur on the Atlantic coast, the Atlantic menhaden, *Brevoortia tyrannus*, and the yellowfin menhaden, *B. smithi*. Yellowfin menhaden range from Cape Lookout, North Carolina, to the Mississippi River delta (Ahrenholz 1991). The numbers of Atlantic menhaden relative to yellowfin menhaden become reduced proceeding southward along the Atlantic coast of Florida. A large amount of hybridization occurs between these two species and areas with pure strains of yellowfin menhaden have yet to be defined. As the relative density of Atlantic menhaden decreases as one proceeds southward, the number of Atlantic x yellowfin menhaden hybrids increases along with pure strains of yellowfin menhaden. Historically, the menhaden gill net fishery in Indian River, Florida, was dominated by yellowfin menhaden and the Atlantic x yellowfin menhaden hybrid (Dahlberg 1970). Yellowfin menhaden were traditionally targeted by specialized bait fisheries in Florida but this may have changed due to the net ban implemented by that state in 1995.

Abundance and status of stocks

(from the 2007 Update to the ASMFC FMP)

Status of the coastwide stock is determined based on the terminal year (2005) estimate relative to its corresponding limit (or threshold). Benchmarks have been estimated based on the results of the updated base run. The terminal year estimate of fishing mortality rate (F2+) was estimated to be 56% of its limit (and 91% of its target). Correspondingly, the terminal year estimate of population fecundity was estimated at 158% of its fecundity target (and 317% of its limit).

Hence, the coastwide stock is not considered to be overfished, nor is overfishing occurring.

The model used in the assessment (ASMFC 2006) calculates the benchmarks referred to above using the method described in Addendum I of Amendment 1 to the Menhaden FMP. The values used for benchmarks change each assessment as new data are added to the model. For a historical comparison of fishing mortality rate relative to its annually estimated threshold benchmark (F/Frep) and population fecundity relative to its annually estimated target (FEC/FECtarget), please see Figure 7.5 of the Stock Assessment Report.

The current coastwide estimate of F is near the lowest of the time series (1955-2005). However, recent recruitment estimates are of concern because they are below the 25th percentile [Table 6.2, ASMFC 2006]. Most of the concern stems from the decline in juveniles seen in Chesapeake Bay as documented by the Virginia and Maryland seine surveys. The Technical Committee has provided research recommendations in the past to better understand poor recruitment in Chesapeake Bay. Several projects are ongoing to address this issue.

The current stock assessment model has several limitations. It cannot provide details on the status of the menhaden stock in geographical areas smaller than coastwide. However, the Stock Assessment Subcommittee is considering how to incorporate a spatial component into the stock assessment prior to the next peer review. In addition, the model is not capable of addressing questions of multispecies interactions. Many ongoing research projects are being conducted and the MSVPA-X is being implemented to provide more information to answer those questions.

4.2.2 Striped Bass

Description and Distribution

(information from the ASMFC's Amendment 6 to the Striped Bass FMP, 2003)
The striped bass is a long-lived (at least up to 29 years of age, Merriman 1941, Secor et al. 1995) species which normally spends the majority of its adult life in the coastal estuaries or the ocean, migrating north and south seasonally, and ascending rivers to spawn in the spring. Mature female striped bass (age 4 and older) produce large quantities of eggs, which are fertilized by mature males (age 2 and older) as they are released into waters of riverine spawning areas. The fertilized eggs drift downstream with currents while developing, eventually hatching into larvae. The larvae and postlarvae begin feeding on microscopic animals during their downstream journey. After their arrival in the nursery areas, located in river deltas and the inland portions of the coastal sounds and estuaries, they mature into juveniles. They typically remain in coastal sound and estuaries for two to four years, and then migrate to the Atlantic Ocean. In the ocean, fish tend to move north during the summer and to the south during the winter. Important wintering grounds for the mixed stocks are located from offshore New Jersey as far south as Cape Hatteras, NC historically including the North Carolina sounds. With warming water temperatures in the

spring, the mature adult fish migrate to the riverine spawning areas to complete their life cycle. In general, the Chesapeake Bay spawning areas produce the majority of coastal migratory striped bass.

Atlantic coastal migratory striped bass live along the eastern coast of North America from the St. Lawrence River in Canada to the Roanoke River and other tributaries of Albemarle Sound in North Carolina. Stocks which occupy coastal rivers from the Tar-Pamlico River in North Carolina south to the St. Johns River in Florida are believed primarily endemic and riverine and apparently do not presently undertake extensive Atlantic Ocean migrations as do stocks from the Roanoke River north (Richkus 1990). Striped bass are also naturally found in the Gulf of Mexico from the western coast of Florida to Louisiana (Musick et al. 1997). Striped bass were introduced to the Pacific Coast using transplants from the Atlantic Coast in 1879. Striped bass also were introduced into rivers, lakes, and reservoirs throughout the US, and to foreign countries such as Russia, France and Portugal (Hill, 1989).

Reproduction

Spawning

Striped bass spawn in freshwater or nearly freshwater of Atlantic Coast rivers and estuaries. They spawn above the tide in mid-February in Florida but in the St. Lawrence River they spawn in June or July. The bass spawn in turbid areas as far upstream as 320 km from the tidal zone (Hill, 1989). The tributaries of the Chesapeake Bay are the primary spawning areas for striped bass, but other major areas include the Hudson River, Delaware Bay and the Roanoke River. Spawning is triggered by increased water temperature (Shepherd, 2000). Spawning occurs between 10 and 23 degrees Celsius, but optimal temperature for spawning is between 17 and 19 degrees Celsius. No spawning occurs below 13 degrees Celsius or above 22 degrees Celsius (Bain, 1982). Spawning is characterized by brief excursions to the surface by females surrounded by males, accompanied by much splashing. Females release eggs in the water. This is where fertilization occurs (Raney, 1952). Striped bass do not eat during spawning but they may eat heavily before and afterward. Spawning occurs in the late afternoon and early evening as well as late evening and early morning.

Development, growth and movement patterns

Eggs and larvae

An egg is only viable for about an hour for fertilization. Following fertilization the fertilized eggs are spherical, non-adhesive, and semi-buoyant and will harden within one to two hours at 18 degrees Celsius (Hill, 1989). Eggs need adequate water velocity, from either current or tidal flow, to keep them suspended in the water column.
Survival of striped bass eggs is dependent on environmental conditions. A temperature range of 17-19 degrees Celsius is important for egg survival as well as for maintaining appropriate dissolved oxygen

Yolk-sac larvae occur in open water but ultimately form schools and migrate inshore. The fin fold larvae and larger larvae have been collected in mid-channel areas near the bottom. Occurrence of fin fold larvae varied with the time of day and the depth of the river (Hill, 1989). Striped bass larvae usually stay in the open surface waters of estuaries.

There are three stages of larval development. These are: yolk-sac larvae, finfold larvae, and post-finfold larvae (Hill, 1989). The yolk-sac larvae occur right after hatching and this stage usually lasts for about 3 to 9 days. They are 2.0 to 3.7 mm in length and contain an easily identified yolk-sac. The yolk-sac is the main source of energy for the striped bass during this time. Also during this time, the mouth has not been formed and the eyes are not pigmented (Mansueti, 1958). This phase is finished when the yolk-sac is absorbed. The finfold phase lasts for about 11 days and the striped bass reach a length of 12mm. The last phase is the post-finfold larvae which lasts for about 20 to 30 days and the larvae reach a length of 20 mm (Bain, 1982).

Survival of the larvae depends on three main factors: temperature, salinity, and dissolved oxygen. The optimal temperature for larvae is 18 to 21 degrees Celsius, but temperatures of 12 to 23 degrees Celsius have been and can be tolerated (Bain, 1982). Studies have shown that striped bass larvae do better and have a higher survival rate when they are in low salinity waters rather than freshwater (Setzler et al. 1980). The third factor, dissolved oxygen, is equally critical for larvae as it was for the egg stage. A reduction in the dissolved oxygen level diminishes the chances of survival of the larvae (Turner and Farley, 1971). Other factors that also influence the survival of striped bass larvae include turbulence. While at first it is necessary for the larvae to reside in turbulent waters to maintain position, the larvae quickly become motile and then are able to maintain position on their own (Doroshev, 1970).

Juveniles

Juvenile striped bass are able to tolerate a wider range in environmental conditions. The habitat requirements for the juvenile fish are much like the habitat required for the adult bass. As the juvenile bass grow, they migrate to nearshore areas and then to higher salinity areas of an estuary (Raney, 1952). Juvenile striped bass prefer clean, sandy bottoms but they have been found in gravel beaches, rock bottoms, and soft mud areas. They are usually found in schools of as many as several thousand fish.

However, the location of the schools depends on the age of the fish (Hill, 1989).
Striped bass become juveniles at about 30 mm, when the fins are fully developed. At this point they resemble adults. Bluefish, weakfish, and other piscivores prey on striped bass (Buckel et al. 1999, Hartman and Brandt 1995b). The location of the striped bass determines the content of its diet. In the diet of the stock from the York River, where the salinity was higher than other places, the fish fed on mysids. In the James River, where the salinity was lower, the same sized fish fed mostly on insects. This and other evidence showed that there is a relationship between the diet of the stock of striped bass and the salinity of the habitat in which the fish live (Setzler et al.1980).

Adults

Mature adult striped bass leave the estuaries and migrate along the coast where they have similar temperature and dissolved oxygen requirements as juvenile bass (Bain, 1982). Tagging studies indicate that fish from all stocks range widely along the Atlantic Coast, generally remaining in state (0-3 miles) waters but in some areas entering the Exclusive Economic Zone (EEZ; 3-200 miles). Studies are presently underway, using Geographic Information Systems (GIS) analysis, to characterize the habitats used by striped bass when they are in nearshore waters during the summer, fall and winter months. Schools of striped bass which winter off North Carolina use nearshore habitats from the surf zone to beyond the state-EEZ boundary line.

Migration Patterns

Migration of striped bass occurs at juvenile and adult stages. Migratory patterns for all life stages vary by location, but in general juveniles migrate downstream in summer and fall, while adults migrate upriver to spawn in spring, afterwards returning to the ocean and moving north along the coast in summer and fall, and south during the winter (Shepherd, 2000).

Juvenile striped bass migration varies by locations. In Virginia, the movement of young bass during their first summer was downstream into waters of higher salinity (Setzler et al. 1980). In the Hudson River, the bass began migrating in July. Migration was documented through an increase in the number of juvenile striped bass caught along the beaches and subsequent decline in the numbers in the channel areas after mid-July. Downstream migration continues through late summer, and by the fall, juveniles start to move offshore into Long Island Sound (Raney, 1952).

Juvenile striped bass rarely complete coastal migrations, but even though fish that are under the age of two are non-migratory, many do leave their birthplaces when they are two or more years old. From Cape Hatteras, North Carolina, to New England, fish may migrate in groups along the coast. They migrate north in the summer and south in the winter, however, the extent of the migration varies between sexes and populations (Hill, 1989). Larger bass, typically the females, tend to migrate farther distances. However, striped bass are not usually found more than 6 to 8 km offshore (Bain, 1982). These coastal migrations are not associated with spawning and usually begin in early spring, but this time period can be prolonged by the migration of bass that are spawning.

Some areas along the coast are used as wintering grounds for adult striped bass. The inshore zones between Cape Henry, Virginia, and Cape Lookout, North Carolina, serve as the wintering grounds for the migratory segment of the Atlantic coast striped bass population (Setzler et al. 1980). There are three groups of fish that are found in nearshore ocean waters of Virginia and North Carolina between the months of November and March, the wintering period. These three groups are bass from Albemarle and Pamlico Sounds, North Carolina, fish from the Chesapeake Bay, and large bass that spend the summer in New Jersey and north (Holland & Yelverton, 1973). Based on tagging studies conducted under the auspices of the Southeast Area Monitoring and Assessment Program (SEAMAP) each winter since 1988, striped bass wintering off Virginia and North Carolina range widely up and down the Atlantic Coast, at least as far north as Nova Scotia, and represent all major migratory stocks (U.S. Fish and Wildlife Service and National Marine Fisheries Service, unpublished data).

Ecological relationships

Striped bass larvae feed only on mobile planktonic food. They pass the prey repeatedly in order to aim and rush at the prey successfully. It was found that the first successful feeding of a 9-day-old larvae occurred at concentrations of 15,000 Cyclops nauplii and copepodites per liter. By the 11th and 12th day, when the air bladder of the larvae is filled, the prey concentration may be reduced to 2,000 and 5,000 per liter. By days 40 to 50, the striped bass feed on plankton and epibenthos and by days 50 to 80, the food of the striped bass larvae includes mysid shrimp, gammarid amphipods, and fish up to 20 mm in length (Doroshev, 1970).

Abundance and status of stocks

At the 2006 Annual Winter Board Meetings, the Striped Bass Technical Committee submitted a request to the Striped Bass Management Board to bypass the 2006 annual update stock assessment in favor of having more time to prepare new methods and better data for the 2007 benchmark stock assessment. The Board approved this request, such that the most recent data on the status of the stock are derived from the 2005 stock assessment.

The estimate of total abundance for January 1, 2005 from the ADAPT VPA was 65.3 million age-1 and older fish. This estimate is about 1.2 million fish lower than the 2004 abundance but 10% higher than the average stock size for the previous five years. Population estimates were calculated for the first time this year from tag-based F estimates using the catch equation. The 2004 population estimate of age 3+ fish was 48.5 million fish; that is, roughly 8 million fish higher than the 2003 estimate. This estimate is higher than the ADAPT VPA estimate of 39.2 million age 3+ fish at the beginning of 2004. This discrepancy in population estimates between the two approaches increased with older age classes. The tag-based approach estimated the 2004 population of age 7+ fish to be 17.1 million, whereas the ADAPT VPA estimated the age 7+ population to number 9.4 million fish. The abundance of older fish (age 13+) in the stock estimated from the ADAPT VPA increased from 382,000 fish at the beginning of 2003 to 547,000 fish on January 1, 2005.

The female spawning stock biomass for 2004 was estimated (from the VPA) at 54.8 million pounds, which is above the recommended biomass threshold of 30.9 millions pounds (13,956 mt) and the target SSB of 38.6 million pounds (17,500 mt). SSB has declined by 9% since 2002 when it peaked at 60.6 million pounds.

Recruitment of the 2004 cohort for all stocks combined is 12.7 million age-1 fish, which is close to the average age-1 recruitment observed since the stocks were declared recovered in 1995.

Based on VPA results, average age 8-11 fishing mortality in 2004 was estimated at F=0.40 which is below the Amendment 6 threshold of 0.41 but exceeds the target of 0.30. However, it was the consensus of the Technical Committee members that this was likely an overestimate of the 2004 F given the uncertainly with the terminal year estimate from the VPA and the systematic positive bias observed in the retrospective analysis. The 2003 value of F from the 2005 VPA is 0.29, which is substantially lower than the terminal year F from the 2004 VPA run of 0.62. This is due not only to the addition of another year’s worth of data, but to the modified suite of tuning indices used in the 2005 VPA and the inclusion of wave 1 (Jan./Feb.) estimates of recreational harvest mortality from NC and VA for 1996 – 2004 (see Data and Uncertainty section in Plan Review Document available at www.asmfc.org).

The 2004 tag-based estimates of F using stock-specific, model-based estimates of fishing mortality and a constant M of 0.15 were as follows. For fish greater than 28 inches, the coast-wide average F was estimated as 0.29 and specific tagging program values ranged from 0.02 in the New York ocean haul survey (NYOHS) to 0.31 in the Maryland (MD) tagging program. This value was similar to the VPA F weighted by N value for age 7-11 fish of 0.32. For fish greater than 18 inches, the coast-wide average F was estimates as 0.29 and specific tagging program values ranging from 0.06 in the Virginia spawning stock (VARAP) program to 0.68 in the New

Jersey Delaware Bay (NJDEL) program. This tag-based F estimate was greater than the VPA F weighted by N value for age 3-11 fish of 0.15.

The 2004 variable M tag-based estimates of F for fish greater than 28 inches indicated the coast-wide average F was 0.14, and specific tagging program values ranged from 0.09 in the VARAP program to 0.26 in the Delaware and Pennsylvania (DE-PA) tagging program. These F estimates were less than the VPA F weight by N, for age 7-11 fish, of 0.32. For fish greater than 18 inches, the coast-wide average was 0.11, and specific tagging program F estimates ranged from 0.05 in three different programs to 0.17 in the MD program. This tag-based F estimate is similar to the VPA F weighted by N value for age 3-11 fish of 0.15. Chesapeake Bay fishing mortality in 2004 was estimated as F=0.16 by the direct enumeration study. This F represents mortality during the June 2003 – June 2004 period, so it is not directly comparable to the average, weighted (by N) VPA calendar-year F on age 3-8 striped bass that is equal to 0.12.

4.2.3 Alewife

Description and Distribution

(all information below from draft ASMFC alewife doc)
The alewife, *Alosa pseudoharengus*, is an anadromous, highly migratory, euryhaline, pelagic, schooling species. Both alewife and blueback herring are often referred to as "river herring," a collective term for these two species, which often school together (Murdy et al. 1997). Although this term is often used generically in commercial harvests and no distinction is made between the two species (ASMFC 1985), landings are reported as alewife (Dixon 1996).

The alewife spends the majority of its life at sea, returning to freshwater river systems along the U.S. Atlantic Coast to spawn. There are also some alewife populations that have been successfully introduced into landlocked freshwater systems, such as the Great Lakes and some of the Finger Lakes of New York (Scott and Crossman 1973), as well as those that have been stocked in man-made reservoirs (Bigelow and Schroeder 2002). Their historical coastal range was South Carolina to Labrador and northeastern Newfoundland (Berry 1964; Winters et al. 1973; Burgess 1978), but more recent surveys indicate that they do not occur in the southern range beyond North Carolina (Rulifson 1982; Rulifson et al. 1994). Alewife from the southernmost range are capable of migrating long distances (over 2000 km) in ocean waters of the Atlantic seaboard and patterns of migration may be similar to those of American shad (Neves 1981). Although alewife and bluebacks co-occur throughout much of their range, alewife are typically more abundant than bluebacks in the northern part of their range (Schmidt et al. 2003).

Several long-term data sets were recently analyzed to determine the current status of alewife in large river systems along the Atlantic Coast, including the Connecticut, Hudson, and Delaware rivers. These analyses suggest that alewife are showing signs of overexploitation in all of these rivers, including reductions in mean age, decreases in percentage of returning spawners, and decreases in abundance. Researchers did note that some runs in the northeastern U.S. and Atlantic Canada have been increasing recently (Schmidt et al. 2003). Alewife appear to be doing well in inland waters, colonizing many freshwater bodies, including all five Great Lakes (Waldman and Limburg 2003). Much of the research regarding specific environmental requirements of alewife, such as temperature, dissolved oxygen, salinity, and pH has been conducted on landlocked populations, not anadromous stocks therefore, data should be interpreted with discretion.

Development, growth and movement patterns

Spawning

Adult alewife populations migration to spawning grounds in freshwater and brackish waters progresses seasonally from south to north, with populations further north returning as the season progresses (and water temperatures increase). Fish typically begin spawning from late February in their southern range and June in their northern range (Neves 1981; Loesch 1987). Neves (1981) suggested that alewife migrate from offshore waters north of Cape Hatteras, encountering the same thermal barrier as American shad, then move south along the coast for fish homing to South Atlantic rivers; northbound pre-spawning adults head north along the coast (Stone and Jessop 1992). They spawn in rivers as far south as North Carolina and as far north as the St. Lawrence River, Canada (Neves 1981). Fish may spawn as late as June in the southern range and through August in their northern range (Marcy 1976a). Spawning is triggered most strongly by a change in the water temperature. Movement upstream may be controlled by water flow, with increased movement occurring during higher flows (Collins 1952; Richkus 1974). Although adult alewife will move upstream at various times, peak migration typically occurs during the day, between dawn and noon, and also from dusk to midnight (Richkus 1974; Rideout 1974; Richkus and Winn 1979). High midday movement is restricted to overcast days, and nocturnal movement occurs when water temperatures are abnormally high (Jones et al. 1978). Males are first to arrive at the mouths of spawning rivers, prior to the arrival of females (Cooper 1961; Tyus 1971; Richkus 1974.

There is strong evidence that suggests that alewife home to their natal rivers to reproduce, but some colonize new areas; they have also been found to reoccupy systems from which they have been extirpated (Havey 1961; Thunberg 1971; Messieh 1977; Loesch 1987). Messieh (1977) found that alewife strayed considerably to adjacent streams in the St. Johns River, Florida, particularly during the prespawning period (late winter, early spring), not during the spawning run. It appears that olfaction is the primary means for homing behavior (Ross and Biagi 1990).

In general, alewife are less selective in choosing their spawning sites than blueback herring. Alewife will select slow-moving sections of rivers or streams to spawn, where the water may be as shallow as 30 cm (Jones et al. 1978). They may enter lakes or ponds, including freshwater coves behind barrier beaches (Smith 1907; Belding 1920; Leim and Scott 1966; Richkus 1974; Bigelow and Schroeder 2002). Alewife often spawn in ponds that form the headwaters of most coastal streams in New England and Nova Scotia (Loesch 1987). They are typically more abundant than bluebacks in rivers where there are well-developed headwater ponds in New England. In rivers where headwater ponds are absent or poorly-developed, alewife may be most abundant further upstream in headwater reaches, while bluebacks may select the mainstream proper for spawning (Ross and Biagi 1990). In tributaries of the Rappahannock River, Virginia, upstream areas were found to be more important than downstream areas for spawning alewife (O’Connell and Angermeier 1997). Although earlier studies suggested that alewife will ascend further upstream than bluebacks (Hildebrand 1963; Scott and Crossman 1973), Loesch (1987) noted that both species have the ability to ascend rivers far upstream.

Alewife are noted for their greater ability than American shad for navigating suitable fishways (Dominy 1973). In rivers where dams are an impediment, spawning may occur in shore-bank eddies or deep pools (Loesch and Lund 1977). Alewife will generally spawn 3-4 weeks before blueback herring in areas where they co-occur; however, there may be considerable overlap (Loesch 1987) and peak spawning periods may differ by only 2-3 weeks (Jones et al. 1978). In a tributary of the Rappahannock River, Virginia, O'Connell and Angermeier (1997) found that blueback eggs and larvae were more abundant than those of alewife, but alewife used the stream over a longer period of time. They also reported that there was only a 3-day overlap of spawning by alewife and bluebacks. Although it has been suggested that alewife and bluebacks select separate spawning sites in sympatric areas to reduce competition (Loesch 1987), O'Connell and Angermeier (1997) reported that the two species used different spawning habitat. They suggested that there was a temporal, rather than spatial segregation that minimized the competition between the two species.

Alewife may spawn throughout the day, but do so more commonly at night (Graham 1956). One female fish and as many as 25 male fish broadcast their eggs and sperm simultaneously just below the surface of the water or over the substrate (Belding 1920; McKenzie 1959; Cooper 1961). Spawning lasts 2-3 days for each group or "wave" of fish that arrives (Cooper 1961; Kissil 1969; Kissil 1974), with older and larger fish usually spawning first (Belding 1920; Cooper 1961; Libby 1981, 1982). Upon spawning, spent fish return quickly downstream (Bigelow and Schroeder 2002).

Alewife are repeat spawners, with some fish spawning up to seven or eight times in a lifetime (Jessop et al. 1983). It is not clear whether there is a clinal trend from south to north for repeat spawners (more repeat spawners in the north than the south) (Klauda et al. 1991), or there is a general overall value (i.e. 30-40% repeat spawners throughout their range) (Richkus and DiNardo 1984).

Tables 4.2-1 and 4.2-2 present percentages of repeat spawners observed in several areas of the species range and spawning seasons, respectively

Table 4.2-1. Percentages of repeat spawners by area for alewife, *Alosa pseudoharengus*.

State	Percentage of repeat spawners	References
Nova Scotia	60%	O'Neill 1980
Maryland	30-72%	Weinrich et al. 1987; Howell et al. 1990
York River, Virginia	61%	Joseph and Davis 1965
North Carolina	13.7% (1993); 61% (1995)	Winslow 1995

Table 4.2-2. Reported spawning seasons for alewife, *Alosa pseudoharengus*, by state or region.

State or Region	Reported Spawning Season	References
Bay of Fundy tributaries	late April or early May	Leim and Scott 1996; Dominy 1971, 1973

Gulf of St. Lawrence tributaries	late May or early June	Leim and Scott 1996; Dominy 1971, 1973
Maine	late April to mid-May	Rounsefell and Stringer 1943; Bigelow and Schroeder 1953; Havey 1961; Libby 1981
Massachusetts	early to mid-April	Belding 1920; Bigelow and Schroeder 1953
Mid-Atlantic and southern New England	late March or early April	Cooper 1961; Kissil 1969; Marcy 1969; Smith 1971; Saila et al. 1972; Richkus 1974; Zich 1978; Wang and Kernehan 1979
Chesapeake Bay region	mid-March	Jones et al. 1978; Loesch 1987
North Carolina	late February	Holland and Yelverton 1973; Frankensteen 1976

Adults will typically spend 2 to 4 years at sea before returning to their natal rivers to spawn (Neves 1981). The majority of adults reach sexual maturity at ages-3, 4, or 5, although some adults from North Carolina (Richkus and DiNardo 1984) returned to spawn at age-2 (Jessop et al. 1983). The oldest fish recorded in North Carolina were age-9 (Street et al. 1975; Johnson et al. 1979), and age-10 fish have been caught in New Brunswick (Jessop et al. 1983) and Nova Scotia (O'Neill 1980). Kissil (1974) found that alewife spawning in Bride Lake, Connecticut, spent 3 to 82 days on the spawning grounds, while Cooper (1961) reported that most fish left within 5 days of spawning. Kissil (1974) suggests that alewife might spawn more than once in a season.

Temperature

There is some discrepancy regarding minimum spawning temperatures for alewife. Although running ripe fish of both sexes have been reported at temperatures as low as 4.2°C in the Chesapeake Bay area (Mansueti and Hardy 1967), it is suggested that the minimum temperature at which adults spawn is 10.5°C (Cianci 1965; Loesch and Lund 1977). Marcy (1976a) suggested that the majority of spawning activity in the lower Connecticut River probably occurs at temperatures between 7.0-10.9°C. There does appear to be a broad range of temperatures for spawning in some regions, such as the Chesapeake Bay, where reported ranges are between 10.5-21.6°C (Jones et al. 1978), and 11-19°C in the Patuxent River, Maryland (Mowrer 1982). Cooper (1961) noted that upstream migration ceased in a Rhode Island stream when temperatures reached 21°C, while Edsall (1970) reported that spawning ceases altogether at 27.8°C. Peak spawning has been reported to occur at 13°C in North Carolina (Tyus 1974) and 14.0-15.5°C in Rhode Island (Jones et al. 1978). Although quantitative data were lacking, Pardue (1983) suggested that the optimum spawning temperature for alewife is 15-20° C, based on available information.

Adults have been collected in temperatures ranging from 5.7-32°C (Marcy 1976b; Jones et al. 1978). Upper incipient lethal temperatures (temperature at which 50% of the population survives) ranged from 23.5-24.0°C for adults that were acclimated at temperatures of 10, 15, and 20°C (Otto et al. 1976). Another study reported upper incipient lethal temperatures of 29.8 and 32.8°C at acclimation temperatures of 16.9 and 24.5°C, respectively (Stanley and Holzer 1961).

McCauley and Binkowski (1982) reported an upper incipient lethal temperature of 31-34°C after acclimation at 27°C for a northern population of adults.

The lower incipient lethal temperature range for adults acclimated at 15.0 and 21.0°C is between 6-8°C (Otto et al. 1976). At temperatures below 4.5°C, normal schooling behavior was significantly reduced for adult alewife from Lake Michigan (Colby 1973). No fish survived below 3°C, regardless of acclimation temperature (Otto et al. 1976).

In general, alewife may prefer cooler water, and northern populations may be more cold tolerant than other migratory anadromous fish (Stone and Jessop 1992). Richkus (1974) showed that the response of migrating adults to a particular hourly temperature was determined by its relationship to a changing baseline temperature and not on the basis of its absolute value. Stanley and Colby (1971) found that decreased temperatures (from 16 to 3°C at a rate of 2.5°C per day) reduced adult alewife ability to osmoregulate. Adults were also shown to survive temperature decreases of 10°C, regardless of acclimation temperature, if the temperature did not drop below 3°C (Otto et al. 1976).

Depth

Water depth in spawning habitat may be a mere 6 inches (15.2 cm) deep (Bigelow and Schroeder 1953; Rothschild 1962), or as deep as 10 feet (3 m) (Edsall 1964); however, it is typically less than 1 m (3.3 ft) (Murdy et al. 1997). Adults may utilize deeper water depths in order to avoid high light intensities (Richkus 1974).

Salinity

While it is known that alewife can adjust to a wide range of salinities, experimental evidence is lacking (Klauda et al. 1991). Richkus (1974) found that adults that were transferred from freshwater to saline water (32 ppt) and vice versa experienced zero mortality. Leim (1924) studied the life history of American shad in its northern range and noted that they do not ascend far beyond the tidal influence of the river, yet alewife migrate as far upstream as they can travel. He concluded that alewife may be less dependent on salt water for development. Also, unlike American shad, some populations of alewife have become landlocked and are not dependent on salt water (Scott and Crossman 1973).

Water Velocity/Flow

Increased movement upstream occurs during higher water flows (Collins 1952; Richkus 1974), while spawning typically takes place in quiet, slow-moving waters for spawning alewife (Smith 1907; Belding 1921; Marcy 1976a).

Differential selection of spawning areas has been noted by some researchers. For example, in Connecticut, alewife choose slower moving waters in Bride Lake (Kissil 1974) and Higganum and Mill creeks, while bluebacks select fast-moving waters in the upper Salmon River and Roaring Brook (Loesch and Lund 1977). In other areas where alewife and bluebacks are forced to spawn in the same vicinity due to blocked passage (Loesch 1987), alewife generally spawn along shorebank eddies or deep pools, whereas, bluebacks will typically select the main stream flow for spawning (Loesch and Lund 1977). In North Carolina, they select slow moving streams and oxbows (Street et. al. 2005).

Bottom composition

The spawning habitat of alewife can range from sand, gravel or coarse stone substrates, to submerged vegetation or organic detritus (Edsall 1964; Mansueti and Hardy 1967; Jones et al. 1978). Boger (2002) found that river herring spawning areas along the Rappahannock River, Virginia had substrates that consisted primarily of sand, pebbles, and cobbles (usually associated with higher-gradient streams), while areas with little or no spawning were dominated by organic matter and finer sediments (usually associated with lower-gradient streams and comparatively more agricultural land use).

Pardue (1983) evaluated studies of cover component in spawning areas, suggesting that substrate characteristics and associated vegetation were a measure of the ability of a habitat to provide cover to spawning adults, their eggs, and developing larvae. In high flow areas, there is little accumulation of vegetation and detritus, while in low flow areas, detritus and silt accumulate and vegetation has the opportunity to grow. Based on a review of the literature, Pardue suggested that substrates with 75% silt or other soft material containing detritus and vegetation, and sluggish waters are optimal for alewife.

pH

There are only a few studies of pH sensitivity in alewife (Klauda et al. 1991). Byrne (1988) found that the average pH level was 5.0 in several streams in New Jersey where alewife spawning was known to occur. Since blueback herring did not spawn in these streams, he suggested that early life history stages of alewife were more tolerant to acidic conditions than bluebacks. Laboratory tests found that fish from those streams could successfully spawn at a pH as low as 4.5. In one pH change study, adults tolerated changes up to 0.8 units within a range of pH 6.5-7.3 (Collins 1952). When aluminum pulses were administered in the laboratory, critical conditions for spawning could occur during an acidic pulse between pH 5.5 and 6.2 with concomitant concentrations of total monomeric aluminum ranging from 15-137 µg/L for a pulse duration of 8-96 h (Klauda 1989). Klauda et al.(1991) suggested a range of 5-8.5 as suitable for alewife eggs, but no range was provided for spawning.

Dissolved Oxygen

There is little information regarding sensitivities of various life history stages of alewife to dissolved oxygen (DO) (Klauda et al. 1991). Adults that were exposed to DO ranging from 2.0-3.0 mg/L for 16 hours in the laboratory experienced a 33% mortality rate (Dorfman and Westman 1970). They were able to withstand DO concentrations as low as 0.5 mg/L for up to five minutes, as long as a minimum of 3.0 mg/L was available, thereafter. Jones et al. (1988) suggested that the minimum DO concentration for adults is 5.0 mg/L.

Egg and Larval Habitat

Eggs may hatch anywhere from 50 to 360 hours, depending on water temperature (Fay et al. 1983), but hatch most often within 80-95 hours (Edsall 1970). Fertilized eggs remain demersal and adhesive for several hours (Mansueti 1956; Jones et al. 1978), after which they become pelagic and are transported downstream (Wang and Kernehan 1979). Marcy (1976a) observed eggs more often nearer the bottom than at the surface in the Connecticut River.

Within 2 to 5 days, the yolk-sac is absorbed and larvae will begin feeding exogenously (Cianci 1965; Jones et al. 1978). Post-yolk-sac larvae are positively phototropic (Odell 1934; Cianci 1965). Dovel (1971) observed larvae near or slightly downstream of presumed spawning areas in the Chesapeake Bay, only where the water was less than 12 ppt salinity (Dovel 1971). Larvae were also found in or close to observed spawning areas in Nova Scotia rivers in relatively shallow water (2 m) over sandy substrate (O'Neill 1980).

Temperature

In general, average time to median hatch varies inversely with temperature. Edsall (1970) reported the following hatch times for alewife eggs taken from Lake Michigan: 2.1 days at 28.9° C, 3.9 days at 20.6°C, and 15 days at 7.2°C. Reported hatch times in saltwater by various researchers are comparable: 2-4 days at 22°C (Belding 1921); 3 days at 23.8-23.9°C and 26.7-26.8° C, and 3-5 days at 20° C (Mansueti and Hardy 1976); and 6 days at 15.5°C (Bigelow and Welsh 1925). Laboratory tests conducted by Kellogg (1982) found that eggs from the Hudson River, New York achieved maximum hatching success at 20.8° C. Edsall (1970) reported some hatching at temperatures as low as 6.9°C for eggs from Lake Michigan (below 11° C caused a high percentage of deformed larvae) and as high as 29.4°C, but optimum hatching occurred between 17.2-21.1°C. Although this was the suggested optimal range, Edsall determined that considerable hatch rates and proper development could occur over a broader range from 10.6°C to 26.7° C. In the upper Chesapeake Bay, alewife eggs were collected where temperatures ranged from 7-14°C and 70% of these eggs were found where temperatures were between 12-14°C (Dovel 1971).

Edsall (1970) correlated egg mortality with incubation temperature. He developed an equation for predicting incubation time for alewife eggs from temperature, which is as follows:

$$t = 6.335 \text{ x } 106 \, (T) -3.1222$$

where t = time in days
T = incubation temperature in degrees °F

Several investigations have been conducted to determine the effects of temperature on alewife eggs. One study examined the effects of power plants on alewife eggs found that they suffered no significant mortality or abnormal egg development, after being acclimated at 17°C, then exposed to 24.5°C for 6-60 minutes (Schubel and Auld 1972). Koo et al. (1976) determined that the critical thermal maximum (CTM) for alewife eggs was 35.6°C, acclimated at 20.6°C, with a critical exposure period of 5-10 minutes.

Larval alewife were collected at water temperatures between 4-27°C in the upper Chesapeake Bay although 98% were collected at water temperatures 25° C (Dovel 1971). In laboratory experiments, larvae acclimated at 18.6°C withstood temperatures as high as 33.6°C for one hour (Koo et al. 1976). The upper temperature tolerance limit for yolk-sac larvae from the Hudson River, New York, acclimated at 14-15°C was 31°C (Kellogg 1982); their preferred range when acclimated at 20°C appears to be 23-29°C (Ecological Analysts Inc. 1978; Kellogg 1982).

Although alewife eggs taken from Lake Michigan were able to hatch at temperatures as low as 6.9°C, larvae held at incubation temperatures below 10.6°C had a 69% rate of deformities

(Edsall 1970). Dovel (1971) found that growth rates of alewife larvae were much lower in freshwater compared to saltwater (1.0-1.3 ppt) at 26.4°C. He also observed substantial growth increases with small temperature increases above 20.8°C. Average daily weight gain for alewife larvae has been directly correlated to water temperature. The maximum larval growth rate was 0.084 g/day at 29.1°C; net gain in biomass (a function of survival and growth) was highest at 26.4° C (Kellogg 1982).

Based on Kellogg's (1982) observations that the optimum growth temperature (26°C) exceeds peak spawning temperatures by about 10-13°C, he suggested that it is not likely that survival and early development of young alewife would be threatened by rapid warming trends following spawning or by moderate thermal discharges. He further indicated that temperature elevations above normal following spawning and hatching would probably be beneficial to alewife populations.

In their review of the literature, Klauda et al. (1991) provided optimal ranges for both the prolarva and postlarva life stages for alewife. They suggested a suitable range of 8-31°C and 14-28°C, and an optimum range of 15-24°C and 20-26°C, respectively, for these two life stages.

Salinity

Alewife eggs have been collected in the upper Chesapeake Bay in salinities between 0-2 ppt; however, almost 99% of these eggs were collected where the salinity was 0 ppt. Larvae were collected where salinities ranged from 0-8 ppt, but again, most (82%) were collected in freshwater (Dovel 1971). Klauda et al. (1991) suggested that the optimal range for egg development for alewife is 0-2 ppt.

Growth rates of larval alewife were demonstrated to be considerably faster in saltwater (1.0-3.0 ppt) compared to growth in freshwater, at temperatures of 26.4°C (Klauda et al. 1991). Later review by Klauda et al. (1991) suggested that the optimal range for the prolarva life stage was 0-3 ppt and for the postlarva life stage was 0-5 ppt.

Water Velocity/Flow

Sismour (1994) observed a rapid decline in abundance of early preflexion river herring larvae (includes both alewife and blueback herring) in the Pamunkey River, Virginia following high river flow in 1989. He speculated that high flow led to increased turbidity, which reduced prey visibility, leading to starvation of larvae. O'Connell and Angermeier (1997) found that current velocity (and DO) were the strongest predictors of alewife early egg presence in a Virginia stream. Findings from Rhode Island suggest the importance of river flow to alewife stocks. Drought conditions in the summer of 1981 were strongly suspected of impacting the 1984 year class, which was only half of its expected size (ASMFC 1985). In tributaries of the Chowan system, North Carolina, water flow was related to recruitment of larval river herring (O'Rear 1983).

Bottom composition

As with spawning habitat, Pardue (1983) suggested that egg and larval habitat with substrates with 75% silt or other soft material containing detritus and vegetation was optimal.

pH and aluminum
Klauda et al. (1991) suggest that a range of pH 5.0-8.5 for both the alewife egg and prolarva life stage was preferred. Klauda (1987) suggested that during an acidic pulse between pH 5.5.-6.2 critical conditions associated with > 50% direct mortality could occur. Klauda et al. (Klauda et al. unpublished, cited in Klauda et al. 1991) found that larvae subjected to a single 24-hour, acid-only pulse of pH 4.5 experienced no mortality, while those subjected to a 24-hour single acid pulse and 446 µg/L inorganic monomeric aluminum pulse suffered a 96% mortality rate. A single 12-hour acid-only pulse of 4.0 resulted in 38% mortality.

Dissolved Oxygen
Jones et al. (1988) determined that the minimum DO concentration requirement for eggs and larvae is 5.0 mg/L. O'Connell and Angermeier (1997) found that DO (and current velocity) were the strongest predictors of alewife early egg presence in a Virginia stream.

Suspended solids/turbidity
Alewife eggs subjected to suspended solids concentrations up to 1000 mg/L did not exhibit a reduction in hatching success (Auld and Schubel 1978). Despite these results, high levels of suspended sediment may significantly increase rates of egg infections from naturally occurring fungi, as was witnessed in earlier experiments (Schubel and Wang 1973), which can lead to delayed mortalities (Klauda et al. 1991).

Juveniles
In North Carolina, juveniles may spend the summer in the lower ends of rivers where they were spawned (Street et al. 1975). In the Chesapeake Bay, juveniles can be found in freshwater tributaries in spring and early summer, but may head upstream in the summer when saline waters encroach on their nursery grounds (Warriner et al. 1970). Some juveniles in the Chesapeake Bay remain in brackish water through the summer (Murdy et al. 1997).

Juveniles in the Hudson River usually remain in freshwater tributaries until June (Schmidt et al. 1988). Juvenile alewife were found to be most abundant in inshore areas at night in the Hudson River, compared to inshore abundance of American shad and blueback herring during the day (McFadden et al. 1978; Dey and Baumann 1978). Hudson River juveniles were observed in shallow portions of the upper and middle estuary in late June and early July, where they remained for several weeks before moving offshore as they grew (Schmidt et al. 1988). They typically spend 3-9 months in their natal rivers before returning to the ocean (Kosa and Mather 2001).

In summer in the Potomac River, juveniles are abundant near surface waters during the day, but shifted to mid-water and bottom depths in September, where they remained until they emigrated in November (Warriner et al. 1970). Juvenile alewife respond negatively to light and follow diel movements similar to blueback herring. There appears to be some separation between the alewife and blueback as they emigrate from nursery grounds in the fall, most notably at night, when alewife can be found more frequently at midwater depths, while bluebacks are found mostly at the surface (Loesch and Kriete 1980). This may reduce interspecific competition for food (Loesch 1987), given that their diets are similar (Davis and Cheek 1966; Burbidge 1974; Weaver 1975).

Once water temperatures begin to drop in the late summer through early winter (depending on geographic area), juveniles start heading downstream, initiating their first phase of seaward migration (Pardue 1983; Loesch 1987). Some researchers found that movement of alewife peaked in the afternoon (Richkus 1975a; Kosa and Mather 2001), while others found that it peaked at night (Stokesbury and Dadswell 1989). Migration downstream is also prompted by changes in water flow, water levels, precipitation, and light intensity (Cooper 1961; Kissil 1974; Richkus 1975a, 1975b; Pardue 1983). Other researchers have suggested that water flow plays little role in providing the migration cue under riverine conditions. Rather, timing is triggered more by water temperature and moon phases that provide dark nights, generally new and quarter moons (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989). Stokesbury and Dadswell (1989) found that alewife remained in the offshore region of the Annapolis estuary, Nova Scotia for almost a month before the correct migration cues triggered emigration. Large juveniles begin moving downstream before smaller juveniles (Schmidt et al. 1988), moving to saline waters before they begin their seaward migration (Loesch 1969; Marcy 1976a; Loesch and Kriete 1980).

Richkus (1975a) observed waves of juveniles leaving following environmental changes but the number of fish leaving was unrelated to the level of magnitude of change. Most fish (60-80%) emigrated during a small percentage (7-8%) of available days. These waves also lasted 2 to 3 days, regardless of the degree of environmental change. Others have also observed the majority (i.e., >80%) of river herring emigrating in waves (Cooper 1961; Huber 1978; Kosa and Mather 2001). Richkus (1975a) also noted that in some instances, high abundances of juveniles may trigger very early (i.e., summer) emigration of large numbers of small juveniles from the nursery area, which is likely a response to a lack of forage. Juvenile migration of alewife is about one month earlier than that of blueback herring (Loesch 1969; Kissil 1974).

Although most juveniles emigrate offshore their first year, some overwinter in the Chesapeake (Hildebrand 1963) and Delaware bays (Smith 1971). Marcy (1969) suggests that many juveniles (age-1+) spend their first winter close to the mouth of their natal river because he found in the lower portion of the Connecticut River in early spring. Some juvenile alewife may remain in deep estuarine waters through the winter (Hildebrand and Schroeder 1928). There is some indication that alewife in northern states may remain in inshore waters for one to two years (Walton 1981). Since juvenile river herring cannot survive water temperatures of 3°C or below (Otto et al. 1976), they likely do not overwinter in coastal systems where temperatures are below 3°C (Kosa and Mather 2001).

Temperature

Juveniles tolerate a broad range of temperatures. Juvenile alewife have been collected in water temperatures between 4-27°C in the upper Chesapeake Bay. Ninety-eight percent of those were collected at 25°C (Dovel 1971). In the Cape Fear River, North Carolina, juveniles have been collected in seasonally in temperatures ranging from 13.5-29°C (Davis and Cheek 1966). The upper lethal temperature for juvenile alewife is about 30°C (McCauley and Binkowski 1982). Young-of-the-year alewife have critical thermal maxima (CTM) that are 3-6°C higher than adults (Otto et al. 1976).

In Lake Michigan, upper incipient lethal limits, the temperature at which 50% of the population survives, for young-of-the-year alewife acclimated at 10, 20, and 25°C was estimated to be slightly less than 26.5°C, 30.3°C, and 32.1°C, respectively (Otto et al. 1976). A separate study found that juveniles exposed to 35°C waters for 24 hours after acclimation to water at 18.9-20.6°C had a 20% survival rate (Dorfman and Westman 1970). When subjected to decreasing temperatures (15.6-2.8°C) over the course of 15 days, juveniles suffered greater than 90% mortality (Colby 1973).

Pardue (1983) suggests that the overall optimal water temperature for juvenile alewife is 15-20°C. Klauda et al. (1991) suggest a broader range of 10-28°C as suitable. Preferred water temperatures in waters with 4-7 ppt salinity were 17-23°C after acclimation at 15-21°C (Meldrim and Gift 1971; PSEGC 1982). In Lake Michigan, juveniles that were acclimated to ambient inshore water temperatures of 15-18°C preferred waters with temperatures of 25.0°C. Juveniles acclimated at 10°C to 20°C had temperature preferences of 25.0°C and 24.0°C, respectively. This preference declined even further to 21.0°C in November and 19.0°C in December (Otto et al. 1976). Juveniles acclimated to 26°C avoided temperatures ≥34°C (PSEGC 1984).

Juveniles exposed to 9°C, following acclimation at 20°C in 5.5 ppt salinity suffered no mortality. However, when the temperature was decreased to 7°C for 96 h, they suffered 27-60% mortality (PSEGC 1984). The lower limit at which juvenile river herring are unable to survive is 3°C or less (Otto et al. 1976).

Depth

Jessop (1990) reported that juvenile alewife were completely absent from near-surface water during daylight hours. No other information was available regarding depth preferences or optima for juvenile alewife.

Salinity

Richkus (1974) reported that juveniles that were transferred from freshwater to saline water (32 ppt), and vice versa, experienced zero mortality. Similar to alewife larvae, juvenile alewife in the upper Chesapeake Bay are found in salinities that range from 0-8 ppt, but most (82%) were collected in freshwater (Dovel 1971). Pardue (1983) suggested that salinities less than or equal to 5 ppt were considered optimal for the juvenile life stage.

Water Velocity/Flow

Water discharge is an important factor influencing variability in relative abundance and emigration of juvenile alewife. Extremely high discharges may adversely affect juvenile emigration, and high or fluctuating discharges may lead to a decrease in the relative abundance of adults and juveniles (Kosa and Mather 2001). Laboratory experiments suggest juvenile alewife avoid water velocities greater than 10 cm/s, especially in narrow channels (Gordon et al. 1992). In large rivers, where greater volumes of water can be transported per unit of time without substantial increases in velocity, the effects of discharge may differ (Kosa and Mather 2001).

Kissil (1974) observed juveniles leaving Lake Bride, Connecticut between June and October and noted especially high migration occurring during times of heavy water flow. These results are consistent with Cooper's (1961) observations that 98 % of juveniles left after periods of heavy rainfall. Huber (1978) also noted that juvenile emigration in the Parker River, Massachusetts was triggered by an increase in water flow. Jessop (1994) found that the juvenile abundance index (JAI) of alewife decreased with mean river discharge during summer. Daily instantaneous mortality increased with mean river discharge from July-August from the Mactaquac Dam headpond on the Saint John River, New Brunswick, Canada.

Bottom composition

Olney and Boehlert (1988) found juvenile alewife among submerged aquatic vegetation (SAV) beds of the lower Chesapeake Bay and suggested that SAV likely confers some level of protection from predation.

pH and aluminum

Kosa and Mather (2001) report that of juvenile river herring abundance peaks at a pH of 8.2 in coastal systems in Massachusetts and suggest that pH appears to contribute to variations in juvenile abundance.

Dissolved Oxygen

Jones et al. (1988) determined that the minimum DO concentration for juveniles is 3.6 mg/L. Dorfman and Westman (1970) reported that at concentrations below 2.0 mg/L, juvenile alewife became stressed. At concentrations as low as 0.5 mg/L, juveniles survived for approximately five minutes in oxygen. In the Cape Fear River system, juveniles preferred waters where DO levels ranged from 2.4-10.0 mg/L (Davis and Cheek 1966).

Subadults

Some young-of-the-year overwinter in deep, high salinity areas of the Chesapeake Bay (Hildebrand and Schroeder 1928). Dovel (1971) reported juvenile populations in the upper Chesapeake Bay that did not emigrate until early spring of their second year. Milstein (1981) found that juveniles overwintered in waters approximately 0.6-7.4 km from the shore of New Jersey, at depths of 2.4-19.2 m, in what is considered an offshore estuary (Cameron and Pritchard, 1963). This area is warmer and has a higher salinity than the cooler, lower salinity river-bay estuarine nurseries where they reside in fall. The majority of fish were present during the month of March, when bottom temperatures ranged from 4.4 to 6.5°C and salinity was between 29.0 and 32.0 ppt. Further south, young alewife have been found overwintering off the North Carolina coast from January to March, concentrated at depths of 20.1-36.6 m (Holland and Yelverton 1973; Street et al. 1973). Other sources have noted that during their first year in saltwater, juveniles tend to remain near the surface (Bigelow and Schroeder 1953). In Lake Michigan, age-1 fish were usually pelagic, except in spring and fall, where they often occurred on the bottom; age-2 fish were typically found on the bottom (Wells 1968).

Information on the life history of young-of-the-year and adult alewife after they emigrate to the sea is sparse (Klauda et al. 1991). But it is generally accepted that juveniles join the adult population at sea within the first year of their lives and follow a north-south seasonal migration along the Atlantic coast, similar to that of American shad (Neves 1981). Sexual maturity is reached at a minimum of age-2 but may vary regionally. In North Carolina, sexual maturity occurs mostly at age-3. In Connecticut, most males achieve maturity at age-4, and most females at age-5 (Jones et al. 1978).

No adults older than age IX have been captured in North Carolina; however age X fish have been recorded in New Brunswick and Nova Scotia.

Despite a lack of conclusive evidence, it is thought that alewife are similar to other anadromous clupeids in that they may undergo seasonal migrations within preferred isotherms (Fay et al. 1983).

While at sea, alewife are more available to bottom trawling gear during the day, leading researchers to conclude that they follow the diel movement of plankton in the water column and are sensitive to light (Neves 1981). Thus, feeding and vertical migration are likely controlled by light intensity patterns within thermal preference zones (Richkus and Winn 1979; Neves 1981).

During spring, alewife from the Mid-Atlantic Bight move inshore and north of 40° latitude to Nantucket Shoals, Georges Bank, coastal Gulf of Maine, and the inner Bay of Fundy for the summer; commercial catch data indicated that they were most frequent on Georges Bank and south of Nantucket Shoals (Neves 1981; Rulifson et al. 1987). Distribution in the fall is similar to the summer, but they are concentrated along the northwest perimeter of the Gulf of Maine. In the fall, they move offshore and southward to the mid-Atlantic coast, with catches reported between latitude 40° and 43° north, where they remain until early spring (Neves 1981). It is unknown to what extent they overwinter in deepwater off the continental shelf, but they have rarely been found more than 130 km from the coast (Jones et al. 1978).

Canadian spring survey results also reveal river herring distributed along the Scotian Gulf, southern Gulf of Maine, and off southwestern Nova Scotia from the Northeast Channel north to the central Bay of Fundy, and to a lesser degree, along the southern edge of Georges Bank and in the canyon between Banquereau and Sable Island Banks (Stone and Jessop 1992). A large component of the overwintering population on the Scotian Shelf moves inshore during spring to spawn in Canadian waters, but may also include the U.S. Gulf of Maine region. Summer aggregations of river herring in the Bay of Fundy/eastern Gulf of Maine may consist of a mixture of stocks from the entire Atlantic coast, as do similar aggregations of American shad (Dadswell et al. 1987). However, based on commercial offshore catches by foreign fleets in the late 1960's, it is believed that coastal river herring stocks do not mingle to the extent that American shad stocks apparently do, at least during the seasons during which foreign harvests were being made (ASMFC 1985). They typically migrate in large schools of fish of similar size and may even form mixed schools with other herring species (Bigelow and Schroeder 2002).

Temperature

Alewife were caught offshore from Cape Hatteras to Nova Scotia where surface water temperatures ranged from 2-23°C and bottom water temperatures ranged from 3-17°C; catches were most frequent where the average bottom water temperature was between 4-7°C (Neves 1981). Stone and Jessop (1992) reported a temperature range of 7-11°C for alewife in their northern range off Nova Scotia, the Bay of Fundy, and the Gulf of Maine. They also noted that the presence of a cold (<5°C) intermediate water mass over warmer, deeper waters on the Scotian Shelf (Hatchey 1942), where the largest catches of river herring occurred, may have restricted the extent of vertical migration during the spring. Since few captures were made where bottom temperatures were <5°C during the spring, vertical migration may be confined by a water temperature inversion in this area at this time of the year.

Alewife may prefer, and be better adapted to cooler water than blueback herring (Loesch 1987; Klauda et al. 1991). Northern populations may exhibit more tolerance to cold temperatures (Stone and Jessop 1992). Additionally, antifreeze activity was found in blood serum from an alewife off Nova Scotia, but not for those from Virginia (Duman and DeVries 1974).

Depth

Sixteen years of National Marine Fisheries Service catch data conducted from Cape Hatteras to Nova Scotia (Neves 1981) found that fish offshore were caught most frequently in the 56-110 m zone (sampling was conducted as deep as 200 m). Their position in the water column may be influenced by zooplankton concentrations (Neves 1981), which are at depths <100m in the Gulf of Maine (Bigelow 1926). Stone and Jessop (1992) found that alewife off Nova Scotia, the Bay of Fundy, and the Gulf of Maine were found offshore at middepths of 101-183 m in the spring, in shallower nearshore waters at 46-82 m in the summer, and in deeper offshore waters at 119-192 m in the fall. They also found differences in depth distribution, with smaller fish (sexually immature) occurring in shallow regions (<93 m) during spring and fall, while larger fish occurred in deeper areas (≥93 m) in all seasons.

In coastal waters (Neves 1981), juvenile alewife are found deeper in the water column than blueback herring, despite their diets being identical in these locations (Davis and Cheek 1967; Burbidge 1974; Watt and Duerden 1974; Weaver 1975). Jansen and Brandt (1980) reported that a nocturnal depth distribution of adult landlocked alewife differed by size-class, with the smaller fish at shallower depths.

Salinity

As noted above, young-of-the-year alewife have been found overwintering offshore of New Jersey (Milstein 1981), where salinities range from 29.0-32.0 ppt. For sub-adults and non-spawning adults that remain in the open ocean, they will reside in full-strength sea water (33.0 ppt). Since it has been suggested that alewives may follow a north-south seasonal migration along the Atlantic coast, similar to that of American shad (Neves 1981), and prespawning adult American shad may detour into estuaries (Neves and Depres 1979), they may be subject to more brackish waters during migration.

Ecological relationships

Adults

Food

Adults do not feed extensively, or typically not at all, during their upstream spawning run (Bigelow and Schroeder 1953; Colby 1973), but spent fish that have reached brackish waters on their downstream migration will feed voraciously, mostly on mysids (Bigelow and Schroeder 2002). Adults may consume their own eggs during the spawning run (Edsall 1964; Carlander 1969), but it is the juveniles that reportedly feed more actively on them (Bigelow and Schroeder 2002).

Competition and Predation

In freshwater, adults may be preyed upon by osprey, green heron, mink (Colby 1973), lake trout (Royce 1943), Atlantic salmon, striped bass (Scott and Scott 1988), and other fish (Loesch et al. 1987). Erkan (2002) notes that predation of alosines has increased dramatically in Rhode Island rivers in recent years, especially by the double-crested cormorant, which often takes advantage of fish staging near the entrance to fishways. Populations of nesting colonies have increased in size and have expanded into areas in which they have previously not been observed. Predation by otters and herons has also increased, but to a lesser extent (Erkan, Rhode Island DEM, 2003, personal communication).

Eggs and larvae

Food

Once larvae begin feeding exogenously, they select relatively small cladocerans and copepods, adding larger species as they grow (Norden 1968; Nigro and Ney 1982). Alewife larvae are highly selective feeders (Norden 1967), usually favoring cladocerans (mainly Cyclops sp. and Limnocalanus sp.) and copepods over other food types (Norden 1968; Johnson 1983).

Competition and Predation

Alewife eggs may be consumed by yellow perch, white perch, spottail shiner, as well as other alewife (Edsall 1964; Kissil 1969). Alewife larvae are preyed upon by both vertebrate and invertebrate predators (Colby 1973).

Juveniles

Food

Juvenile alewife are opportunistic feeders and usually favor items that are seasonally available (Gregory et al. 1983).). For example, in the Hamilton Reservoir, Rhode Island, juveniles fed primarily on dipteran midges in July and cladocerans in August and September (Vigerstad and Colb 1978). Juveniles either select their prey individually or switch to a non-selective filter-feeding mode, which they do more at night (Janssen 1976). Grabe (1996) found that juvenile alewife fed on chironomids, odonates, amphipods, and other amphipods during the day and early evening hours in the Hudson River. Juveniles have also been observed consuming epiphytic fauna (Grabe 1996), especially at night (Weaver 1975).

Juveniles may also feed extensively on benthic organisms, including ostracods, chironomid larvae, and oligochaete worms (Watt and Duerden 1974). Morsell and Norden (1968) found that juveniles will consume zooplankton until they reach 12 cm TL, and may then switch to increasing amounts of the more benthic amphipod Pontoporeia sp.

The number of zooplankton per liter is assumed to be critical for the survival and growth of juvenile alewife. Pardue (1983) suggested that habitats that contained 100 or more individuals of zooplankton per liter are optimal. Walton (1987) found that juvenile abundance in Damariscotta Lake, Maine was controlled by competition for zooplankton, rather than parental stock abundance and recruitment. It has been suggested that clupeids evolved so as to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter and Hunter 1982). Several researchers (Vigerstad and Colb 1978; O'Neill 1980; Yako 1998) hypothesize that a change in food availability may provide a cue for juvenile anadromous herring to begin emigrating seaward, but no causal link has been established.

Invasive species may threaten food sources for alewife. There is strong evidence that juveniles in the Hudson River have experienced a reduced forage base as a result of zebra mussel colonization (Waldman and Limburg 2003).

Competition and Predation

Juvenile alewife are consumed by American eel, white perch, yellow perch, grass pickerel, largemouth bass, pumpkinseed, shiners, walleye and other fishes, as well as turtles, snakes, birds, and mink (Kissil 1969; Colby 1973; Loesch 1987). In estuarine waters of Maine, juvenile bluefish preyed heavily on alewife (Creaser and Perkins 1994). In Massachusetts rivers, juvenile alewife were an energetically valuable and a key food source for largemouth bass during late summer (Yako et al. 2000).

It is often noted throughout the literature, that alewife and blueback herring co-exist in the same geographic regions, yet interspecific competition is often reduced through several mechanisms. For example, juveniles of both species in the Connecticut River consume or select different sizes of prey (Crecco and Blake 1983). Juvenile alewife in the Minas Basin, Nova Scotia favor larger, more benthic prey (particulate-feeding strategy) than do juvenile bluebacks (filter feeding strategy) (Stone 1985; Stone and Daborn 1987). In the Cape Fear River, North Carolina, juvenile alewife consumed more ostracods, insect eggs, and insect parts than did blueback herring (Davis and Cheek 1966).

Alewife also spawn earlier than bluebacks, thereby giving juvenile alewife a relative size advantage over juvenile bluebacks, allowing them a larger selection of prey (Jessop 1990). Difference in juvenile diel feeding activity further reduces competition. One study noted diurnal feeding by juvenile alewife was bimodal, with peak consumption about one to three hours before sunset and a minor peak occurring about two hours after sunrise (Weaver 1975). Another study found that juvenile blueback herring began to feed actively at dawn, increasing throughout the day and maximizing at dusk, then diminishing from dusk until dawn (Burbidge 1974).

Contaminants

A 24 hour LC_{50} of 2.25 mg/L for total residual chlorine (TRC) was reported for juveniles exposed for 30 minutes at 10°C (Seegert et al. 1977). Thirty-minute LC_{50} values for TRC were 2.27 mg/L for juveniles exposed at 10°C, and 0.30 mg/L when fish were exposed at 30°C (Brooks and Seegert 1978; Seegert and Brooks 1978). Juvenile alewife held at 15°C in 7 ppt salinity exhibited an avoidance response to 0.06 mg/L TRC (PSEGC 1978). Juveniles held at 19-24° C in freshwater exhibited an avoidance response at <0.03 mg/L (Bogardus et al. 1978). Juvenile alewife subjected to 0.48 mg/L total chlorine for 2 hours in freshwater (at 22°C) suffered 100% mortality.

<u>Subadults</u>

Food

At sea, alewife feed largely on particulate zooplankton including euphausiids, calanoid copepods, mysids, hyperiid amphipods, chaetognaths, pteropods, decapod larvae, and salps (Edwards and Bowman 1979; Neves 1981; Vinogradov 1984; Stone and Daborn 1987; Bowman et al. 2000). Alewife also consume small fishes, including Atlantic herring, other alewife, eel, sand lance, and cunner (Bigelow and Schroeder 2002). They feed either by selectively preying on individuals or non-selectively filter-feeding with their gill rakers. Feeding mode depends mostly on prey density, prey size, and water visibility, as well as size of the alewife (Janssen 1976, 1978a, 1978b). In Minas Basin, Bay of Fundy, alewife diets shifted from micro-zooplankton in small fish to mysids and amphipods in larger fish. Feeding intensity also decreased with increasing age of fish (Stone 1985).

Alewife generally follow the diel movement of zooplankton, feeding most actively during the day; nighttime predation is usually restricted to larger zooplankton, which are easier to detect (Janssen 1978b; Janssen and Brandt 1980; Stone and Jessop 1993). In Nova Scotia, alewife feeding peaked at midday during the summer and mid-afternoon during the winter. Alewife were also found to have a higher daily ration in the summer than in the winter (Stone and Jessop 1993). Although direct evidence is lacking, catches of alewife in specific areas along Georges Bank, the perimeter of the Gulf of Maine, and south of Nantucket Shoals may be related to zooplankton abundance (Neves 1981).

Competition and Predation

At sea, schooling fish such as bluefish, weakfish, and striped bass prey upon alewife (Bigelow and Schroeder 1953; Ross 1991). Other fish such as dusky shark, spiny dogfish, Atlantic salmon, goosefish, cod, pollock, and silver hake also prey on alewife (Rountree 1999; Bowman et al. 2000). Of these species, spiny dogfish had the greatest quantity of alewife in their stomachs (Rountree 1999).

Abundance and status of stocks

Factors affecting stock size

At low stock levels, Havey (1973) and Walton (1987) demonstrated a weak relationship between spawning stock and juvenile migrant alewife. Jessop (1990) found a stock recruitment relationship for the spawning stock of river herring and year-class abundance at age 3. Despite these results, most studies have been unable to detect a strong relationship between adult and juvenile abundance of clupeids (Crecco and Savoy 1984; Henderson and Brown 1985; Gibson 1994; Jessop et al. 1994). Researchers have suggested that although year-class is driven mostly by environmental factors (see subsequent sections), if the parent stock size falls below a critical level, the size of the spawning stock may become a factor in determining juvenile abundance (Kosa and Mather 2001).

The 2006 Plan Review of the Shad and River Herring Fishery Management Plan (ASMFC, 2006) states:

While the FMP addresses four species including American shad, hickory shad, alewife, and blueback herring, lack of comprehensive and accurate commercial and recreational fishery data for the latter three species make it difficult to ascertain the status of these stocks. A stock assessment for American shad was completed in 1997 and submitted for peer review in early 1998 based on new information and Management Board recommended terms of reference. The 1998 assessment estimated fishing mortality rates for nine shad stocks and general trends in abundance for 13 shad stocks. The next stock assessment update to be externally peer reviewed is scheduled for 2007.

4.2.4 American Shad

Description and Distribution

(all information from ASMFC's doc)
American shad (Alosa sapidissima) (Wilson, 1811) are anadromous, coastal pelagic, highly migratory, schooling species (Bigelow and Schroeder 2002), whose original range occurred from Sand Hill River, Labrador, to Indian River, Florida in the Atlantic Ocean (Lee et al. 1980; Morrow 1980). There are no spawning populations north of the St. Lawrence River, Quebec (Leggett 1976). Since their introduction to the Sacramento, Columbia, Snake, and Willamette rivers in California and Oregon, in the late 1800's, their range in the Pacific Ocean has increased to Cook Inlet, Alaska, and the Kamchatka Peninsula, Asia in the north, to Todos Santos Bay, Baja California in the south (Lee et al. 1980; Howe 1981). Attempts to introduce the species in the Gulf of Mexico (Whitehead 1985), Mississippi River drainage, rivers of peninsular Florida, Colorado streams, and the Great Lakes were unsuccessful (Walburg and Nichols 1967). Although a landlocked population exists in a reservoir of the San Joaquin River on the Pacific coast, no landlocked populations have been reported along the Atlantic coast (Zydlewski and McCormick 1997a).

American shad spend most of their life in the Atlantic Ocean then migrate to coastal rivers and tributaries for spawning. It is likely that all accessible rivers and tributaries within their range along the Atlantic coast have historically been used for spawning by this species (MacKenzie et al. 1985). Rivers, bays, and estuaries associated with spawning rivers are used as nursery areas by American shad (ASMFC 1999). During an average life span of 4-5 years at sea, American shad from the southernmost range may travel over 20,000 km (Dadswell et al. 1987).

Reproduction

Spawning

Atlantic coast stocks of American shad have a geographic range that extends from the St. Johns River, Florida to the St. Lawrence River, Canada (Walburg and Nichols 1967). It is estimated that they once ascended at least 130 rivers throughout this range to spawn, but now, fewer than 70 systems have runs (Limburg et al. 2003). The majority of shad return to their natal rivers and tributaries to spawn (Fredin 1954; Talbot 1954; Hill 1959; Nichols 1966; Carscadden and Leggett 1975), with an average straying rate of about 3% (Mansueti and Kolb 1953; Williams and Daborn 1984; Melvin et al. 1985). Hendricks et al. (2002) demonstrated that hatchery-reared American shad not only homed to a specific tributary (Lehigh River, Pennsylvania) within a major river system (Delaware River) several years after stocking, but also that they prefer the side of the river influenced by the plume of their natal river. It is hypothesized that the degree of homing by shad may be dependent on the nature of the drainage system. If this theory is correct, more mixing and consequent straying would likely occur in large and diversified estuarine systems, such as the Chesapeake Bay, while more precise homing could be expected in other systems that have a single large river, such as the Hudson River (Richkus and DiNardo 1984).

Spawning runs begin in the south and move progressively north as the season progresses and water temperatures increase (Walburg 1960). Shad first appear in the St. Johns River, Florida in mid-November, begin spawning as early as December (Williams and Bruger 1972) with peak spawning occurring in January (Leggett 1976); in Georgia and South Carolina rivers, the runs begin in mid-January; in North Carolina and Virginia bays and inlets, shad are returning by mid-February and peak spawning occurs in March; abundance peaks in April in the Potomac River, and early May in the Delaware River; fish begin their upstream migration in the Hudson and Connecticut Rivers at the end of March and continue until June (Walburg and Nichols 1967; Leggett and Whitney 1972). Shad in some Canadian rivers may spawn as late as July, and in some years, as late as August (MacKenzie et al. 1985; Scott and Scott 1988; Bigelow and Schroeder 2002).

Spawning runs typically last 2-3 months, but can vary depending on weather conditions (Limburg et al. 2003). Spawning adult shad migrating up the James River, Virginia were found to ascend mostly between 0900 and 1600 hours (Weaver et al. 2003). Arnold (2000) reported similar results in the Lehigh River where shad passed primarily between 0900 and 1400 hours.

Although Leim (1924) observed spawning by shad in brackish waters, other researchers have claimed that spawning occurs only in freshwater (Massman 1952; MacKenzie et al. 1985). There does not appear to be a minimum distance from brackish waters at which spawning occurs, (Leim 1924; Massmann 1952) but upstream and mid-river segments appear to be favored (Massmann 1952; Bilkovic et al. 2002a). It is not unusual for shad to migrate between 25 to 100 miles upstream to spawn, and some populations historically traveled over 300 miles upstream (Stevenson 1899; Walburg and Nichols 1967). In the eighteenth and nineteenth centuries, shad runs were reported as far inland as 451 miles along the Great Pee Dee and Yadkin rivers (N.C. Geol. and Econ. Survey 1925) and over 500 miles in the Susquehanna River (Stevenson 1899).

Males arrive on the spawning grounds before females (Leim 1924). Females release their eggs close to the surface, where they are fertilized by one or several males. Eggs are released and fertilized in open water after sunset in clear water, (Leim 1924; Whitney 1961) or during the day in turbid rivers (Chittenden 1976a) or on overcast days (Miller et al. 1982). In the Pamunkey River, Virginia, spawning has been observed throughout the day. This may be due to its relatively turbid waters, which controls light intensity to some degree (Massmann 1952). These findings support the hypothesis that daily spawning is regulated by light intensity (Miller et al. 1982). Spawning activity usually peaks around midnight (Massmann 1952; Miller et al. 1971; 1975).

Fish that spawn north of Cape Hatteras are iteroparous (repeat spawners), while almost all of the fish that spawn to the south are semelparous (die after spawning). This may be due to the fact that south of the Carolinas, the physiological limits of shad are exceeded during the long oceanic migrations, and from the rapidly rising temperatures in southern rivers (Leggett 1969). Shad will spawn repeatedly as they progressively move upriver, (Glebe and Leggett 1981a) which may be a function of their high fecundity (Bigelow and Schroeder 2002). They exhibit asynchronous ovarian development and are batch spawners. Preliminary estimates for the York River, Virginia are 20,000-70,000 eggs per kg somatic weight, spawned every four days (Olney et al. 2001).

Studies have shown that the percentage of adults that are iteroparous increases northward along the Atlantic coast. For example, 3% of adults in the Neuse River, North Carolina were reported as repeat spawners, 24% in the York River, Virginia, 63% in the Connecticut River (Leggett and Carscadden 1978), and 73% in the Saint John River, Canada (Bigelow and Schroeder 2002). Percentage of repeat spawners may change over time within the same river as a result of pollution (Delaware River), fishing pressure (Hudson River), or other unknown causes (Connecticut River) (Limburg et al. 2003). A large percentage (58.5%) of shad in the St. Lawrence River did not spawn every year following the onset of maturation, but skipped one or more seasons (Provost 1987). Some fish spawn up to five times before they die (Carscadden and Leggett 1975).

Earlier studies suggested that southern stocks produce more eggs per unit of body weight than northern populations to compensate for their seeming disadvantage, which would result in about the same lifetime reproductive potential of fish throughout their range (Leggett and Carscadden 1978). Results from another study found that fecundity in shad may be indeterminate, and that previous annual or life-time fecundity estimates may not be accurate (Olney et al. 2001). Researchers examined batch fecundity of American shad in the St. Johns River, Florida (semelparous population), York and Connecticut rivers (iteroparous populations) and found no statistically significant differences in batch fecundity among semelparous and iteroparous populations. Thus, their results do not confirm the findings of Leggett and Carscadden. Until spawning frequency, duration, and batch size throughout the spawning season are known, lifetime fecundity for these stocks cannot be determined and previous methods to determine fecundity throughout the coastal range are inadequate (Olney and McBride 2003).

It is interesting to note that Olney et al. (2001) found that for postspawning females leaving the York River, approximately 70% of post-spawning fish had only partially spent ovaries, suggesting that the annual fecundity of most female shad in the river system is not achieved. Researchers hypothesize that these fish draw upon partially spent ovaries by resorping un-spawned yolked oocytes, which could supplement somatic energy sources as they return to the ocean. These fish would have a greater potential for surviving to become repeat spawners than fish that are fully spent and have no such energy reserves.

Despite a large potential area for spawning in the Connecticut River, shad were observed selecting discrete sites and remaining there for most of the season (Layzer 1974). Sometimes, spawners will forego areas with highly suitable habitats that are further downstream, suggesting that there are other, unaccounted for variables that influence habitat choice (Bilkovic 2000). Choice of spawning habitat may even be unrelated to physical variables and may reflect some unknown ecological selective pressure, such as fewer egg predators in selected habitats (Ross et al. 1993).

Spent adults are very emaciated, and will return to the sea soon after spawning (Chittenden 1976b), sometimes feeding before reaching saltwater (Atkins 1887). Studies along the Connecticut River found that the majority (86%) of spent adult shad emigrated seaward during daylight hours between 0700 and 2100 hours (O'Leary and Kynard 1982; Taylor and Kynard 1984). The oldest reported living shad in the United States was 11 years of age (Cating 1953), while a female from the Annapolis River, Nova Scotia was estimated to be 13 (Melvin et al. 1985).

Studies have attempted to demonstrate a stock-recruitment relationship among clupeids, but most have been unable to detect a strong relationship between adult and juvenile abundance (Crecco and Savoy 1984; Henderson and Brown 1985; Gibson 1994; Jessop 1994). Crecco et al. (1983) have suggested that year-class strength for American shad is driven by environmental factors.

Temperature

Water temperature is the primary factor that triggers spawning, but photoperiod, water flow and velocity, and turbidity also exert some influence (Leggett and Whitney 1972). The oceanic temperature range that triggers fish to begin migrating inshore is quite broad, which is between 5-23°C, (Walburg and Nichols 1967) but is most common in the range of 16-19°C (Leggett and Whitney 1972). Shad moving into nearshore waters of North Carolina were captured where bottom temperatures ranged from 8.6 to 19.9°C, with peak captures occurring at 13.2°C. Based on these results and the temperature range reported by Leggett and Whitney, Parker (1990) suggested that prespawning adults tolerate higher temperatures as they become sexually "ripe" and undergo physiological changes.

Estuarine temperatures along the Atlantic East Coast will vary between 3-15°C, from the time that pre-spawning fish first begin arriving at their natal rivers and peak spawning occurs (Talbot 1954; Massmann and Pacheco 1957; Walburg and Nichols 1967; Leggett 1972; Leggett and Whitney 1972). Egg development in the ovaries may occur slowly at first as water temperatures are increasing, and then mature rapidly at the onset of higher temperatures (DBFWMC 1980). The southern populations are the first to arrive at South Atlantic rivers since these waters are the first to warm up, with temperatures in the higher range of tolerance. As the year progresses and water temperatures in Middle Atlantic and North Atlantic rivers continue to rise, prespawning adults will return to their natal rivers. Peak movement into east coast rivers occurs when temperatures are between 16.5-21.5° C, (Leggett 1976) but fish have been reported to move into natal rivers when temperatures are 4° C or less (Jones et al. 1978).

Throughout their geographic range, the water temperature at which American shad begin spawning is between 8-26°C, (Walburg and Nichols 1967; Stier and Crance 1985) but generally occurs between 12-21°C (Walburg and Nichols 1967; Leggett and Whitney 1972). At the northern limit of the shad's range, temperatures below 12° C will cause total or partial cessation of spawning (Leim 1924).

Shad ovaries develop more slowly at 12.8°C than at 20-25°C (Mansueti and Kolb 1953). Marcy (1976a) found that peak spawning temperatures varied from year to year. For example, a peak spawning temperature of 22°C was reported in 1968 and 14.8°C in 1969 in the Connecticut River. Stier and Crance (1985) assigned an optimum range for surface water temperature during spawning, between 14-20°C. Later analysis by Ross et al. (1993) suggested raising the upper optimum to 24.5°C.

Depth

Although Witherell and Kynard (1990) observed adult shad in the lower half of the water column as they migrated upstream, depth is not considered a critical factor after they reach their spawning habitat (Weiss-Glanz et al. 1986). Once they reach preferred areas, spawning adults have been found at river depths ranging from 0.45 to 10 m, (Mansueti and Kolb 1953; Walburg and Nichols 1967) but depths less than 4 m are often considered ideal (Bilkovic 2000). Ross et al. (1993) observed that the greatest level of spawning occurred where the water depth was less than 1 m in the Delaware River. Several studies have suggested that adults appear to select river areas that are less than 10 ft deep (3.3 m) or have broad flats (Mansueti and Kolb 1953; Leggett 1976; Kuzmeskus 1977).

Researchers have observed adults residing in slow, deep pools during the day, then moving to shallower water dominated by broad flats (where riffle-pools may be present) in the evening to spawn (Chittenden 1969; Layzer 1974). During the act of spawning, females and males can be found close to the surface during release and fertilization of eggs (Medcof 1957).

Despite little information on optimum and suitable depth ranges for this life stage, a suitability index was developed by Stier and Crance (1985), based on input from qualified researchers. They suggested that for all life history stages, including spawning, egg incubation, larvae, and juveniles, the optimum range for river depth is between 1.5-6.1 m. Depths less than 0.46 m (for spawning adults, larvae, and juveniles) and 0.15 m (for egg incubation), and greater than 15.24 (all life history stages) were designated unsuitable. Recent field studies based on spawning events, rather than egg collection, indicate that optimal habitat may be defined more narrowly. For example, sites deeper than 2 m in the Neuse River, North Carolina were used less extensively for spawning than expected based on their availability within the spawning grounds and over the entire river (Beasley and Hightower 2000; Bowman and Hightower 2001).

Salinity

Prior to migrating upstream, prespawning adults may spend two to three days in estuarine waters prior to moving upriver (Dodson et al. 1972; Leggett 1976). To test whether this acclimation period was necessary, Leggett and O'Boyle (1976) found that fish transferred from seawater to freshwater (accompanied by a 5-6°C temperature increase) over a 2.5-hour period experienced physiologic stress and a 54% mortality rate, 5 hours later. Additionally, adults did not survive transfers from saltwater (27 ppt) to freshwater with an accompanying 14°C temperature increase. Mortality varied from 0-40% for transfers from salinities ranging from 13-25 ppt to freshwater, with accompanying temperature increases up to 5.6°C. Adults appear to be better adapted to transfers from freshwater to saltwater, where they tolerated transfers from 23-24 ppt to freshwater, accompanied by temperature increases up to 9° C (Leggett and O'Boyle 1976).

Spawning typically occurs in tidal (Chittenden 1976a) and non-tidal freshwater regions of rivers and tributaries. In some rivers, adult spawners have historically migrated beyond tidal freshwater areas prior to dam blockages, but can no longer ascend these reaches (Mansueti and Kolb 1953). American shad exhibit a great tolerance to a wide range of salinities during their early developmental stages (Chittenden 1969), as well as, during their adult years (Dodson et al. 1972). Despite their tolerance to a wide range of salinities at this life history stage, American shad eggs are always deposited in freshwater (Weiss-Glanz 1986). Leim (1924) observed that eggs were typically deposited in waters of the Shubenacadie River, Canada slightly above the range of tide. In the Hudson River, shad ascend much further beyond the salt front, as far upstream as they can travel (Schmidt et al. 1988). Limburg and Ross (1995) concluded that the shad's preference for upriver spawning sites may be a genetically fixed character, but its advantage or significance does not appear to lie in salt intolerance of eggs and larvae.

Water velocity/flow

Stier and Crance (1985) considered temperature and water velocity to be the two most important variables for evaluating shad spawning habitat. Areas with high water flows provide a cue for spawning American shad (Orth and White 1993). Walburg (1960) found that spawning and egg incubation most often occurred where water velocity was 0.3-0.9 m/sec. Stier and Crance (1985) suggested that this was the optimum range for spawning areas. Ross et al. (1993) observed that spawning activity was highest in areas that ranged from 0-0.7 m/sec, suggesting that there is no lower suitability limit during this stage and that the upper limit should be modified. Although Bilkovic (2000) observed live eggs where the water velocity ranged from 0-1.0 m/s and larvae where water velocity ranged from 0-0.6 m/s, she further modified the optimum range to 0.3-0.7 m/sec. In order to prevent siltation and to insure that conditions conducive to spawning and egg incubation occur (Williams and Bruger 1972), she reasoned that some minimum velocity is required (Bilkovic 2000).

Appropriate water velocity at the entrance of fishways is also important for fish migrating upstream to spawning areas. Researchers found that water velocities of 0.6-0.9 m/sec at the entrance to pool-and-weir fishways (with a combined difference in pool elevations of 23 cm) was required to sufficiently attract fish (Walburg and Nichols 1967). Entrance velocities of 2-3 m/sec are routinely and effectively used at the Conowingo Dam fish lift on the Susquehanna River (St. Pierre, pers. comm.). At other sites, such as the Holyoke Dam, Massachusetts, American shad had trouble locating fishway entrances among turbulent discharges and avoided the area; thus, too much water velocity may actually deter fish (Barry and Kynard 1986).

Ross et al. (1993) noted that habitat selection seemed evident among spawning adults, which favored mid-river runs, defined as being relatively shallow (0.5-1.5 m) and moderate to high current velocity (0.3-0.7 m/s); to a lesser degree channels (deeper, greater current velocities, little if any SAV) and SAV shallows (inshore, high densities of SAV, low current velocities); and to a much lesser degree pools (wide river segment, deep, low current velocities) and riffle pools (immediately downstream of riffles, deepwater, variable current velocity and direction). They found that pools and riffle pools contain both deep and slow water, physical characteristics that adults seem to avoid. While runs may contain both swift and shallow water characteristics, and channels and SAV shallows may contain one or the other, but not both, this may help explain choice of habitats, which may confer higher survivability to newly spawned eggs. Bilkovic et al. (2002a) also found the greatest level of spawning activity in runs.

In 1985, a rediversion canal and hydroelectric dam with a fish passage facility were constructed between the Cooper River and Santee River, South Carolina, which increased the average flow of the Santee River from 63 m^3/s to 295 m^3/s. (Cooke and Leach 2003). This increased river flow and access to spawning grounds have contributed to increases in American shad populations. Although the importance of instream flow requirements has been previously recognized (Crecco and Savoy 1984; ASMFC 1985; Crecco et al. 1986; Ross et al. 1993), it has usually been with regard to spawning habitat requirements or recruitment potential (Moser and Ross 1994). Cooke and Leach's results suggest that the study of and possible adjustment of river flow may be an important consideration for restoring alosine habitat.

Water velocity may also contribute in some way to weight loss and mortality during the annual spawning migration, especially for males. Since they typically migrate upstream earlier when water velocities are greater, they tend to expend more energy than females (Glebe and Leggett 1973; DBFWMC 1980).

Although Summers and Rose (1987) could not detect direct relationships between stock size and river flow or water temperature, they found that spawning stock size, river flow rate, and temperature were important predictors of future American shad population sizes. They suggest that future studies incorporate a combination of environmental variables, rather than a single environmental variable, to determine what stimuli affect stock size.

Bottom composition

Spawning often occurs far upstream or in adjacent river channels along areas dominated by flats where the bottom substrate often consists of sand, silt, muck, gravel, or boulders (Mansueti and Kolb 1953; Walburg 1960; Walburg and Nichols 1967; Leggett 1976; Jones et al. 1978). Substrate type is not considered an important factor at the spawning site since eggs are released into the water column (Krauthamer and Richkus 1987); however, eggs are semibuoyant and may eventually sink to the bottom. Thus, areas predominated by sand and gravel may be better for survival because there is sufficient water velocity to remove silt or sand to prevent suffocation if eggs settle to the bottom (Walburg and Nichols 1967). Other researchers have also observed shad spawning primarily over sandy bottoms that were free of mud and silt (Williams and Bruger 1972). Bilkovic et al. (2002a) concluded that substrate type was not predictive of spawning and nursery habitat in two Virginia rivers she surveyed, although Layzer (1974) noted that survival rates of shad eggs were highest where gravel and rubble substrates were present. Finally, Hightower and Sparks (2003) hypothesized that larger substrates are important for American shad reproduction, based on their observations of spawning in the Roanoke River, North Carolina.

pH

No information found; refer to discussion of pH under Egg and Larval Habitat Section. Presumably, spawners will avoid waters with adverse pH conditions.

Dissolved oxygen

Shad require well-oxygenated waters in both rivers and at sea (MacKenzie et al. 1985). Jessop (1975) found that migrating adults require minimum dissolved oxygen (DO) levels between 4-5 mg/L in the headponds of the Saint John River, New Brunswick. Levels below 3.5 mg/L have shown sublethal effects (Chittenden 1973a), less than 3.0 mg/L blocked upstream migration in the Delaware River (Miller et al. 1982), and less than 2.0 mg/L caused a high incidence of mortality (Tagatz 1961; Chittenden 1969). Dissolved oxygen levels below 0.6 mg/L will result in 100% mortality of all fish (Chittenden 1969). Although minimum daily DO levels of 2.5-3.0 should be sufficient to allow shad to migrate through polluted areas, Chittenden (1973a) recommended that suitable spawning areas have a minimum of 4.0 mg/L of DO. Miller et al. (1982) proposed even higher minimum DO levels, suggesting that anything below 5.0 ppm (mg/L) should be considered potentially hazardous to adult and juvenile shad.

Suspended solids/turbidity

Adults appear to be quite tolerant of suspended solids, where concentrations as high as 1000 mg/L in the Shuebenacadie River, Nova Scotia, did not deter migrating adults (Leim 1924). Auld and Schubel (1978) found that similar concentrations of 1000 mg/L did not significantly affect hatching success of eggs.

Development, growth and movement patterns

Eggs and larvae

In general, eggs and larvae are found at, or downstream, of spawning locations. In the Mattaponi and Pamunkey rivers, Virginia, eggs were predominantly found in the upper and mid-river segments. Upstream areas typically have extensive deadfall (where important larval and juvenile shad prey items originate), and spawning there may ensure that eggs (and larvae) are retained within favorable habitats (Bilkovic et al. 2002a).

Once eggs are released into the water column, they are initially semibuoyant to demersal. Researchers followed shad eggs after they were broadcast and found that they traveled a distance of 5 to 35 m downstream until they sank or were lodged on the bottom (Whitworth and Bennett 1970). Other researchers (Barker 1965; Carlson 1968; Chittenden 1969) have reported similar observations. Laboratory experiments, which did not factor in hydrodynamic and tidal effects, found that sinking rates for eggs were 0.5-0.7 m/min (1.6-2.4 ft/min), with newly spawned eggs sinking at a quicker rate (Massmann 1952; Chittenden 1969). Other factors can influence how far eggs travel, such as extensive deadfall and other debris, which may prevent eggs from settling far from the spawning site (Bilkovic 2000). Once eggs sink to the bottom, they are swept under rocks and boulders by eddy currents and are kept in place as they increase in diameter from water absorption. They may become dislodged and be swept downstream for short distances, especially to nearby pools (DBFWMC 1980). Survival of eggs is dependent on several factors, including current velocity, dissolved oxygen, water temperature, suspended sediments, pollution, and predation (Krauthamer and Richkus 1987; Bailey and Houde 1989).

Yolk-sac larvae may not use inshore habitat as extensively as post yolk-sac larvae (Limburg 1996). One early study (Mitchell 1925, cited in Crecco et al. 1983) found that yolk-sac larvae were near the bottom and swam to shore as the yolk-sac reabsorbed. Metzger et al. (1992) also found yolk-sac larvae mostly in offshore areas along the bottom, while post yolk-sac larvae were more concentrated in quiet areas nearshorelines (Cave 1978; Metzger et al. 1992). Yolk-sac larvae are typically found deeper in the water column than postlarvae, due to their semi-buoyant nature and aversion to light, while postlarvae are more abundant in surface waters, especially in downstream waters (Marcy 1976a).

After hatching, yolk-sac larvae will exhaust their food supply within 4-7 days (Walburg and Nichols 1967), when they are about 10-12 mm total length (TL) (Marcy 1972). Larval survival may be dependent on water temperature, water flow, food production and density, and predation (State of Maryland 1985; Bailey and Houde 1989; Limburg 1996). Larvae may drift passively into brackish water shortly after hatching occurs, or can remain in freshwater for the remainder of the summer (State of Maine 1982). Larvae often aggregate in eddies and backwaters (Stier and Crance 1985). Ross et al. (1993) reported that shad larvae frequent riffle pools where water is of moderate depth and variable velocity and direction. Larvae in the Mattaponi and Pamunkey rivers, Virginia, were dispersed from the upper through the downriver areas. Unlike the presence of eggs, which could be predicted in most cases using physical habitat and shoreline/land use ratings, distinct habitat associations could not be discerned for larval distributions. This may be due to the fact that larvae are carried further downstream than eggs, dispersing them into more variable habitats (Bilkovic et al. 2002a).

Temperature

Rate of development of shad eggs has been linearly correlated to water temperature (Mansueti and Kolb 1953) and hatching times were observed at the following temperatures: 15.5 (Leim 1924) and 17 days at 12°C (Ryder 1887); 7 days at 16.1°C (Hendricks, cited in Boreman 1981) and 17°C (Leim 1924); 3 days at 24°C (MacKenzie et al. 1985); and 2 days at 27°C (Rice 1878). Within the range of 11-27°C, the time it takes for eggs to develop can be expressed as (Limburg 1996):

$$\mathrm{loge}(EDT) = 8.9 - 2.484 \times \mathrm{loge}(T)$$

where EDT is egg development time in days and T is temperature in degrees Celsius

Most eggs typically hatch in 3 to 6 days (Krauthamer and Richkus 1987). Temperatures below 8-10°C are unsuitable (Bradford et al. 1968), and at 8°C eggs will stop developing (Leim 1924). Several researchers have suggested suitable near-surface water temperatures for development and survival of American shad eggs, including 8-26°C (Walburg and Nichols 1967; Ross et al. 1993) and 10-30°C (Stier and Crance 1985). Leim (1924) suggested that overall optimal conditions for American shad egg development occur at 17°C, 7.5 ppt salinity, and darkness.

Temperatures above 27°C resulted in abnormalities or total cessation of larval development (Bradford et al. 1968). Few larvae have been found living in temperatures above 28° C (Marcy 1971; 1973), and no viable larvae developed from eggs incubated above 29°C (Bradford et al. 1968). The range of suggested suitable water temperatures for the larval stage includes 10-27°C (Bradford et al. 1968), 13.0-26.2°C (Ross et al. 1993), and 10-30° C (Stier and Crance 1985). The optimal temperature range for maximum hatching and egg and larval development combined is suggested to be 15.5-26.5°C (Leim 1924) and 15-25°C (Stier and Crance 1985). Ross et al. (1993) have recommended that further sampling be conducted for postlarval stages at temperatures ≥27°C to confirm upper optimal temperature preferences. In their studies, they found no reduction in density of larvae at the upper thermal limit (26-27°C) in areas sampled along the Delaware River.

Laboratory experiments conducted on shad eggs reveal that they can tolerate extreme temperature changes as long as exposure duration is relatively short (Klauda et al. 1991). Temperature increases after acclimation at various temperatures produced variable results, but of note, is the ability of eggs to withstand temperatures of 30.5°C for 30 minutes and 35.2°C for 5 minutes (Schubel and Koo 1976). Also, sensitivity to increases in temperature decreased as eggs matured (Koo et al. 1976). Larvae could also withstand temperatures as high as 29.5° C after acclimation, but only for 15 minutes (Koo et al. 1976; Koo 1979).

Shoubridge (1977) analyzed temperature regimes in several coastal rivers throughout the range of American shad (Florida to New Brunswick, Canada), and found that as latitude increased: 1) the duration of the temperature optima for egg and larval development decreased; and 2) the variability of the temperature regime increased. Based on Shoubridge's work, Leggett and Carscadden (1978) suggested that variation in shad egg and larval survival, year-class strength, and recruitment also increases with latitude.

Crecco and Savoy (1984) found that low water temperatures (and high rainfall and high river flow) were significantly correlated with low shad juvenile abundance during the month of June in the Connecticut River, while high water temperatures (and low river flow and low rainfall) were significantly correlated with high juvenile abundance (Crecco and Savoy 1984). Depressed water temperatures can retard the onset and duration of shad spawning (Leggett and Whitney 1972), the growth rates of larvae (Murai et al. 1979), and the production of riverine zooplankton (Chandler 1937; Beach 1960).

Depth

Eggs are slightly heavier than water, but may be buoyed by prevailing currents and the tide. Eventually, many of the eggs will eventually settle at or near the bottom of the river during the water-hardening stage (Jones et al. 1978). Shad eggs were found to be distributed almost equally between the surface and the bottom of the Connecticut River, while larvae were more than twice as abundant in surface waters, becoming increasingly pelagic as they moved downstream (Marcy 1976a). Most of the larvae caught by Leim (1924) were obtained in surface tows.

One study in the Connecticut River found that 49 percent of the eggs were found in water less than 10 feet (3.3 m) deep, 30 percent in water between 11 to 20 feet (3.7-6.7 m) deep, and the rest were collected in water between 21 to 30 feet (7-10 m) (Walburg and Nichols, 1967). Massman (1952) reported that five times as many eggs per hour were collected at depths ranging from 1.5 to 6.1 m (4.9-20.0 ft), than in deeper waters of the Pamunkey and Mattaponi rivers. Approximately 40% of spawned eggs were reported at depths less than 3 m (9.8 ft) by Walburg and Nichols (1967).

Despite a lack of data for depth optima, Stier and Crance (1985) developed a suitability index based on input from qualified researchers, and suggested that for all life history stages, including spawning, egg incubation, larvae, and juveniles, the optimum range for river depth is between 1.5-6.1 m. Depths less than 0.46 m (for spawning adults, larvae, and juveniles) and 0.15 m (for egg incubation) and greater than 15.24 (all life history stages) were designated unsuitable. Bilkovic et al. (2002a) found eggs at depths of 0.9-5.0 m along the Mattaponi and Pamunkey rivers, while larvae were more widely distributed in the range of 1-10 m. Thus, she suggested that larval shad may occupy a broader range of optimal depths.

Salinity

Although American shad eggs are always deposited in freshwater, it is unknown whether they hatch only in freshwater, only brackish water, or in both (Weiss-Glanz 1986). Leim (1924) noted that shad in their northern range do not spawn very far beyond the tidal portion of rivers, even though they had the ability to migrate further upstream in some areas. Also, unlike alewives, there are no landlocked populations on the East Coast. His experiments found that successful development of embryos and larvae occurred under low salinity conditions, and larvae were able to survive longer without food compared with freshwater conditions.

Eggs and larvae were observed in salinities ranging from 0-7.6 ppt, but most often at 0 ppt in the Shubenacadie River, Canada. Although larvae could tolerate salinities as high as 15 ppt in laboratory studies, premature death often resulted. At 22.5 ppt, egg development was poor or hatching occurred prematurely (Leim 1924). Early attempts to gradually acclimate larval shad to full-strength seawater resulted in high mortality and 20-24 ppt also met with unfavorable results (Milner 1876). Temperature was found to influence salinity sensitivities, with lower temperatures (12°C) resulting in more abnormalities at 15 and 22.5 ppt, than at higher temperatures (17°C) (Leim 1924).

Limburg and Ross (1995) found that salinities of 10-20% were favorable for post-yolk sac shad larvae under experimental conditions, and concluded that estuarine salinities neither depressed growth rates nor elevated mortality rates of larval American shad, compared with freshwater conditions. They concluded that ecological factors other than the physiological effects of salinity may have played a greater role in influencing spawning site selection by shad.

Water velocity/flow

Kuzmeskus (1977) found fresh spawn in areas where water velocity rates were between 9.5 and 132 cm/sec. Williams and Bruger (1972) noted that increased siltation may result if water velocities are less than 0.3 m/s, causing increased egg mortality from suffocation and bacterial infection. Early studies suggested that optimal conditions for eggs and larval stages occur where water velocity is between 0.3-0.9 m/sec (Walburg 1960; Walburg and Nichols 1967; Stier and Crance 1985). Ross et al (1993) later modified this range to 0-0.7 m/sec. Bilkovic et al. (2002a) collected eggs within a broader range of water velocities of 0-1.0 m/s in the Mattaponi and Pamunkey rivers, Virginia. She suggested that a suitable range for both the egg and larval stage combined would incorporate this range (0-1.0 m/s), but that future research should facilitate the development of distinct models for the egg and larval stages.

Freshwater discharges can influence developing eggs and larvae. Increased river flow can carry eggs from favorable nursery habitat to unfavorable areas that reduce their chance for survival, while lower flows may result in favorable hydrodynamic, thermal, and feeding conditions (Crecco and Savoy 1987a; Limburg 1996). Crecco and Savoy (1987b) observed that larval and juvenile shad selected eddies and backwater areas where water flow was greatly reduced. Limburg's (1996) observations in the Hudson River led her to postulate that high May river discharges, and associated low temperatures and low food availability, contributed to high larval mortality, while larvae hatched after May had a much higher survival rate due to more favorable conditions. Marcy (1976) discovered significant correlations between year-class strength and river flow in the Connecticut River. He found that from 1966 through 1973 during the month of June, increased river flows and decreased water temperatures accounted for reduced year-class abundance. Larval survival rates in the Connecticut River have also been negatively correlated with increased river flow in June and positively correlated with June river temperatures (Savoy and Crecco 1988).

Although hydrographic turbulence may affect larval shad survival rates, the precise mechanisms are uncertain because daily river flow and rainfall levels are nonlinear, time-dependent processes (Sharp 1980) that may act singularly or in combination with other factors. There are numerous potential interactions of flow rates with climatic, physical, and biological processes (Turner and Chadwick 1972). For example, decreased temperatures can delay and shorten the spawning season of shad (Leggett and Whitney 1972), impact the growth rates of larvae (Murai et al. 1979), and affect riverine zooplankton production (Chandler 1937; Beach 1960). Transparency of the water may also be reduced, compromising the ability of larval fish to see their prey (Theilacker and Dorsey 1980). Increased turbidity may also affect photosynthesis among river phytoplankton, which in turn may lead to elimination of cladocerans and copepods (Chandler 1937; Hynes 1970), a favored prey item among larval shad (Crecco and Blake 1983; Johnson and Dropkin 1995). Thus, there are many ways in which river flow can alter survival rates of shad larvae, and it is unreasonable to assume that a single causal mechanism will operate under all circumstances (Crecco and Savoy 1984).

Bottom composition

Once eggs become fertilized, they can either sink to the bottom, becoming lodged under rocks and boulders, or be swept along by currents, usually to the nearest pool (Chittenden 1969). As discussed above, bottom composition does not appear to be a critical factor for spawning (Krauthamer and Richkus 1987), and Bilkovic (2000) concluded that substrate type was not predictive of spawning and nursery habitat in rivers she surveyed in Virginia. Spawning over sand and/or gravel substrates may be preferred however, because there is sufficient water velocity to remove silt or sand and prevent suffocation, if eggs settle to the bottom (Walburg and Nichols 1967). Survival rates of shad eggs have been found to be highest for those that settled over gravel and rubble substrates (Layzer 1974).

pH

Early laboratory studies of pH tolerance of American shad from the Shuebenacadie River, Canada found that values between 6.0-9.0 had no negative effects on eggs and larvae (Leim 1924). When subjected to a pH of 10.0 and higher, eggs did not develop properly and larvae were less active. Bradford et al. (1968) found that American shad eggs developed successfully at pH 5.5-9.5 (18-19° C), but most eggs (100-68%) died at a pH of less than 5.2. The lethal dose for 50% of the population (LD50) was calculated at about pH 5.5, but many of the larvae that hatched were deformed. The most successful range for hatching was between 6.0-7.5 and researchers concluded that a pH of at least 6.0 was necessary for suitable egg incubation. When eggs were also subjected to aluminum pulses, critical conditions were met at pH 5.7 + 50 or 200 µg/L Al for 96 h or pH 6.5 + 100 µg/L Al for 96 h (Klauda 1994).

Klauda (1989) concluded that shad larvae required a minimum of pH 6.7 and a maximum of 9.9 for survival; pH >7.0 is considered optimal for larvae (Leach and Houde 1999). Bilkovic et al. (2002a) surveyed shad eggs and larvae within waters with pH values from 5.9-9.3, and observed shad eggs associated with a pH between 6.5-8.5, and larvae in the range of 6.5-9.3.

Yolksac larvae (1-3 days old) that were subjected to an array of acid and aluminum conditions appeared to be more sensitive to acid and aluminum pulses than eggs. The least severe treatment that resulted in critical conditions of acid and aluminum was a 24 h exposure to pH 6.1 with 92 g/L of total dissolved aluminum. The least severe treatment that resulted in a lethal condition was a 24 h exposure to pH 5.5 with 214 g/L of total dissolved aluminum.

Postlarvae (6-16 days old) were found to be more sensitive to acid and aluminum pulses than both eggs and yolksac larvae. Critical conditions occurred at pH 5.2 + 46 µg/L and pH 6.2 + 54 or 79 µg/L aluminum for 8 hours, and lethal conditions occurred at pH 5.2 + 63 µg/L aluminum for 16 hours (Klauda 1994).

In general, fertilized eggs, yolk-sac larvae, and to a lesser degree, post yolk-sac larvae have the highest probability of temporary acidic conditions and elevated aluminum levels in or near their freshwater spawning sites in streams that are poorly buffered (low alkalinity) (Klauda 1989). American shad stocks that spawn in poorly buffered Eastern Shore Maryland rivers, like the Nanticoke and Choptank, may be more vulnerable to storm-induced, toxic pulses of low pH and elevated aluminum, and thus, recover at a much slower rate than stocks that spawn in well-buffered Western Shore rivers. Klauda (1994) hypothesized that whenever the abundance of an acid-sensitive fish species like American shad is as low as most Maryland stocks are today, and annual climatic conditions are less than favorable for good reproduction, even infrequent and temporary episodes of critical or lethal pH and aluminum exposures in the spawning and nursery areas could contribute to significant reductions in egg or larval survival and slow stock recovery. Leach and Houde (1999) noted that sudden drops in pH levels, such as those associated with rainfall, can impose high and sudden mortalities on larvae.

Dissolved oxygen

Few specific egg and larval DO tolerance or optima data were found in the literature, however there are several studies that note presence or absence of eggs and larvae under certain DO conditions (Bilkovic et al. 2002a). American shad eggs were collected in the Neuse River, North Carolina, where DO ranged from 6-10 mg/L (Hawkins 1979). No eggs could be found in the Connecticut River when the DO concentrations were less than 5 mg/L (Marcy 1976a). Bilkovic (2000) found that in the Mattaponi and Pamunkey Rivers, associated DO median values for eggs (10.8, 10.2 mg/L, respectively) were greater than for yolksac larvae (8.2, 9.6 mg/L, respectively) and postlarvae (8.1, 8.2 mg/L, respectively).

One study determined that the LC_{50} values for Connecticut River eggs were between 2.0-2.5 mg/L (Marcy 1976a). In the Columbia River the LC50 was close to 3.5 mg/L for eggs and at least 4.0 mg/L was required for a high percentage of hatched eggs and healthy larvae; less than 1.0 mg/L resulted in total mortality (Bradford et al. 1968). Klauda et al. (1991) concluded that a good hatch with a high percentage of normal larvae required DO levels during egg incubation of at least 4.0 mg/L, based on observations by both Maurice et al. (1987) and Chittenden (1973a). Miller et al. (1982) concluded the minimum DO level for both eggs and larvae is approximately 5 mg/L. This is the value that Bilkovic (2000) assigned for optimum conditions for survival, growth, and development of American shad. Finally, it is worth noting that cleanup of the Delaware River has had a measurably positive effect on increasing DO concentrations there (Maurice et al. 1987).

Suspended solids/turbidity

Eggs seem to be less vulnerable to the effects of suspended solids than larvae. For example, levels of up to 1000 mg/L did not significantly reduce hatching success, while larvae exposed to levels of 100 mg/L or greater significantly reduced survival rates (Auld and Schubel 1978).

Juveniles

Shad larvae are transformed into juveniles 3-5 weeks after hatching at about 28 mm total length (TL), (Jones et al. 1978; Crecco and Blake 1983; Klauda et al. 1991; McCormick et al. 1996) and disperse at or downstream of the spawning grounds, where they spend their first summer in the lower portion of the river where they were spawned. Juvenile American shad (and blueback herring) were found inshore in the Hudson River during the day, while alewives predominated inshore at night (McFadden et al. 1978; Dey and Baumann 1978).

While most young shad use freshwater nursery reaches, (McCormick et al. 1996) it is thought that their early ability to hypo-osmoregulate allows them to utilize brackish nursery areas during years of high juvenile populations (Crecco et al. 1983). American shad juveniles use the headpond of the Annapolis River, Nova Scotia, as a nursery area, which has surface water salinities of 25-30% (Stokesbury and Dadswell 1989).

O'Donnell (2000) found that juveniles in the Connecticut River began their seaward emigration at approximately 80 days post hatch. They are typically 7-15 cm in length before they leave the river and enter the ocean (Talbot and Sykes 1958). Shad were observed remaining in the offshore region of the Annapolis estuary (Nova Scotia) for almost a month before the correct cues triggered emigration (Stokesbury and Dadswell 1989). Some researchers (Chittenden 1969; Limburg 1996) found evidence that juvenile emigration was already underway by midsummer, indicating that movement may be triggered by cues other than declining fall temperatures. Juveniles in northern rivers emigrate seaward first, and those from southern rivers emigrate progressively later in the year (Leggett 1977a). For example, downstream emigration peaks in September and October in the Connecticut River, late October in the Hudson River (Schmidt et al. 1988), and late October through late November in the Upper Delaware River and Chesapeake Bay (Krauthamer and Richkus 1987). Although juveniles were still found in the Cape Fear River, North Carolina in December, seaward migration took place mostly in November (Fischer 1980). Emigration usually peaks at night (i.e. at 1800-2300 hours) (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989).

The combination of factors that trigger juvenile emigration is uncertain, but researchers suggest decreasing water temperatures, reduced water flow, or a combination of both during autumn appear to be key factors (Sykes and Lehman 1957; Walburg and Nichols 1967; Moss 1970). In the Susquehanna River, an increase in river flow from October through November may actually help push juveniles downstream (St. Pierre, pers. comm.). Miller et al. (1973) suggested that water temperature was more important than all other factors, because it directly affects the shad, with time of season being secondary (which also influences temperature). Several researchers (Chittenden 1969; Miller et al. 1973; Limburg 1996; O'Donnell 2000) have observed younger, smaller young-of-the-year fish in upstream reaches, while older and larger (within age cohorts) fish were found downstream earlier in the season, which led them to hypothesize that as fish grow and age, they move downstream. Both Chittenden (1969) and Marcy (1976a) suggested that factors associated with size appear to initiate the earlier stages of seaward emigration; larger fish that were already downstream by mid-summer when temperatures were higher than 21° C was interpreted as emigration in progress.

Results from another study (Stokesbury and Dadswell 1989) suggest that size at emigration may not be an important factor that triggers migration, but that environmental stress may reach a point where seaward movement is necessary regardless of a critical size. O'Leary and Kynard (1986) and Stokesbury and Dadswell (1989) found that shad movement typically occurred during quarter to new-moon periods when water temperatures dropped below 19°C and 12°C, respectively. Decreasing water temperatures and the new moon phase, which provided dark nights, were considered to be more important in providing cues for emigration than increased river flow. The lower lethal temperature limit that triggers the final movement of juveniles from fresh water is approximately 4-6°C (Chittenden 1969; Marcy 1976a). Zydlewski and McCormick (1997a) observed changes in osmoregulatory physiology in migrating juvenile shad, and concluded that these were part of a suite of changes that occur at the time of migration. While this set of changes has been shown to be strongly affected by temperature in several studies, they suggested that other environmental and/or ontogenetic factors may have an influence on timing of migration.

Upon leaving their nursery habitat in the late fall, juveniles may spend their first year near the mouths of streams, in estuaries, and other nearshore waters (Hildebrand 1963; Bigelow and Schroeder 2002), or may move to deeper, higher salinity areas, such as may exist in portions of the Chesapeake Bay (Hildebrand and Schroeder 1928). Milstein (1981) found juveniles overwintering in warmer, higher salinity waters 0.6-7.4 km from the shore of New Jersey, in what is considered an offshore estuary (Cameron and Pritchard 1963). Hammer (1942) reported catches of 1- and 2-year old shad in brackish and fresh water of the Potomac River. Juvenile shad from the Connecticut River may remain in Long Island Sound for one or two years before joining the coastal migratory stocks in the Gulf of Maine during their second or third year of life (Savoy 1993). Juveniles may overwinter in estuarine waters of the lower Neuse River, NC, with emigration occurring as late as February (Holland and Yelverton 1973). In their southern range, some juveniles may stay in the river for up to one full year (Williams and Bruger 1972). In South Carolina, juvenile American shad were found predominantly in deeper, channel habitats of estuarine systems, during fall and winter. Small crustaceans preyed upon by American shad are generally abundant near the bottom in these areas (McCord 2005).

Temperature

Young shad are sensitive to water temperature changes, and actively avoid temperature extremes, if possible. Laboratory tests suggest that juveniles can tolerate temperature increases >1° and <4° C above ambient temperature, but above that, shad will avoid changes, if given a choice (Moss 1970).

The lower range of thermal tolerance for juveniles appears to be about 2°C, but sublethal effects have been observed between 4-6°C (Chittenden 1972). Juveniles have a preference for temperatures of at least 8°C (MacKenzie et al. 1985) and have a natural upper temperature limit near 30° C (Marcy et al. 1972). Juveniles collected from the Connecticut River were found where temperatures ranged from 10-30°C, with one fish found where the temperature was 31°C (Marcy et al. 1972). Leim (1924) found that juveniles captured in the Shubenacadie River, Canada were usually found where temperatures tended to be the highest compared to other regions of the river. Limburg (1996) found that juveniles in the lab had higher initial growth rates at 28.5°C than fish reared at lower temperatures. O'Donnell (2000) concluded that it may be advantageous for fish to hatch later in the year because temperatures are higher and growth rates for juveniles will be faster. Disadvantages to later hatching later in the year include increased competition and predation rates.

The lethal upper water temperature limit that killed 50% of juveniles tested (TL50) was 31.6°C, but acclimation at 24°C prior to exposure, was first necessary (Ecological Analysts Inc. 1978). A critical thermal maximum of 34-35°C has been reported for juveniles in the Neuse River, North Carolina (Horton and Bridges 1973). Unlike shad eggs, juveniles do not appear to be as tolerant to temperature changes. For example, juveniles acclimated to 25°C suffered a 100% mortality rate when the temperature was decreased to 15°C. There was also a 100% mortality rate for juveniles acclimated to 15°C and then subjected to temperatures <5°C. Finally, no survival was reported for juveniles acclimated to 5°C and then exposed to 1°C (PSE&G 1978).

Crance (1985) suggested an optimum range between 15.5-23.9°C for the juvenile life stage. Stier and Crance (1985) suggested an optimal near-bottom temperature range for juveniles during the winter and spring in estuarine waters was 10-25°C, and below 3°C and above 35°C were unsuitable.

In the Connecticut River, seaward migration was observed when temperatures dropped below 19°C (Leggett 1976; O'Leary and Kynard 1986), but juveniles have also been observed moving downstream when temperatures were higher than 19° C (between 26-23°C), which was interpreted by researchers as active emigration (Marcy 1976a). Watson (1970) observed a similar pattern, with juveniles beginning to migrate once temperatures reached 18.3°C, during the month of September. Migration peaks when temperatures decline to 16-9°C (Leggett and Whitney 1972; O'Leary and Kynard 1986). In the Delaware River, emigration was complete at 8.3°C (Chittenden and Westman 1967), and in the Chesapeake Bay watershed, all juveniles had left once temperatures reached 8.3°C (Chesapeake Bay Program 1988). In North Carolina rivers, juvenile peak emigration was observed when temperatures fell below 15.1°C (Neves and Depres 1979; Boreman 1981). Limburg (1996) and O'Donnell (2000) found evidence that emigration downstream had already begun by mid-summer, before fall temperatures decreased. Limburg (1996) suggested that at the population level, temperature may provide the stimulus for fish to emigrate, or it may be a gradual process that is cued by size of fish, with early cohorts leaving first.

Depth

Juveniles have been observed at depths ranging from 0.9 m to 4.9 m in the Connecticut River (Marcy 1976a); however, abundance was related to the distance upstream and not to depth (MacKenzie et al. 1985). Chittenden (1969) observed juveniles in the Delaware River most often in deeper pools away from the shoreline in non-tidal areas during daylight hours, and to a much lesser degree, in shallow riffles. In the Connecticut River, juveniles were caught primarily at the bottom during the day (87%) and all were caught at the surface at night (Marcy 1976a). After sunset, juveniles will scatter and can be found at all depths (Miller et al. 1973).

Although there were a lack of data for depth optima for juveniles, Stier and Crance (1985) developed a suitability index based on input provided by research scientists. They suggested that for all life history stages, including juveniles, the optimum range for river depth is between 1.5-6.1 m. Depths less than 0.46 m and greater than 15.24 were designated as unsuitable.

Salinity

Early studies of juveniles provide conflicting results of responses to changes in salinity. For example, Tagatz (1961) observed 60% mortality for juveniles in isothermal transfers (21° C) from freshwater to 30-ppt seawater, while Chittenden (1973) observed 100% survival in isothermal (17° C) transfers from freshwater or 5 ppt to 32 ppt salinities. Juveniles that were transferred from 30 ppt seawater to freshwater suffered 100% mortality, but no mortalities resulted when they were transferred from 5 ppt to freshwater (Chittenden 1973b). In general, shad are considered to be capable of enduring a wide range of salinities at an early stage in their life, especially if salinity changes are gradual (Chittenden 1969).

When accompanied by temperature changes, juveniles could generally adapt to abrupt transfers from freshwater to saltwater, but high mortality resulted when transferred from saltwater to freshwater (Tagatz 1961). At temperature increases <14°C, all juvenile fish survived abrupt transfers from saltwater (15 ppt and 33 ppt salinity) to freshwater. Conversely, no fish survived transfers from freshwater (at 21.1°C) to saltwater (33 ppt) at 7.2-12.8°C. Freshwater transfers to 15 ppt in association with temperature decreases <4° C also resulted in high mortalities (30-50%).

Experiments conducted on shad and other anadromous fish (Rounsefell and Everhart 1953; Houston 1957; Tagatz 1961; Zydlewski and McCormick 1997a, 1997b) have found that fish undergo physiological changes before emigrating to saltwater. This ability to adapt to changes in salinity occurs at the onset of metamorphosis, between 26 and 45 days post-hatch. Researchers noted that the ability to osmoregulate in full-strength seawater is an important factor that limits the early life history to freshwater and low-salinity estuaries (Zydlewski and McCormick 1997b). It was suggested that a decrease and subsequent loss of hyperosmoregulatory ability in shad may serve as a proximate cue for juveniles to begin their downstream migration (Zydlewski and McCormick 1997b).

Water velocity/flow

Ideal water velocity rates are thought to range between 6-75 cm/sec (0.06-0.75 m/sec) for the juvenile non-migration stage (Klauda et al. 1991). The rate of water velocity is also critical for fish migrating downstream that pass over spillways (MacKenzie et al. 1985). It has been suggested that water flow may serve to orient emigrating juveniles in the downstream direction. Studies conducted on shad in the St. Johns River, Florida led researchers to speculate that lack of current from low water levels could result in the inability of juveniles to find their way downstream (Williams and Bruger 1972).

Bottom composition

Although juveniles were found to be most abundant where boulder, cobble, gravel and sand were present, (Walburg and Nichols 1967; Odom 1997), substrate type is not considered to be a critical factor in nursery areas (Krauthamer and Richkus 1987). Estuarine productivity is linked to freshwater nutrient (detritus) input to the estuary (Biggs and Flemer 1972; Hobbie et al. 1973; Saila 1973; Day et al.1975) and detritus production in the salt marsh (Teal 1962; Odum and

Heald 1973; Reimhold et al. 1973; Stevenson et al. 1975). Based on the assumption that the amount of submerged and emergent vegetation will be a qualitative estimate of the estuary's secondary productivity, and therefore, food availability (zooplankton) to juvenile shad, Stier and Crance (1985) suggested that estuarine habitat with 50% or more vegetation coverage is optimal.

It is important to note that, although no link has been made between the presence of SAV and abundance of alosines, there seems to be a general agreement that there is a correlation between water quality and alosid abundance (Sadzinski 2003). Abundance of SAV is often used as an indirect measure of water quality, with factors such as available light (Livingston et al. 1998), salinity, temperature, water depth, tidal range, grazers, suitable sediment quality, sediment nutrients, wave action, current velocity, and chemical contaminants controlling the distribution of underwater grasses (Koch 2001). Maryland has made it a priority to increase the amount of SAV within the Chesapeake Bay watershed in order to improve water quality. If SAV in a given area increases, this can be used as an indicator of improved water quality, which in turn, will likely benefit alosine species (Sadzinski 2003).

Ross et al. (1997) found no overall effect of habitat type on juvenile relative abundance in the upper Delaware River, indicating that juveniles use a wide variety of habitat types to their advantage in many nursery areas. They suggested that in contrast to earlier life stages and spawning adults, premigratory juveniles may be habitat generalists. They did however, find a positive relationship between abundance of juvenile American shad and percent of SAV cover in SAV habitats only. Odom (1997) found that juvenile American shad favored riffle/run habitat in the James River, especially areas with extensive beds of water stargrass (Heteranthera dubia). These areas provided flow-boundary feeding stations where juvenile shad could feed on drifting macroinvertebrates while reducing their energy costs. Finally, it should be noted that Dixon (2004, per. comm.) commented that since juvenile blueback herring (another alosine species) are a pelagic schooling fish, they likely do not rely on SAV to the extent that other anadromous fish do for predator avoidance, such as striped bass.

pH

Areas that are poorly buffered (low alkalinity) and subject to episodic or chronic acidification may provide less suitable nursery habitat than areas that have higher alkalinities and are less subject to episodic or chronic acidification (Klauda et al. 1991). Juveniles may be less at risk to changes in pH because they move downstream to brackish areas that may have a higher buffering capacity (Klauda 1989). No additional information regarding different pH effects on juveniles could be found.

Dissolved oxygen

Seemingly healthy juvenile shad have been collected in the Hudson River, New York, where dissolved oxygen (DO) concentrations were 4-5 mg/L (Burdick 1954). Similarly, in headponds above hydroelectric dams on the St. John River, New Brunswick, DO must be at least 4-5 mg/L for migrating juveniles to pass through (Jessop 1975). Under laboratory conditions, juveniles did not lose equilibrium until DO decreased to 2.5-3.5 mg/L (Chittenden 1969; 1973a). In the Delaware River, DO concentrations less than 3.0 mg/L blocked juvenile migration, and DO below 2.0 mg/L was lethal. Emigrating juveniles have historically arrived at the upper tidal section of the Delaware River by mid-October, but could not continue further seaward movement until November or December, when the pollution/low oxygen conditions dissipated (Miller et al. 1982). Juveniles have been reported to survive brief exposure to DO concentrations of as little as 0.5 mg/L, but survived only if >3 mg/L was available immediately thereafter (Dorfman and Westman 1970).

Because minimum dissolved oxygen values have a more adverse effect upon fish than average dissolved oxygen values, minimum criteria has been recommended. Dissolved oxygen concentrations less than 5.0 mg/L are considered sublethal to juvenile American shad (Miller et al. 1982). As with spawning areas, Bilkovic (2000) assigned a value of >5.0 mg/L dissolved oxygen as optimal for nursery areas.

Turbidity

Ross et al. (1997) suggested that optimal turbidity values for premigratory juveniles in tributaries only is between 0.75-2.2 nephelometric turbidity units (NTU). While preliminary, these results could be cautiously applied to other river systems, but consideration should be given to the range and diversity of habitat types in the river system under study before applying the models.

Subadults

Fish remain in the ocean for 2-6 years before becoming sexually mature, whereupon, they return to their natal rivers to spawn (Talbot and Sykes 1958; Walburg and Nichols 1967). Both sexes mature at a minimum of 2 years, with males maturing on average in 4.3 years and females maturing on average in 4.6 years (Leggett 1969). Fish north of Cape Hatteras are repeat spawners and will return to rivers to spawn when temperatures are suitable. American shad typically live to be 5 to 7 years of age.

Results from 50 years of tagging indicate that discrete aggregations of fish occur at sea, comprised of juveniles and adults (Talbot and Sykes 1958; Leggett 1977a, c; Dadswell et al. 1987; Melvin et al. 1992), at the same time, at widely separated geographic locations (Dadswell et al. 1987). These aggregations are a heterogeneous mixture from many rivers (Dadswell et al. 1987), but it is unknown if fish from all river systems along the East Coast intermingle at all times of the year (Neves and Depres 1979). Populations that return to rivers to spawn are a relatively homogeneous group, (Dadswell et al. 1987) and fish from all river systems can be found entering coastal waters as far south as North Carolina in the winter and spring (Neves and Depres 1979).

Dadswell et al. (1987) summarized the following seasonal time/locations for American shad: 1) January-February – fish are off Florida, the Middle Atlantic Bight, and Nova Scotia and entering streams to spawn from Florida to South Carolina; 2) March and April – fish are moving onshore and northward, from the Middle Atlantic Bight and Nova Scotia, with spawning underway from North Carolina to the Bay of Fundy; 3) Late June – concentrated in the inner Bay of Fundy, in the inner Gulf of St. Lawrence, the Gulf of Maine, and off Newfoundland and Labrador; however, spawning fish are still upstream from the Delaware River to the St. Lawrence River; 4) Autumn – fish leaving the St. Lawrence estuary are captured across the southern Gulf of St. Lawrence, while fish leaving the Bay of Fundy are found from Maine to Long Island, and some have already arrived as far south as Georgia and Florida.

Dadswell et al. (1987) analyzed tag returns, occurrence records, and trawl survey data and found that there are three primary offshore areas where fish aggregations spend the winter at sea: off the Scotian Shelf/Bay of Fundy region, in the Middle Atlantic Bight, and off the Florida coast. It appears that the majority of fish overwintering along the Scotian Shelf region spawn in rivers in Canada (Vladykov 1936; Melvin et al. 1985), and to a lesser degree, in the mid-Atlantic region and off the Florida coast (Williams 1985). Fish aggregations that overwinter off the mid-Atlantic coast represent populations that spawn in rivers from Georgia to Quebec (Talbot and Sykes 1958; White et al. 1969; Miller et al. 1982; Dadswell et al. 1987). Winter habitat in the mid-Atlantic region occurs primarily from Maryland to North Carolina (ASMFC 1999). The regional composition of aggregations overwintering off the Florida coast is unknown. Leggett (1977a) proposed the approximate time and location of fish heading south to overwinter off Florida based on migration rates and an average departure date of October 1 from the Gulf of Maine/Bay of Fundy area: Rhode Island/Long Island coast in mid-to-late October, off Delaware Bay in early November, and off the coast of North Carolina, Georgia, and Florida in early December. Early migration studies of shad found that during mild winters, fish in small quantities sometimes entered sounds of North Carolina during November and December, but disappeared if the weather became cold (Talbot and Sykes 1958).

Most shad populations overwintering off the mid-Atlantic coast migrate shoreward in waters between 36° to 40° N in the winter and early spring. Prespawning adults homing to rivers in the South Atlantic migrate shoreward north of Cape Hatteras, North Carolina, then head south along the coast to their natal rivers. The proximity of the Gulf Stream to North Carolina provides a narrow migrational corridor at Cape Hatteras if fish are to remain within their preferred temperature range of 3-15°C. Although prespawning adults are not required to follow a coastal route to North Atlantic rivers because temperatures in the Mid-Atlantic Bight are well within the shad’s range of oceanic occurrence in the spring, tag returns indicate that they most likely enter waters in the lower Mid-Atlantic region, then migrate north along the coast. South of Cape Cod, prespawning shad migrate close inshore (Leggett and Whitney 1972), but north of there, the migration corridor is less clear (Dadswell et al. 1987). Prespawning adults may detour into estuaries during their coastal migration, but the timing and duration of stay is unknown (Neves and Depres 1979). Although poorly documented, immature American shad (age 1+) may also enter estuaries and accompany adults to the spawning grounds, more than 150 km upstream (Limburg 1995, 1998).

Neves and Depres (1979) determined that a second group of fish were found offshore mostly at depths of 50-100 m and limited to near-bottom temperatures of 3-15°C; however, these fish are likely juveniles and nonspawning adults that join spent adults in their summer grounds (Dadswell et al. 1987). Nonspawning adults have also been recorded in brackish estuaries (Hildebrand 1963; Gabriel et al. 1976).

Dadswell et al. (1987) found three primary summer aggregations of shad at sea: the Bay of Fundy / Gulf of Maine, the St. Lawrence estuary, and off the Newfound and Labrador coast. Neves and Depres (1979) also found distinct summer aggregations on Georges Bank and south of Nantucket Shoals. Shad from all river systems, including those from South Atlantic rivers, have been collected in the Gulf of Maine during the summer (Neves and Depres 1979), their summer feeding grounds. Fish from north Atlantic rivers are most abundant in the Bay of Fundy in the early summer, while abundance of fish from the southern range does not peak until mid-summer (Melvin 1984; Dadswell et al. 1987). These migrating shad groups are a mixture of juveniles, immature subadults, and spent and resting adults that originate from rivers along the entire East coast (Dadswell et al., 1983). Since there are very few repeat spawners in the southern range, the majority of fish that migrate to the Bay of Fundy from areas south of Cape Lookout, North Carolina are juveniles (76%) (Melvin et al. 1992).

Fish enter the Bay of Fundy in early summer and move throughout the inner Bay of Fundy in a counterclockwise direction with the residual current, with the entire run lasting four months (Dadswell et al. 1987). As water temperatures decline in the fall, shad begin moving through the Gulf of Maine by October, and continue to their offshore wintering grounds. Offshore, they have been captured in late fall and winter 80-95 km offshore of eastern Nova Scoatia (Vladykov 1936), 65-80 km off the coast of Maine, 40-145 k, off southern New England, and the southern part of Georges Bank, 175 km from the nearest land (Bigelow and Schroeder 2002; Dadswell et al. 1987).

Temperature

Early studies by Leggett and Whitney (1972) found that shad moved along the coast within a "migrational corridor" where water temperatures were between 13-18°C. Neves and Depres (1979) later modified the near-bottom temperature range from 3-15°C, with a preferred range of 7-13°C. They also hypothesized that seasonal movements are broadly controlled by climate, and that shad followed paths along migration corridors or oceanic paths of "preferred" isotherms. This theory has been revised with supporting data that indicate shad cross thermal barriers, remain for extended periods in temperatures outside their "preferred" range, and migrate rapidly between regions regardless of currents and temperatures (Melvin et al. 1985; Dadswell et al. 1987). More recent studies have documented nonreproductive shad migrating from wintering grounds in the Mid-Atlantic Bight through the Gulf of Maine during May-June, where a constant sub-surface temperature of 6°C prevails, to reach the Bay of Fundy by mid-summer (Dadswell et al. 1987).

Temperature change and some aspect of seasonality (i.e. day length) may initiate migratory behavior, but timing of the behavior by different fish may be influenced by intrinsic (genetic) factors and life history stage of the fish; chance may also play a small role in determining which direction a fish will follow, at least within a confined coastal region. Dadswell et al. (1987) concluded that extrinsic factors related to ocean climate, seasonality, and currents may provide cues and clues for portions of nongoal-oriented migration, while intrinsic cues and bicoordinate navigation appear to be important during goal-oriented migration.

Depth

While it is known that adults move offshore to deeper waters during the fall and early winter, information regarding preferred depths is lacking. Shad have been found throughout a broad depth range in the ocean, from surface waters to 340 m (Walburg and Nichols 1967; Facey and Van Den Avyle 1986). Catch data analyses showed that they were caught at depths ranging from surface waters to 220 m (Walburg and Nichols 1967), but are most commonly found at intermediate depths of 50-100 m (Neves and Depres 1979). Seasonal migrations are thought to occur mainly in surface waters (Neves and Depres 1979).

The summer and autumn months are a time of active feeding, and analyzing stomach contents has served as a means for inferring distribution in the water column. Studies by Neves and Depres (1979) suggested that American shad follow diel movements of zooplankton, staying near the bottom during the day and dispersing in the water column at night. It was also thought that water temperature preference confined their depth range to 50-200 m. Other researchers (Dadswell et al. 1983) have suggested that light intensity may control depth selection by shad. For example, shad swim much higher in the water column in the turbid waters of Cumberland Basin, Bay of Fundy than they do in clear coastal waters, where they select deeper water. Both areas are within the same light intensity range.

Salinity

During their residence in the open ocean, sub-adults and adults will live in sea water that is approximately 33.0 ppt. During their coastal migration, prespawning adults may detour into estuaries, where water is more brackish, but the timing and duration of stay is unknown (Neves and Depres 1979).

Suspended solids/turbidity

The preference zone for light intensity was found to be limited to surface waters (2-10 m) for shad in the Bay of Fundy during the summer and fall because of extreme turbidity (Dadswell et al. 1983). Although this made them more susceptible to fishing gear that operated near surface waters, these waters are highly productive sources of zooplankton. Sight-oriented planktivores may be at a disadvantage in these turbid waters, but shad, which can use a filter-feeding mechanism, may have a competitive advantage.

Ecological relationships

Adults

Food

Recent feeding studies (Walters and Olney 2003) of American shad during spawning migrations in the York River, Virginia found that fish continued to feed actively as they moved from the open ocean into coastal waters. Diet composition changed as coastal and estuarine copepods (*C. typicus, Acartia* spp.) replaced the oceanic C. finmarchicus as the major constituents of the diet and the estuarine mysid shrimp *N. americana* increased in importance, replacing euphausids. Feeding intensity decreased as fish entered the estuary, but fish still selected for the most abundant and larger planktonic crustaceans. Minor amounts of other crustaceans were found in stomachs including cumaceans, sevenspine bay shrimp *Crangon septemspinosa*, and gammarid amphipods.

Early researchers thought that adult American shad typically do not feed in freshwater during upstream migration or after spawning until they leave the river (Hatton 1940; Moss 1946; Nichols 1959). One theory was that cessation of feeding may stem from the fact that most of the available food in the freshwater environment may be too small to be retained by adult gill rakers (Walburg and Nichols 1967). Atkinson (1951) proposed that fish stop feeding because of the physical separation from suitable food sources rather than a behavioral or physiological reduction in feeding. Chittenden (1969; 1976b) found minor quantities of insects and juvenile fish in the stomachs of migrating fish, and Atkinson (1951) found that fish would feed in experimental enclosures. Adult shad have even been known to strike at fishing lures. Atkinson's theory would seem to support the observations of these latter studies.

Walter and Olney (2003) found woody and green plant debris in the stomachs of adult shad at the spawning grounds, which has little or no nutritional value; however, they discovered that shad resumed feeding during postspawning migration. Stomach fullness was comparable to those values observed for shad feeding in the open ocean and estuary, with spent and partially spent adults feeding on mostly mysid shrimp. These results further support Atkinson's theory that adults feed if there is suitable prey available. Walter and Olney (2003) suggested that the ability to feed during some portion of migration and soon after spawning may be important in decreasing postspawning mortality. Given their significant energetic expenditures and weight losses during their migration (Glebe and Leggett 1981a; 1981b), the resumption of feeding likely represents a return to natural feeding patterns, which allows the fish to begin regaining lost energy reserves (Walter and Olney 2003). Finally, the ability to survive spawning has been correlated with the degree of energy lost (Glebe and Leggett 1981b; Bernatchez and Dodson 1987), and fish that feed actively before and after spawning may have a higher likelihood of repeat spawning. Fish whose spawning grounds are in closer proximity to estuarine food sources (and don't expend as much energy as fish that have to travel farther), and emigrating fish that have partially spent ovaries that can be resorped for energy (Olney et al. 2001) may have a high frequency of repeat spawning and lower energy expenditures (Walter and Olney 2003).

Competition and predation

Earlier studies found that adult shad were preyed upon primarily by seals and humans (Scott and Crossman 1973), and had few other predators (Scott and Scott 1988). More recent studies (Erkan 2002) have found that predation of alosines has increased dramatically in Rhode Island rivers in recent years, especially by the double-crested cormorant, which often takes advantage of fish staging near the entrance to fishways. Predation by otters and herons has also increased, but to a lesser extent (Erkan 2003). A recent study strongly supports the hypothesis that striped bass predation on adult American shad in the Connecticut River has resulted in a dramatic and unexpected decline in shad abundance since 1992 (Savoy and Crecco in press). Researchers further suggest that striped bass prey primarily on spawning adults because their predator avoidance capability may be compromised at this time, due to their strong drive to spawn during upstream migration. Rates of predation on ages 0 and 1 alosines was also much lower.

In South Atlantic coastal rivers where the percentage of repeat spawning is low or non-existent, adult shad that die after spawning may contribute significant nutrient input from the marine system into freshwater interior rivers (ASMFC 1999). Garman (1992) hypothesized that before recent declines in abundance, the annual input of marine-derived biomass of postspawning alosines was an important seasonal source of energy and nutrients for the non-tidal James River.

<u>Eggs and larvae</u>

Food

Once the yolk sac is absorbed, larvae initially consume zooplankton, and add copepods, immature insects (i.e. midge larvae and midge pupae), and adult aquatic and terrestrial insects as they grow (Leim 1924; Mitchell et al. 1925; Maxfield 1953; Crecco and Blake 1983; Facey and Van Den Avyle 1986). Several studies (Crecco and Blake 1983; Johnson and Dropkin 1995) have noted varying levels of selectivity for copepods and cladocerans, but zooplankton and chironomids generally comprise the bulk of their diets (Maxfield 1953; Levesque and Reed 1972). Feeding occurs most actively in late afternoon/early evening, peaking between 1200 h and 2000 h (Johnson and Dropkin 1995), and least intensively near dawn (Massman 1963; Grabe 1996). They are opportunistic feeders, shifting their diet depending on availability, river location, and their size (Leim 1924; Maxfield 1953; Walburg 1956; Levesque and Reed 1972; Marcy 1976a).

Researchers have also attempted to determine if the patchiness of planktonic prey has any effect on cohort survival. The effect of prey patchiness on cohort survival will vary with overall prey density such that increasing levels of patchiness will enhance survival when productivity or average prey density is low, but will reduce cohort survival when productivity is high. Thus, except when average prey densities of plankton are particularly high, prey patchiness may be a requirement for survival of fish larvae (Letcher and Rice 1997).

Predation and starvation are thought to be the primary causes of mortality among larval fish (May 1974; Hunter 1981), with some studies showing that starving larvae are more susceptible to predation than non-starving larvae (Rice et al. 1987). Newly-hatched larvae must begin feeding within 5 days; otherwise, they will succumb to death from malnutrition (Wiggins et al. 1984). Older larvae have significantly reduced survival rates if they are deprived of food for as little as 2 days (Johnson and Dropkin 1995). Researchers have also found that larvae fed at intermediate prey densities of 500 l-1 survived as well as those fed at high prey densities, and significantly higher than starved larvae, which indicates that some minimal level of feeding in riverine reaches can increase survival (Johnson and Dropkin 1995).

It has been suggested that clupeids evolved so as to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter and Hunter 1982). Shad larval survival rates have been found to vary in proportion to May-July zooplankton densities (Crecco et al. 1983). Limburg (1996) determined that zooplankton densities corresponded with times of larval stages of recruited juveniles, with the year-class being established by cohorts hatched after June 1, despite larval abundance being highest during May. She attributed higher growth rates for fish hatched in June to more favorable conditions that were present then, including warmer temperatures, lower flow rates, and high zooplankton densities.

Competition and predation

American shad eggs and larvae are primarily preyed upon by American eels and striped bass (Mansueti and Kolb 1953; Walburg and Nichols 1967; Facey et al. 1986). Once shad fry hatch from their eggs, they are eaten by minnows, shiners, and likely, any fish that is large enough to consume them (McPhee 2002).

American shad larvae that were stocked in the Susquehanna River, PA were found to experience the lowest percentage mortality at releases of 400,000 to 700,00 larvae (Johnson and Ringler 1998). A high rate of larval mortality at releases up to 400,000 may have been due to depensatory mechanisms operating as small releases, and releases above 700,000 may have resulted in increased predator aggregation at the site. Although individual predators were found to contain up to 900 shad larvae, mortality of shad larvae at the stocking site was usually less than 2%, an insignificant source of mortality.

Contaminants

The lethal dose (LD_{50}) of sulfates for eggs was >1000 mg/L at 15.5°C. The LD_{50} of iron for eggs was greater than 40 mg/L between pH 5.5-7.2 (Bradford et al. 1968). Eggs that were exposed to zinc and lead concentrations of 0.03 and 0.01 mg/L experienced high mortality rates within 36 hours (Meade 1976). When water hardness was low (i.e. 12 mg/L), the toxicity of the zinc and lead were intensified (Klauda et al. 1991).

<u>Juveniles</u>

Food

Juveniles favor zooplankton over phytoplankton (Maxfield 1953; Walburg 1956), and in general, have a wider selection of prey taxa than larvae. Their long, closely-spaced gill rakers enable shad to effectively filter plankton from the water column during respiratory movements (Leim 1924). They are opportunistic feeders, whose freshwater diet includes copepods, crustacean zooplankton, cladocerans, aquatic insect larvae, and adult aquatic and terrestrial insects (Leim 1924; Maxfield 1953; Massmann 1963; Levesque and Reed 1972; Marcy 1976a). Although juveniles consume most of their food from the water column (ASMFC 1999), many of the crustacean organisms that juveniles feed upon are benthic (Krauthamer and Richkus 1987). Leim (1924) speculated that although shad obtain a minor amount of food near the bottom, they do not pick if off the bottom, but capture items as they are carried up into the water column a short distance by tidal currents, including molluscs.

Walburg (1956) found that juveniles fed primarily on suitable organisms that were readily available. In contrast, Ross et al. (1997) found that juveniles in SAV habitat fed principally on chironomids, while those feeding in tributaries fed almost exclusively on terrestrial insects, despite the fact that they were less available than other food sources. Researchers did not attribute the differences to developmental limitations, but concluded that there were true habitat feeding differences. Other studies have noted different selection of organisms along the same river, but at different locations, such as above a dam (Levesque and Reed 1972) or downstream of a dam (Domermuth and Reed 1980).

In waters of Virginia, Massman (1963) found that juveniles upstream consumed more food than juveniles that remained downstream near their spawning grounds. The upstream sections of the river had a greater shoreline to open water ratio that may have provided a greater source of terrestrial insects, a favored prey item (Massman 1963; Levesque and Reed 1972), while the downstream sections provided a greater source of autochthonously-derived prey. In contrast, the lower reach of the Hudson River was found to be more productive (as a function of primary productivity and respiration rates) than upper and middle reaches (Sirois and Fredrick 1978; Howarth et al. 1992). This greater productivity may have led to observed higher fish production in the lower estuary, as well as a higher relative condition of downriver juvenile shad earlier in the season, compared to upriver and midriver fish (Limburg 1994).

Juveniles increase feeding as the day progresses, achieving a maximum at 2000 h (Johnson and Dropkin 1995). Juveniles in the Mattaponi and Pamunkey Rivers, Virginia, were found feeding during the day with stomachs reaching maximum fullness by early evening (Massman 1963). After juveniles leave coastal rivers and estuaries for nearshore waters, they may prey on some fish, such as smelt, sand lance, silver hake, bay anchovy, striped anchovy, and mosquitofish (Leidy 1868; Bowman et al. 2000).

At least one non-native species has proven to have an impact on young-of-the-year shad. In the Hudson River, there is strong evidence that zebra mussel colonization has reduced the forage base of American shad (Waldman and Limburg 2003).

Competition and predation

Juveniles in freshwater may be preyed upon by American eels, bluefish, weakfish, striped bass, and birds (Mansueti and Kolb 1953; Walburg and Nichols 1967; Facey et al. 1986).

There are three species of alosines (American shad, alewife, and blueback herring) common to many east coast river systems, including the Hudson River (hickory shad is more scarce). Differences in distribution, diel activity patterns, and feeding habits are evident in the Hudson River, and are likely mechanisms that may reduce competition between juveniles (Schmidt et al. 1988). For example, several researchers have noted that larger individuals of shad (Chittenden 1969; Marcy 1976a; Schmidt et al. 1988) and alewives (Loesch et al. 1982; Schmidt et al. 1988) move downstream first, which helps to segregate the species. All three Alosa species exhibited diel vertical migrations from near the bottom during the day to the surface at night in the Mattaponi River, Virginia (Loesch et al. 1982). In addition to vertical segregation, there is also diel, inshore-offshore segregation. Both American shad and blueback herring juveniles occur in shallow nearshore waters during the day. Competition for prey between shad and bluebacks is often reduced by: 1) more opportunistic feeding by shad; 2) differential selection for cladoceran prey; and 3) higher utilization of copepods by blueback herring (Domermuth and Reed 1980). Shad feed most often in the upper water column, the air-water interface (Loesch et al. 1982), and even leap from the water (Massman 1963), feeding on Chironomidae larvae, Formicidae, and Cladocera; they are highly selective for terrestrial insects (Davis and Cheek 1966; Levesque and Reed 1972). Juvenile bluebacks are more planktivorous, feeding on copepods, larval dipterans, and Cladocera (Hirschfield et al. 1966), but not the same cladoceran families that alewives feed on (Domermuth and Reed 1980).

Physical habitat variables

Although considered preliminary, Ross et al. (1997) found optimum suitability for juveniles in the Delaware River at temperatures of 19.5-24.5° C in riffle habitat only. They also found maximum suitability for juveniles at depths between 0.5-1.5 m in SAV habitat only. It is not known if the same conditions in other rivers would have similar results; comparable results may be more likely if the range and proportion of habitat types were similar to those that were studied.

Contaminants

The 48 h lethal concentrations (LC_{50}) for juvenile shad ranged from 2,417-91,167 mg/L for gasoline, No. 2 diesel fuel, and bunker oil. The effects of gasoline and diesel fuel were exacerbated when DO was simultaneously reduced. Juveniles exposed to gasoline concentrations of 68 mg/L at 21-23° C resulted in a lethal time (LT_{50}) of 50 minutes when DO was reduced to 2.6-3.2 mg/L. Juveniles that were exposed to 84 mg/L of diesel fuel at 21-23°C and DO between 1.9-3.1 mg/L experienced an LT_{50} of 270 minutes (Tagatz 1961).

Subadults

Food

While they are offshore, shad are primarily planktivorous, feeding on whatever is most readily available, such as copepods, mysid shrimps, ostracods, amphipods, isopods, euphausids, larval barnacles, jellyfish, small fish, and fish eggs (Willey 1923; Leim 1924, Bigelow and Schroeder 1953; Maxfield 1953; Massmann 1963; Levesque and Reed 1972; Marcy 1976a). In the Bay of Fundy, shad were found to consume mostly planktonic and epibenthic crustaceans, while benthic organisms were rare (Themelis 1986). Differences in dominant prey items were attributed to changing availability of zooplankton assemblages and the size of the shad. Juveniles fed more extensively on copepods than adults and a smaller proportion of their diet was composed of large prey items such as euphausids and mysids. In earlier studies, Leim (1924) reported similar observations, with copepods decreasing in importance in the diets of shad over 400 mm in length. Detritus has also been found in the stomachs of shad, but it probably provides little nutritional value and is simply ingested during the course of feeding (Themelis 1982).

The Bay of Fundy is regarded as the primary summer feeding grounds for American shad, however, the entire Bay does not provide optimal feeding conditions for adults. For example, although both adult and juvenile shad feed readily in the oceanic lower Bay of Fundy, only juveniles feed to a large extent within the turbid and estuarine waters of the upper Bay. This is attributed to their ability to successfully filter smaller prey items that dominate the upper Bay (Themelis 1982).

Competition and predation

Once they are in the ocean, American shad are undoubtedly preyed upon by many species including sharks, tunas, king mackerel, seals, and porpoises, given their schooling nature and their lack of dorsal or opercular spines (Melvin et al. 1985; Weiss-Glanz et al. 1986).

Current research has found that American shad can detect ultrasonic signals to at least 180 kHz, which is within the range that echolocating harbour porpoises and bottlenose dolphins use to track shad and herring. In the laboratory environment, shad have been observed modifying their behavior in response to echolocation beams, such as turning slowly away from the sound source, forming very compact groups, and displaying a quick “panic” response. Although behavior in a natural environment may be different from that observed in experimental tanks, this study suggests that shad may have evolved a mechanism to make themselves less “conspicuous” or less easily preyed upon by echolocating odontocetes (Plachta and Popper 2003).

Abundance and status of stocks

Stock declines have been attributed to overfishing, habitat loss, and pollution over the past 170 years (Limburg et al. 2003). Historic catch levels of 30,000 metric kg at the turn of the century (Walburg and Nichols 1967) have dropped considerably since then, to a low of 0.6 million kg in 1996 (AMSFC 1999). Stocks continue to decline in many of the coastal rivers along the East Coast, including the Hudson River, New York populations. There are some populations, however, that have either stabilized for the time being, or have actually increased in numbers, such as stocks in the Connecticut River, the Pawcatuck River, Rhode Island, and the Santee River, South Carolina (ASMFC 1988; Cooke and Leach 2003). Although overfishing was attributed to the decline in American shad landings in many East Coast rivers during the 1950s-1970s (Talbot 1954; Walburg 1955; Walburg 1963; Williams and Bruger 1972; Sholar 1976;), by 1987, it was determined that overfishing was no longer occurring for 12 coastal stocks, and that stock sizes were generally stable (Gibson et al. 1988). The most recent coastwide assessment of American shad (1998) has re-affirmed that most of the stocks are still not overfished; however, overall stock abundance is still historically low. Thus, researchers have concluded that "The current strategy to restore American shad stocks by improving habitat and fish passage, stocking, and inter-basin transfers will yield much stronger dividends than a strategy of stock restoration based solely on reduction of fishing mortality (Boreman and Friedland 2003)."

Information on adult migration trends, migration physiology, and young-of-the-year ecology is good (Limburg et al. 2003) but data for some habitat requirements are lacking. Much of the information contained in this document was derived from fisheries surveys, and research studies on American shad and other fish from the sub-family Alosinae (also referred to as "alosines").

Refer to Abundance and Status of Stocks in section 4.2.3.

4.2.5 Atlantic Sturgeon

Description and Distribution

Atlantic sturgeon, *Acipenser oxyrinchus*, are an anadromous species found in Atlantic coastal waters and major river basins from the Hamilton River and George River, Ungava Bay, Labrador, to Port Canaveral and Hutchinson Island, Florida (Van den Avyle, 1983). Based on historical records, important sturgeon fisheries existed in essentially all Piedmont river basins on the Atlantic coast (Goode, 1887). The early accounts of the sturgeon fishery landings did not distinguish between Atlantic sturgeon and the smaller shortnose sturgeon (*Acipenser breivirostrum*); however it is likely that accounts referred to the larger and more valuable Atlantic sturgeon. Following intense exploitation for food and construction of mainstem river dams during the 19th and early 20th centuries, sturgeon populations were drastically reduced throughout their range and extirpated in some rivers (ASMFC, 1998; NMFS and U.S. FWS, 1998). Spawning populations of Atlantic sturgeon are thought to be extirpated in the St. Marys River, Georgia, as well as in the Connecticut River and in all Maryland and Pennsylvania tributaries of the Chesapeake Bay (Rogers and Weber 1995; ASMFC, 1998; NMFS and U.S. FWS, 1998).

This anadromous species is motile, long lived and utilizes a wide variety of habitats. Atlantic sturgeon require either estuaries or upriver habitats for reproduction and early life stages, along with a hard substrate bottom for spawning (Vladykov and Greeley, 1963; Huff, 1975; T. Smith, 1985). Coastal migrations and frequent movements between the estuarine and upstream riverine habitats are characteristic of this species. Historical accounts describe captures of large sturgeon, most probably Atlantics, during the summer and fall months in fall-line habitats on the Savannah River (Lawson, 1711). In some systems, Atlantic sturgeon may prefer extensive reaches of higher gradient boulder, bedrock, cobble-gravel, and coarse sand substrates free of siltation for spawning habitat (Brownell et al., 2001). Juvenile and adult Atlantic sturgeon frequently congregate in the upper estuary habitats in the vicinity of the saltwater interface, and may move to and from the upstream areas during the summer and fall months, and during late winter and spring spawning periods. Adult Atlantic sturgeon may spend many years between spawning seasons in marine waters.

Much of the habitat information on Atlantic sturgeon remains incomplete. Due to the relatively low numbers of fish in many river basins, habitat utilization patterns have been difficult to establish with certainty (Collins et al., 2000a). Life history, behavior, and movements have been more thoroughly documented in the Hudson River, while many other river systems are lacking in vital life history information (Gross et al., 2002).

Reproduction

Spawning and Spawning Habitat

Atlantic sturgeon are thought to spawn in freshwater (Van den Avyle, 1983), although sturgeon might also spawn in the tidal freshwater regions of large estuaries. This trend however has been seen in the north where obstructions occur on the estuarine portion of the rivers. In the south, where many rivers remain unblocked, sturgeon have been documented ascending hundreds of miles upstream into freshwater rivers to spawn (M. Collins, Personal Communication). Spawning migrations are likely cued to temperature and occur earlier in the South Atlantic in comparison to those located to the North (T. Smith 1985). In Florida, Georgia, and South Carolina, spawning migrations begin in February. In the Edisto River, South Carolina, ripe males were captured as early as March 2nd and a single ripe female was captured on March 7th (Collins et al., 2000b). Spent males were captured as early as late March, and spent females were caught as late as mid-May (Collins et al., 2000b). In the Chesapeake Bay, spawning migrations historically began in April (Hildebrand and Schroeder, 1928), and in the Delaware Bay, spawning migrations occur April through May (Secor and Waldman, 1999). Spawning also begins in May in the Hudson River (Dovel and Berggren, 1983). In New England and Canada, spawning migrations occur May through July (Bigelow and Schroeder, 2002). Hatin et al. (2002) reported that spawning occurred from early June to approximately the 20th of July in the St. Lawrence River, Québec.

In addition to a spring migration, many studies document the occurrence of a fall migration (Smith et al., 1984; T. Smith, 1985; Collins et al., 2000b; Laney et al. in prep). Most fall migrations are movements out of the estuaries into marine habitat. Fall migrations occur from about September through December, again, depending on the latitude (Smith, 1985). An alternate fall migration into estuaries has been proposed to be related to spawning (Smith et al., 1984; Collins et al., 2000b; Laney et al. in prep).

Smith et al. (1984) reported an upriver migration of fish in late August and September in South Carolina, but did not identify any further signs of spawning. Collins et al. (2000b) documented similar behavior. They noted the reappearance of ripe males in South Carolina at the end of August and September. By October, 86% of the males were ripe. Furthermore, Collins et al. (2000b) tracked two sturgeon via radio and acoustic transmitters in the Edisto River, South Carolina. After spending the summer in the lower river, these fish migrated upriver to RKM 190 in October. Based on this upriver movement, they hypothesized that a fall spawning migration was occurring. An alternative explanation is that the fall migration represented fish that would reside through the winter and spawn the following spring as reported to occur in Russian sturgeons (D. Secor, Personal Communication.).

In support of fall-spawning, Collins et al. (2000b) observed spent females, including one that had spawned very recently (postovulatory follicles were still present) in late September and October in South Carolina. Although no eggs were collected, a recently spawned female was captured at RKM 56 in the fall at the same location that a ripe female had been captured in a previous year (Collins et al., 2000b). Thus, they concluded that a fall spawning migration might occur in the Edisto River, South Carolina. Laney et al. (in prep) reported a running ripe male captured by electrofishing, and other Atlantic sturgeon seen but not captured in the Pee Dee River, SC in early October. Dovel and Berggren (1983), however, found no evidence of a fall spawning migration in sturgeon in the Hudson River. The general phenomenon of fall spawning remains uncertain and merits further study. Spring spawning, however, has been well documented in the literature (ASMFC, 1998; NMFS and U.S. FWS, 1998), and may be the dominant behavior by all North American sturgeon species.

Atlantic sturgeon mature at different times along the Atlantic coast, with maturity occurring earlier in the Southern regions (Vladykov and Greeley, 1963). Females in South Carolina first spawn at ages 7-19, and males first spawn at 5-13 years. In the Hudson River, New York, females first spawn at 15-30 years and males at 8-20 years (Dovel, 1979; Smith et al., 1982; C. Smith, 1985; T. Smith 1985; Stevenson and Secor, 2000). Scott and Crossman (1973) report that in the St. Lawrence River, Canada, female Atlantic sturgeon mature at 27-28 years, and males mature at 22-34 years. There has not been much work done to verify age determination methods; Stevenson and Secor (2000) used marginal increment analysis and rearing studies to confirm the seasonality of annulus formation, and reported an aging precision of + 5 years for Hudson River Atlantic sturgeon.

Spawning Periodicity

Sexually mature Atlantic sturgeon do not spawn every year (Van Eenennam et al., 1996; Caron et al., 2002). However, some fish participate in spawning migrations even when they do not spawn (T. Smith, 1985). In South Carolina, females are thought to spawn every 3 to 5 years, while males spawn at 1 to 5 year intervals (T. Smith, 1985). During their study, Collins et al. (2000b) caught and recaught a male sturgeon in 1998 and 1999 that was in spawning condition both years. Vladykov and Greeley (1963) state that females spawn once every 2 to 3 years, while Smith et al. (1982) found that in South Carolina, an average interval of 5.4 years occurred between first and second spawnings, and 3.5 years between second and third spawnings. Results from recent research on gonad histology and hard part analysis of Hudson River Atlantic sturgeon suggest a spawning frequency of 3-5 years (Van Eenennam et al., 1996; Stevenson and Secor, 2000). Scott and Crossman (1973) indicated that spawning might occur every year in some females.

Spawning Location

The precise location of most spawning locations remains unknown. To date, spawning sites have never been verified with the collection of eggs. Spawning is thought to occur on fourteen major rivers on the Atlantic coast, with another five possibly supporting spawning stocks of Atlantic sturgeon (NMFS and U.S. FWS 1998).

As of the year 2000, spawning areas have not been identified in any of the southeastern rivers, nor have any spawning conditions been defined (Collins et al. 2000b). However, Collins et al. (2000b) state that it is possible that spawning is occurring in the Comabahee and Edisto rivers, South Carolina. Although these locations have not been verified by the collection of eggs, ripe females and one recently spawned female were collected in this area. Based on the capture of ripe, running ripe, and spent adults, Collins et al. (2000b) suggests that spawning is occurring at RKM 105 and RKM 190 in the Edisto River, South Carolina, and at RKM 55 in the Combahee River, South Carolina.

Spawning may be occurring in the Pee Dee River, North Carolina and South Carolina. Electrofishing operations directed at capturing imperiled robust redhorse suckers, conducted in 2003 by Progress Energy Carolinas, Inc., in partnership with federal and state fishery management agencies, detected five Atlantic sturgeon during October. The single sturgeon captured and examined was a running ripe male (Laney et al., in prep).

Most studies indicate that after spawning, Atlantic sturgeon migrate to salt water (Vladykov and Greeley 1963), and that down-estuary migrations may occur over several months (Bain 1997).

Physical factors affecting spawning success

Substrate is a key habitat parameter for Atlantic sturgeon, because a hardbottom substrate is required for successful egg attachment and incubation (Vladykov and Greeley 1963; Huff 1975; T. Smith 1985; Secor et al. 2002). Within rivers, the areas of cobble-gravel, coarse sand, and bedrock outcrops, which occur in the rapids complex, may be considered prime habitat. In northern rivers, these areas are nearer to the estuary than in southern rivers. South of the Chesapeake Bay, nearly all rivers have extensive rapid-complex habitats in and near the fall line zone; generally at least 100km upstream from the saltwater interface (P. Brownell, Personal Communication). This habitat provides Atlantic sturgeon with well oxygenated water, clean substrates for egg adhesion, crevices that serve as shelter for post-hatch larvae, and macroinvertebrates for food (P. Brownell, Personal Communication).

Brownell et al. (2001) developed a Habitat Suitability Index (HSI) model for spawning Atlantic sturgeon and early egg development, and found that cobble/gravel (>64 mm to 250 mm) was the optimal spawning substrate for Atlantic sturgeon. Boulder (250-4000mm) scored the second highest in the model, and silt/sand (<2.0mm) and mud/soft clay/fines scored the lowest. The curve and the data values were based on the shortnose sturgeon model, and factors such as oxygenation, substrate embeddedness, available egg attachment sites, protection of eggs from predators, light intensity, and solar warming were all hypothesized to be available in gravel, boulder, and cobble gravel substrates (Brownell et al. 2001).

Collins et al. (2000b) caught a female in the Edisto River, South Carolina, which was believed to be in the process of spawning, in an area of limestone substrate. Collins et al. (2000b) also found adult Atlantic sturgeon using fine mud, sand, pebbles, and shell substrate as a summer habitat in the Edisto River, South Carolina.

Collins et al. (2000b) reported that adult sturgeon in the Edisto River, South Carolina during the summer were at depths ranging from 1.5-13 m. They reported that the majority of sturgeons were caught at the greatest depths available for the area. The HSI model mentioned above (Brownell et al. 2001) showed that the optimal depth range in the South for spawning Atlantic sturgeon and egg incubation ranged from 2.4 m to 8 m. It should be noted that depth in this model had a maximum range of 8 m, because areas where spawning is likely to occur (areas above the fall zone) in the South are not much deeper than 8 m (Brownell, Personal Communication).

In South Carolina, ripe fish migrating to spawning areas were captured at temperatures as high as 21-23°C; the majority of ripe males were caught in water temperatures between 13-19°C (T. Smith 1985). In late September and October, spent females were caught in the Edisto River, South Carolina in waters that were 17-18°C, and a running ripe female was caught during March when the temperature was 13.6°C (Collins et al. 2000b). Collins et al. (2000b) captured a running ripe male during early March when temperatures were 13.6°C. Smith et al. (1982) recorded water temperatures of 7-8°C during the second and third week of February 1979, 1980, and 1982, in South Carolina during Atlantic sturgeon migrations. During the summer months, Collins et al. (2000b) documented adult Atlantic sturgeon in the Edisto and Combahee Rivers in temperatures as high as 33.1°C. A HSI model (Brownell et al. 2001) showed that the optimal temperature for spawning Atlantic sturgeon was 16-21 A HSI model by Brownell et al. (2001) showed that the optimal temperature for spawning Atlantic sturgeon was 16-21°C.

Atlantic sturgeon spawn in freshwater rivers, and may spawn in the tidal freshwater portion of estuaries in northeastern rivers where appropriate habitats are located in such reaches. Most studies however, report that sturgeon spawn well above the salt wedge in rivers (Dovel 1978; 1979; T. Smith 1985; Van Eenennamm et al. 1996). Collins et al. (2000b) found adult Atlantic sturgeon in salinities varying from 0-28.6 ppt in the Edisto River, South Carolina during the summer.

Sturgeon lay their eggs in flowing water (Vladykov and Greeley 1963; Van den Avyle 1983). Research suggests that the optimal water velocities for Atlantic sturgeon spawning range from 46-76 cm/s. Velocities lower than 6cm/s and higher than 107 cm/s are unsuitable for spawning (Crance 1987). A recent HSI developed for spawning Atlantic sturgeon showed that optimal water velocity for spawning and egg incubation ranged from .2 to .76 m/sec (Brownell et al. 2001).

It has been hypothesized that Atlantic sturgeon do not feed during spawning migrations. Research is currently being conducted to test this hypothesis (M. Collins, Personal Communication).

Eggs are laid into flowing water and become widespread after fertilization. After about twenty minutes, the demersal eggs become strongly adhesive and attach to hard substrates (Murawski and Pacheco 1977; Van den Avyle 1983). The eggs hatch after 94-140 hours, and after a yolksac larval period of about 10 days in the water column, late-stage larvae settle to the demersal habitat. This will be the principal type of habitat for the remainder of the sturgeon's life (NMFS and U.S. FWS 1998).

Atlantic sturgeon eggs hatch in 94-140 hours at temperatures ranging from 18-20°C (Smith et al. 1980). Mohler (2003) states that for cultured sturgeon, a temperature range of 20-21°C is favorable for incubation. Temperatures below 18°C prolong hatching and increase the risk of fungal infestation to dead eggs, which in turn can kill the viable ones. Hatching occurs in 60 hours at this temperature range (Mohler 2003).

Development, growth and movement patterns

Early life stages

Little is known about the habitat of larval Atlantic sturgeon. Larval sturgeon are assumed to be found in the same riverine or estuarine habitats where they were spawned (Kynard and Horgan 2002). Newly hatched larvae are active swimmers and leave the bottom to swim in the water column. Once the yolk sac is absorbed, the larvae exhibit benthic behavior (Smith et al. 1980, 1981). Bath et al. (1981) caught free embryos by active bottom netting near the spawning area, demonstrating that early life stages are benthic. Kynard and Horgan (2002) raised Atlantic sturgeon in chambers. They found that upon hatching, the embryos sought cover and remained there for a few days. The fish left cover and began to migrate around day 8. After a couple of days, the larvae stopped migrating and exhibited foraging behavior. Downstream migration resumed again during the juvenile period when the temperature dropped. Atlantic sturgeon larvae are capable of dispersing long distances. Migration occurs at night during the first half of their migration, and eventually, the fish become active during both the day and night (Kynard and Horgan 2002). Kynard and Horgan (2002) hypothesize that this foraging behavior is a way to reduce daytime predation while the larvae are still developing, yet still enable them to forage when there is daylight to aid in the visual detection of prey. Mohler (2003) found similar results. Cultured Atlantic sturgeon were mostly pelagic after hatching and exhibited a "swim up and drift down" behavior. After 3-4 days fry began to exhibit benthic clumping behavior and swam against the flow direction of the tank. Fry remained benthic for about 4 days, before moving around the tank in search of food. At this stage, the sturgeon were noted to be pelagic, until live brine shrimp were thrown into the tank and the fry moved to the bottom of the tank to feed. Atlantic sturgeon fry did not actively seek out their food source, but waited till the currents brought it to them (Mohler 2003).

There are no studies to indicate what larval Atlantic sturgeon prey upon in the wild. However, it is assumed that after they absorb the yolk sac, they feed on tiny bottom dwelling organisms (Gilbert 1989). Studies of other sturgeon species indicate that larvae in rivers feed on small mobile invertebrates, including cladocerans and copepods (Baranova and Miroshnichenko 1969; Miller et al. 1991). Miller et al. (1991) found that white sturgeon larvae primarily fed on amphipods.

Juveniles

Juvenile sturgeon are thought to remain close to their natal habitats within the riverine portion of the estuary for a year before migrating out to sea (Secor et al. 2000). Migrations out to coastal areas occur between 2 and 6 years of age (T. Smith 1985) and are seasonal, with movement occurring north in the late winter, and south in fall and early winter (Dovel 1978; T. Smith 1985; NMFS and U.S. FWS 1998).

Interestuarine migrations have been documented extensively in the literature (Dovel and Berggren 1983; T. Smith 1985; Welsh et al. 2002; Savoy and Pacileo 2003). These non-natal estuarine habitats serve as nursery areas and are very important to the Atlantic sturgeon's life history. They can provide additional foraging opportunities, as well as thermal and salinity refuges (Moser and Ross 1995). Sub-adults tagged in the Hudson River, New York were recaptured in Nantucket, Massachusetts, and North Carolina (C. Smith 1985). Sub-adults tagged in the lower Delaware River were recaptured within several other estuaries including Pamlico Sound, North Carolina Chesapeake Bay, Virginia/Maryland, the Hudson River, New York, and Narragansett Bay, RI (C. Shirey, Personal Communication). Dovel and Berggren (1983) report that juvenile Atlantic sturgeon were recaptured in estuaries from Massachusetts to Cape Hatteras, North Carolina. T. Smith (1985) stated that fish tagged off South Carolina migrated as far north as Pamlico Sound, North Carolina, and the Chesapeake Bay, Maryland/Virginia. Most data indicates that sturgeon in the northern rivers travel more extensively than those in the southern rivers (ASMFC 1998). However, research in the southern region has not adequately addressed inter-basin movements in the south (P. Brownell, Personal Communication).

Seasonal migrations of juveniles and sub-adults are regulated by changes in temperature gradients between fresh and brackish waters (Van Den Avyle 1983). Juveniles released in the Chesapeake Bay, Maryland/Virginia, used the brackish waters close to the estuary mouth during the colder months and moved upriver during the warmer months (Secor et al. 2000). This behavior has been seen in a number of river systems including the Delaware River, Hudson River, New York, and the Winyah Bay system, South Carolina (Brundage and Meadows 1982; Smith et al. 1982; Dovel and Berggren 1983; Gilbert 1989). Dovel and Berggren (1983) report a mass down-estuary migration in the Hudson Estuary, New York, of juvenile Atlantic sturgeon when the temperature drops below 20°C. Migrations down-river/down-estuary peak at the end of October. At this time, many juveniles overwinter in deep holes, while others leave the Hudson River and move south along the Atlantic coast (Dovel and Berggren 1983). Moser and Ross (1995) found that juvenile sturgeon in the Cape Fear River, North Carolina, kept the same center of distribution near the saltwater-freshwater interface year round. However, these fish are unable to move upriver because of the location of the Cape Fear Lock and Dam No. 1, just above the estuary (0.5 ppt interface) (P. Brownell, Personal Communication).

Juvenile Atlantic sturgeon tend to congregate in deepwaters (Moser and Ross 1995; Savoy and Pacileo 2003). Moser and Ross (1995) report that juvenile sturgeon use deep and cool areas, particularly in the summertime. They state that in North Carolina, juvenile Atlantic sturgeon utilize very deep holes as thermal refuges in the summer. Juvenile sturgeon caught in the upper Cape Fear River, North Carolina, were found in waters deeper than 10 m, and sturgeon caught in the Brunswick River, North Carolina, were caught in depths less than 7 m.

While the majority of Atlantic sturgeon have been collected at the deepest depths available, they have also been collected in shallower waters (2.5 m) (Savoy and Pacileo 2003). Kynard et al. (2000) reported tracking fish at depths ranging from 2-12 m. The mean depth of the six Atlantic sturgeon tracked was 7 m. Musick et al. (1994) found that juvenile Atlantic sturgeon in the

Chesapeake Bay, Virginia were captured in depths less than 20 m, and that the fish were located within 10 km from shore. Similarly, a telemetry study on hatchery-released age-1 juveniles showed that most Atlantic sturgeon used depths <6 m (Secor et al. 2000). In a gill net survey in the Brunswick River, North Carolina, Moser and Ross (1995) captured Atlantic sturgeon over shoals less than 7 m, even though nets extended down to deeper areas. Lazzari et al. (1986) caught juvenile Atlantic sturgeon at depths ranging from 7-16 m in the Delaware River. In the Albemarle Sound, North Carolina, juvenile sturgeons were located in sites ranging from 1.8 to 5.4 m (Armstrong and Hightower 2002). Shirey et al. (1999) conducted biotelemetry studies and found Atlantic sturgeon preferred depths ranging from 5.5-11 m in the lower Delaware River during the summer even though deeper channel areas were nearby.

Sub-adults are known to emigrate out of their natal estuarine habitats and migrate long distances in the marine environment (Murawski and Pacheco 1977); the longest oceanic journey recorded was 1,450 km (Mangin and Beaulieu 1963). A total of 120 tag returns by commercial fisheries of sub-adult Atlantic sturgeon that were originally tagged in Delaware River provide insight into a coastal migration for this life stage that encompasses a broad size range (Delaware Fish and Wildlife, unpublished data). After leaving the Delaware Estuary during the fall, sturgeon were recaptured in the near-shore waters along the coast as far south as Cape Hatteras, North Carolina where they were recaptured from November through early March. Sturgeon moved back and forth across the mouth of the Chesapeake Bay and the Delmarva Peninsula in March and April with a portion of the tagged fish re-entering the Delaware Estuary. However, many continued this northerly coastal migration through the mid-Atlantic and into southern New England waters where they were recovered throughout the summer months, primarily in the waters of Massachusetts, Rhode Island, and Long Island, New York. Movements as far north as Maine were documented. A southerly coastal migration was apparent from tag returns reported in the fall. The majority of these tag returns were reported from relatively shallow nearshore fisheries with few fish reported from waters in excess of 25 m (Shirey, in prep).

Adults

Little is known about the habitat use of adult Atlantic sturgeon during the non-spawning season, particularly when the sturgeon return to marine waters (Bain 1997; Collins et al. 2000b). While at sea, Atlantic sturgeon have been documented using relatively shallow nearshore habitats (10-20 m) (Laney et al. in prep; Stein et al. 2004). It is possible that individual fish select habitats in the same areas, or even possibly school to some extent (Laney et al. in prep; Stein et al. 2004).

A study by Collins et al. (2000b) indicated that adult Atlantic sturgeon in South Carolina utilize a wide variety of habitats during the summer. They found sturgeon in the upper fresh/brackish interface zone, the lower interface zone, and in the high salinity portions of the estuary in the Edisto River, South Carolina. Atlantic sturgeon were present in this river from March to October. During the winter, southern Atlantic sturgeon overwinter in the ocean (Collins et al. 2000b). Adult Atlantic sturgeon in southern rivers exhibit behavior much like gulf sturgeon (*Acipenser oxyrinxhus desotoi*) in that they spend 9 months within the river system and 3 months during the winter in marine waters (M. Collins, Personal Communication).

In marine waters, Stein et al. (2004) reported that Atlantic sturgeon were found mostly over sand and gravel substrate, and that they were associated with specific coastal features, such as the mouths of the Chesapeake and Narragansett Bay, and inlets in the North Carolina Outer Banks. In their study, Stein et al. (2004) found Atlantic sturgeon over four types of substrate in Massachusetts, including silt, sand, clay, and gravel. The authors state that Atlantic sturgeon use any substrate that supports their food resources and that habitat use is strongly associated with prey availability.

Laney et al. (in prep.) found similar results off the coasts of Virginia and North Carolina. They used GIS layers to analyze data from the Cooperative Winter Tagging Cruise, and found that Atlantic sturgeon were located primarily in sandy substrates. However, the authors state that GIS does not depict small-scale sediment distribution, thus only a broad overview of sediment types was used. They also state that sediment sampling done along the North Carolina coast shows that gravel substrates are found a little farther offshore from where the sturgeon were found.

The greatest depth in the ocean at which Atlantic sturgeon were caught was 75 m (Bigelow and Schroeder 2002). Collins and Smith (1997) report that Atlantic sturgeon were captured at depths of 40 m in marine waters off South Carolina. Stein et al. (2004) investigated data collected by on-board fishery observers from 1989-2000 to determine habitat preferences of Atlantic sturgeon. They found that Atlantic sturgeon were caught in shallow inshore areas of the Continental Shelf. Bycatch on the Continental Shelf occurred in areas where the depth was less than 60 m. Sturgeon were captured in depths less than 25 m along the Mid-Atlantic Bight, and in deeper waters in the Gulf of Maine (Stein et al. 2004).

The Northeast Fisheries Science Center bottom trawl survey caught 139 Atlantic sturgeon from 1972-1996 in waters from Canada to South Carolina. They found the fish in depths of 7m to 75m, with a mean depth of 17.3m. Of the fish caught, 40% were collected at 15m, 13% at 13m, and 5% or less at all the depth strata (NEFC, unpublished data, reviewed in Savoy and Pacileo 2003).

Upon entering the marine habitat, Atlantic sturgeon have been documented near the shore in shallow waters where the depths measure less than 20 m (Gilbert 1989; Johnson et al. 1997). During their tagging cruise off the coasts of Virginia and North Carolina, Laney et al. (in prep.) captured Atlantic sturgeon at depths up to 20 ft (~6 m). The majority of sturgeon were found in depths less than 10 m. Vladykov and Greeley (1963) record a maximum depth of at least 60 ft (~18 m).

Ecological relationships

Post-spawning adults remaining in freshwater systems have been documented feeding on gastropods and other benthic organisms (Scott and Crossman 1973). Adult Atlantic sturgeon feed indiscriminately throughout their lives and are considered to be opportunistic feeders (Vladykov and Greeley 1963; Murawski and Pacheco 1977; Van den Avyle 1983; Bigelow and Schroeder 2002). They feed on mollusks, as well as polychaetes, gastropods, shrimps, isopods, and benthic fish in estuarine areas (Dadswell et al. 1984; Bigelow and Schroeder 2002). In freshwater, they feed on aquatic insects, amphipods, and oligochaetes (Bigelow and Schroeder 2002). Hatin et al. (2002) reported that Atlantic sturgeon in the St. Lawrence River fed on oliogochaetes, nematodes, and amphipods.

Adult Atlantic sturgeon appear to have few ecological competitors. They spawn later in the season and in different areas than shortnose sturgeon, thus avoiding competition in areas where their habitat overlaps (Bath et al. 1981; Gilbert 1989; see discussion in Kynard and Horgan 2002). Other species that might utilize the same spawning habitat includes the walleye (*Stizostedion vitreum vitreum*) and the rainbow trout (*Salmo gairdneri*). Both of these species have been introduced into the range of the Atlantic sturgeon (Gilbert 1989).

Kynard and Horgan (2002) hypothesize that larval and juvenile Atlantic sturgeon have a low predation risk. This is based on the idea that migration upon hatching is stimulated by predation risk to embryos. Species that undergo high predation tend to migrate from the area immediately after hatching (Kynard and Horgan 2002). While this has not been fully tested, Kynard and Horgan (2002) have found that shortnose sturgeon embryos have few predators. After sampling predators in a spawning area, they found that only one fish, the fallfish (*Semotilus corporalis*), had sturgeon eggs in its stomach.

The range of salinities in which Atlantic sturgeon are found vary greatly. Some Atlantic sturgeon may occupy freshwater habitats for a couple of years, while others move downstream to brackish waters when the water temperature drops (Scott and Crossman 1973; Dovel 1978; Hoff 1980; Lazzari et al. 1986). Dadswell (1979), Brundage and Meadows (1982), T. Smith (1985), and Haley et al. (1996) report that young sturgeon primarily use brackish water habitats. Large juvenile sturgeon are found predominately in areas where salinity is greater than 3 ppt (Appy and Dadswell 1978). Haley et al. (1996) generally caught Atlantic sturgeon in the Hudson River, New York in areas where salinity ranged from 3-16 ppt. Dovel and Berggren (1983) found that juvenile sturgeon were concentrated in areas with a salinity range of 0-6 ppt. In their study, Moser and Ross (1995) reported that the majority of Catch Per Unit Effort (CPUE) in the Brunswick River, North Carolina, occurred in an area near the head of the salt wedge where the salinity did not exceed 10 ppt.

Dissolved oxygen is a very important habitat parameter for Atlantic sturgeon. As a result of decreased dissolved oxygen, much of sturgeon nursery habitat has been degraded (see sections II and III). Secor and Niklitschek (2001) report that in habitats with less than 60% oxygen saturation, young of the year fish age 30-200 days, will experience a loss in production. This level is 4.3-4.7 mg/L for summer temperatures ranging from 22°C to 27°C. Mortality of Atlantic sturgeon has been observed for summer temperatures at levels of <3.3 mg/L (Secor and Niklitschek 2001). Secor and Gunderson (1998) also found that juvenile sturgeon were affected negatively by high temperatures and low oxygen. In their experiment, mortality occurred at 26C and ~3 mg/L. Recently, the Chesapeake Bay Program adopted dissolved oxygen guidelines based upon levels that would protect Atlantic and shortnose sturgeon, which show unusually high sensitivity to low oxygen among estuarine living resources (Secor and Niklitschek 2002; Anon. 2003).

Pottle and Dadswell (1982) examined the gut contents of juvenile sturgeon. They found that juvenile Atlantic sturgeon fed on diptera and trichoptera, as well as amphipods in the St. Johns River, Florida. Secor et al. (2000) found that juvenile Atlantic sturgeon in the Chesapeake Bay preyed upon annelid worms, isopods, amphipods, chironomid larvae, and mysids. Moser and

Ross (1995) found polycheate worms, isopods, and mollusk shell fragments in the stomachs of juvenile sturgeon in North Carolina. An examination of 12 juvenile Atlantic sturgeon in the Connecticut and Merrimack Rivers showed a mix of amphipods and polychaetes (Kynard et al. 2000). In freshwater, juvenile sturgeon ate plant and animal matter, sludgeworms, chironomid larvae, mayfly larvae, isopods, amphipods, and small bivalve mollusks (Scott and Crossman 1973). Scott and Crossman (1973) also noted that sturgeon consumed mud while rooting on the bottom.

Both juvenile Atlantic sturgeon and shortnose sturgeon occupy the same freshwater/saltwater interface nursery habitat (Dadswell 1979; Dovel and Berggren 1983; Dovel et al. 1992). However, shortnose sturgeon tend to be located in freshwater, while Atlantic sturgeon utilize more saline areas (Dovel and Berggren 1983; Dovel et al. 1992; Kieffer and Kynard 1993; Haley et al. 1996). Haley et al. (1996) collected the majority of juvenile Atlantic sturgeon in the Hudson River in deeper, mesohaline (3.0-16.0 ppt) regions of the river, while juvenile shortnose sturgeon were found most often in the shallower, freshwater (<.5 ppt) zones of the river. Furthermore, bioenergetic comparisons show that age-1 Atlantic sturgeon showed better growth in brackish water (1-10 ppt), than sympatric shortnose sturgeon juveniles (Niklitschek 2001).

Haley et al. (1996) hypothesize that the freshwater/saltwater interface where both sturgeon species concentrate, may serve as a foraging ground, and that Atlantic and shortnose sturgeon may compete for food in this area. However, Pottle and Dadswell (1982) found that juvenile Atlantic and shortnose sturgeon in the St. Johns River preyed on different species. They found that Atlantic sturgeon preyed upon diptera, trichoptera, and some amphipods, while shortnose sturgeon preyed mostly upon cladocerans, amphipods, mollusks, and insect larvae (Pottle and Dadswell 1982).

In the more southern rivers, juvenile Atlantic sturgeon and adult shortnose sturgeon may share parts of the river with similar salinity levels. This has been documented in the Savannah River during the fall and winter and in the Altamaha River, during warm summers (Reviewed in Kieffer and Kynard 1993).

Atlantic sturgeon juveniles and sub-adults would be expected to compete with other demersal feeding fishes in estuaries. In mid-Atlantic estuaries these include catfishes, white perch, carp, spot, croaker, and hogchokers (Murdy et al. 1997).

There is little information regarding the marine diet of Atlantic sturgeon. Johnson et al. (1997) suggest that this is because of the low population density of sturgeon offshore, and the fact that most studies have focused on rivers and estuaries. A stomach content study by Johnson et al. (1997) found that Atlantic sturgeon off the coast of New Jersey preyed upon polychaetes, isopods, decapods, and amphipods. They also found that mollusks and fish contributed little to the diet, and that sand and organic debris were major components (Johnson et al. 1997). Scott and Crossman (1973) stated that in marine waters, Atlantic sturgeon fed on mollusks, polychaete worms, gastropods, shrimps, amphipods, isopods, and small fish (particularly sand lances).

Gilbert (1989) lists suckers (*Moxostoma* sp.), winter flounder (*Pleuronectes americanus*), tautog (*Tautoga onitis*), cunner (*Tautogolabrus adspersus*), porgies (Sparidae), croakers (Sciaenidae), and stingrays (*Dasyatis* sp.) as possible competitors. Scott and Crossman (1973) report that Atlantic sturgeon are killed by sea lampreys, *Petromyzon marinus*, and in South Carolina, longnose gar have been reported attacking sturgeon (Reviewed in T. Smith 1985).

Abundance and status of stocks

Due to a variety of anthropogenic impacts, including river blockages, water quality deterioration, and overfishing, an estimated 38-59% (based on 14 of the 21 extant stocks reproducing, of 39 historically present) of Atlantic sturgeon stocks are extirpated and the rest are likely at historically low levels (ASMFC 1998; NMFS and U.S. FWS 1998). In 1991, Atlantic sturgeon was listed as a candidate species (56 FR 26797) under the Endangered Species Act (ESA) and remained on the revised list in 1997 (62 FR 37560). In 1998, a status review of Atlantic sturgeon found that the continued existence of Atlantic sturgeon was not threatened by any of the five ESA listing factors. Therefore, Atlantic sturgeon was not listed as a threatened or endangered species (NMFS and U.S. FWS 1998). However, in 2006 the Atlantic sturgeon was listed as a Federal Candidate species. In 1990, the Atlantic States Marine Fisheries Commission wrote a Fisheries Management Plan (FMP) for Atlantic sturgeon and amended it in 1998. In 1998, the ASMFC closed all sturgeon fisheries coastwide in the United States and recommended a 20-40 year moratorium, so that the spawning stock could be restored to a level where 20 protected year classes of adult females are present (ASMFC 1998).

(from the 2006 ASFMC FMP Review)
Reported landings of Atlantic sturgeon peaked in 1890 at 3.4 million kilograms and declined precipitously thereafter. Currently, populations throughout the species' range are either extirpated or at historically low abundance. Recruitment is variable at low levels in most regions. Survival of Atlantic sturgeon during the 20th Century implies that enough spawning and nursery habitats exist to perpetuate the species. In the absence of major threats to existing habitat, reduced fishing mortality is of greater importance to stock restoration efforts than habitat limitations. Adult population abundance in some systems may be so low as to significantly impede reproduction success and timely recovery.

The target fishing rate was defined as that level of F that generated an eggs-per-recruit (EPR) equal to 50% of the EPR at F = 0.0 (i.e., virgin stock). This rate (F50) equals 0.03 (annual harvest rate of 3%) for a restored population. This target is far below recent estimates of F prior to enactment of fishing moratoria, which ranged from 0.01 - 0.12 for females and 0.15 - 0.24 for males in the Hudson River. These numbers may not apply to southern stocks, where more signs toward recovery are being seen.

Based on information presented at a technical workshop in November 2003, the population abundance in various rivers appears to vary substantially. The Hudson River stock may be showing a small increase in abundance, little or no signs of recovery are apparent in most if not all northern stocks, while certain rivers in Georgia and South Carolina are showing increasing numbers of sub-adults, suggesting some population rebuilding.

Currently, all states and the National Marine Fisheries Service have enacted bans on harvest and possession of Atlantic sturgeon and sturgeon parts. As per Amendment 1, these moratoria will remain in effect until stocks exhibit a minimum of 20 protected yearclasses of spawning females and the FMP is modified to permit harvest and possession.

Addendum I to the Interstate Fishery Management Plan for Atlantic sturgeon exempts the State of Florida from the possession moratorium for the purposes of developing private aquaculture facilities for cultivation and propagation of the species. Addendum II exempts a private company in North Carolina from the moratorium on possession, propagation, and sale of Atlantic sturgeon meat and eggs. Addendum III was approved on November 17, 2006, exempting a private company in North Carolina from a moratorium on possession, propagation, and sale of Atlantic sturgeon meat and eggs and exempting a Canadian exporter from exporting Atlantic sturgeon fry and fingerlings into North Carolina.

The November 2003 technical workshop on status of Atlantic sturgeon identified several new issues regarding bycatch of Atlantic sturgeon. Another workshop focused on recovery techniques was held in November 2004 and provided more recommendations for dealing with bycatch. ASMFC hosted an Atlantic sturgeon bycatch workshop in February 2006 that: (1) evaluated genetic and mark-recapture data and approaches to identifying stock composition of bycatch; (2) reviewed and summarized jurisdictional reports on bycatch; and (3) estimated fishery-specific bycatch and bycatch mortality of Atlantic sturgeon during the past ten years in New England and Mid-Atlantic waters. In early 2007, ASMFC will host another bycatch workshop that will focus on the NMFS observer dataset for the period of 2000-2005.

4.2.6 Blueback Herring

Description and Distribution

Blueback herring are anadromous, highly migratory, euryhaline, pelagic, schooling species. Both blueback herring and alewife are often referred to as "river herring," a collective term for these two species combined, which often school together (Murdy et al. 1997). Although this term is often used generically in commercial harvests and no distinction is made between the two species (ASMFC 1985), landings are reported as alewife (Loesch 1987). Bluebacks spend most of their life at sea, returning to freshwater only to spawn (Bigelow and Schroeder 2002). Their range is commonly cited as the St. Johns River, Florida (Hildebrand 1963; Williams et al. 1975) to Cape Breton, Nova Scotia (Scott and Crossman 1973) and the Miramichi River, New Brunswick (Bigelow and Schroeder 1953; Leim and Scott 1966); however, Williams and Grey (undated) reported that they occur as far south as Tomoka River, a small freshwater tributary of the Halifax River in Florida (a brackish coastal lagoon). There are also some landlocked populations in the Southeast (Klauda et al. 1991), but landlocking occurs less in bluebacks than in alewife (Schmidt et al. 2003).

Results from 16 years of catch data reveal that blueback herring are distributed throughout the continental shelf from Cape Hatteras, NC to Nova Scotia during the spring. Most are found south of Cape Cod, but, unlike alewife, no blueback catches were recorded for Georges Bank. During the summer, they move north and inshore, but catch records were too infrequent to determine summer occurrence for bluebacks, although several catches were made near Nantucket Shoals and Georges Bank and they were never collected south of 40°N. By early fall, they are found along Nantucket Shoals, Georges Bank, the inner Bay of Fundy, but concentrated mostly along the northwest perimeter of the Gulf of Maine (Neves 1981). In the autumn, they begin moving southward and offshore to the mid-Atlantic coast to overwinter until early spring (Neves 1981; Rulifson et al. 1987). Although winter sampling stations were inadequate to define wintering grounds, the few catches that were reported were primarily between latitude 40° and 43° N. It is unknown to what extent they overwinter in deepwater off the continental shelf of the U.S. (Neves 1981). They have been found offshore as far as 200 km (Bigelow and Schroeder 1953; Netzel and Stanek 1966), but they are rarely collected more than 130 km from shore (Jones et al. 1978).

Reproduction

Spawning and Spawning Habitat

Blueback herring generally spawn in freshwater above the head of tide; brackish and tidal areas are rarely used for spawning by this species (Nichols and Breder 1927; Hildebrand 1963; Fay et al. 1983; Murdy et al. 1997). In areas where blueback herring and alewife co-occur (sympatric region), bluebacks prefer to spawn over gravel and clean sand substrates, where the flow is relatively swift, and actively avoid areas with slow-moving or standing water (Bigelow and Welsh 1925; Marcy 1976b; Loesch and Lund 1977; Johnston and Cheverie 1988). Bluebacks are also abundant in tributaries and flooded low-lying areas adjacent to main streams (Erkan 2002). If bluebacks and alewife are forced to spawn in the same vicinity (i.e. due to blocked passage) (Loesch 1987), some researchers have suggested that the two species occupy separate spawning sites to reduce competition. For example, Loesch and Lund (1977) note that bluebacks will typically select the main stream flow for spawning, while alewife will spawn along shorebank eddies or deep pools. In rivers where headwater ponds are absent or poorly-developed, alewife may be most abundant further upstream in headwater reaches, while bluebacks select the mainstream proper for spawning (Ross and Biagi 1990).

In the allopatric range, where there is no co-occurrence with alewife (south of North Carolina), bluebacks favor lentic sites, but may also occupy lotic sites (Loesch 1987; Klauda et al. 1991). In the allopatric range, bluebacks select a greater variety of spawning habitat types (Street 1970; Frankensteen 1976; Christie 1978), including small tributaries upstream from the tidal zone (ASMFC 1999), seasonally flooded rice fields, small densely vegetated streams, cypress swamps, and oxbows, where the substrate is soft and detritus is present (Adams and Street 1969; Godwin and Adams 1969; Adams 1970; Street 1970; Curtis et al. 1982; Meador et al. 1984). Despite the fact that bluebacks generally do not spawn in ponds in their northern range (possibly to reduce competition), they have the ability to do so (Loesch 1987).

Bluebacks will ascend freshwater far upstream (Massman 1953; Davis and Cheek 1967; Perlmutter et al. 1967; Crecco 1982), their distribution being a function of habitat suitability and hydrological conditions, such as swifter waters (Loesch and Lund 1977). Earlier suggestions that bluebacks do not ascend as far upstream as alewife are unfounded (Loesch 1987). In tributaries of the Rappahannock River, VA, upstream areas were found to be more important for spawning than downstream areas (O'Connell and Angermeier 1997).

Blueback herring will generally spawn 3-4 weeks after alewife in areas where they co-occur; however, there may be considerable overlap (Loesch 1987) and peak spawning periods may differ by only 2-3 weeks (Hildebrand and Schroeder 1928). In a tributary of the Rappahannock

River, VA, O'Connell and Angermeier (1997) found that blueback eggs and larvae were more abundant than those of alewife, but alewife used the stream over a longer period of time. They also reported that there was only a 3-day overlap of spawning by alewife and bluebacks. Although it has been suggested that alewife and bluebacks select separate spawning sites in sympatric areas to reduce competition (Loesch 1987), O'Connell and Angermeier (1997) did not find that the two species used different spawning habitat in the areas they examined. They suggested that there was a temporal, rather than spatial segregation that minimized the competition between the two species.

Spawning may occur during the day, but most spawning activity is greatest from late afternoon (Loesch and Lund 1977) into the night (Johnston and Cheverie 1988). A female and two or more males will swim approximately 1m below the surface of the water, whereupon they will dive to the bottom (Loesch and Lund 1977), simultaneously releasing eggs and sperm over the substrate (Bigelow and Schroeder 2002). Spawning typically occurs over an extended period, with groups or "waves" of migrants staying 4-5 days before quickly returning to sea (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Klauda et al. 1991). The majority of spent adult blueback herring emigrating from the Connecticut River moved through fish passage facilities between 1700 and 2100 hours (Taylor and Kynard 1984).

Spawning typically begins in the given regions at the following times: 1) Florida – as early as December (McLane 1955); 2) South Carolina (Santee River) – present in February (Bulak and Christie 1981), but spawning begins in early March (Christie 1978; Meador 1982); 3) Chesapeake Bay region - lower tributaries – early April and upper reaches – late April (Hildebrand and Schroeder 1928); 4) Mid-Atlantic region – late April (Smith 1971; Zich 1978; Wang and Kernehan 1979); 5) Susquehanna River - abundance peaks in early to mid-May (St. Pierre, pers. comm.); 6) Connecticut River – present in lower river mid-April, but spawning begins in mid-May (Loesch and Lund 1977); and 7) Saint John River, New Brunswick – present in May (Messieh 1977; Jessop et al. 1983), but spawning doesn't commence until June and may run through August (Leim and Scott 1966; Marcy 1976b).

Blueback herring are repeat spawners at an average rate of 30-40% (Richkus and DiNardo 1984). In general, there appears to be a general increase in repeat spawners from south to north (Rulifson et al. 1982). About 44-65% of the spawners in the Chesapeake Bay tributaries had previously spawned (Joseph and Davis 1965), while 75% of those in Nova Scotia had previously spawned (O'Neill 1980). In the Chowan River, North Carolina virgins comprised as high as 78% (Winslow and Rawls 1992) and as low as 35.9% of the spawning population (Winslow 1995). First spawning occurs when adults are between 3 and 6 years old, but virgin spawners are strongly represented by age 4 fish (Messieh 1977; Loesch 1987). Joseph and Davis (1965) reported some bluebacks spawning as many as six times in Virginia. The average life expectancy of blueback herring is less than that of alewife, with adults living up to 7 to 8 years of age (Kocik 2000).

Loesch (1987) has reported that blueback herring can adapt their spawning behavior under certain environmental conditions and disperse to new areas if the conditions are suitable. This was demonstrated in the Santee-Cooper System, South Carolina, where the creation of a rediversion canal and resultant hydrological alterations led to changes in spawning site selection in both rivers. In the Cooper River, bluebacks lost access to formerly impounded rice fields along the river, which were important spawning areas. Following the construction of the rediversion canal, there was an increase in the number and length of tributaries along the river that were used as spawning habitat. In the adjacent Santee River, adults dispersed into the rediversion canal itself in favor of their former habitat, which was further upstream (Eversole et al. 1994).

Jessop (1990) found a stock recruitment relationship for the spawning stock of river herring and year-class abundance at age 3. Despite these results, most studies have been unable to detect a strong relationship between adult and juvenile abundance of clupeids (Crecco and Savoy 1984; Henderson and Brown 1985; Gibson 1994; Jessop 1994). Researchers have suggested that although year-class is driven mostly by environmental factors, if the parent stock size falls below a critical level, the size of the spawning stock may become a factor in determining juvenile abundance (Kosa and Mather 2001). To the extent that environmental factors have been linked to year-class abundance, they will be discussed in subsequent sections.

O'Connell and Angermeier (1997) found that temperature was the strongest predictor of blueback herring adult and early egg presence in a tributary of the Rappahannock River, VA. Blueback herring are reported to spawn at temperatures ranging from a minimum of 13°C (Hawkins 1979; Rulifson et al. 1982) to a maximum of 27°C (Loesch 1968). Loesch and Lund (1977) noted that spawning adults were found in the lower Connecticut River in mid-April when water temperatures were as low as 4.7°C, but spawning did not occur till several weeks later when water temperature had risen. Meador et al. (1984) noted that rapid changes in water temperature appeared to be an important factor influencing the timing of spawning. Optimal spawning temperature range is suggested to be 21-25°C (Cianci 1969; Marcy 1976b; Klauda et al. 1991) and 20-24°C (Pardue 1983). Fish in the laboratory acclimated to 15° C and 29 ppt salinity exhibited a final temperature preference of 22.8°C (Terpin et al. 1977).

During their freshwater migration, blueback herring swim at midwater depths (compared to deeper water used by American shad) (Witherell 1987). They are reported to spawn in both shallow (Jones et al. 1978) and deep streams (Johnston and Cheverie 1988).

Adults, eggs, larvae, and juveniles can tolerate a wide range of salinities (Klauda et al. 1991), but may prefer a more narrow range, depending on life history stage. For example, spawning may occur in salinities ranging from 0-6 ppt, but typically occurs in waters that are less than 1 ppt (Klauda et al. 1991). Boger (2002) modified Klauda et al.'s salinity range for Virginia rivers, suggesting that a suitable salinity range for spawning adults is 0-5. Spawning adults have also been found in brackish ponds at Woods Hole, Massachusetts (Nichols and Breder 1927; Hildebrand 1963).

In the sympatric range, blueback herring prefer spawning in large rivers and tributaries where the flow is relatively swift, actively avoiding areas with slow-moving or standing water (Bigelow and Welsh 1925; Marcy 1976b; Johnston and Cheverie 1988). In such areas, they will concentrate and spawn in the main stream flow, while alewife favor shorebank eddies or deep pools for spawning (Loesch and Lund 1977). In Connecticut, bluebacks were found to select fast-moving waters of the upper Salmon River and Roaring Brook, while alewife chose the slower-moving waters of Higganum and Mill creeks (Loesch and Lund 1977) and Bride Lake (Kissil 1974); researchers suggested that there was differential selection of spawning in these areas. In regions where bluebacks do not co-occur with alewife (allopatric range), they may select slower-flowing tributaries and flooded low-lying areas adjacent to main streams with soft substrates and detritus (Street et al. 1975; Sholar 1975; 1977; Fischer 1980; Hawkins 1980).

Meador et al. (1984) found that high flows (and accompanying low water temperatures) associated with flood control discharges in the Santee River immediately prior to the spawning season resulted in lower numbers of larvae that year. The preceding year, spawning occurred further upstream, when no flood control discharges occurred. Furthermore, ripe adults were found below the sampling site heading downstream the year that high flows occurred, apparently without having spawned (Bulak and Christie 1982). Other studies (Bulak and Curtis 1977; West et al. 1988) have found spawning adults moving downstream from spawning areas, following a sudden change in water discharge.

In 1985, a rediversion canal and hydroelectric dam with a fish passage facility were constructed between the Cooper River and Santee River, South Carolina, which increased the average flow of the Santee River from 63 m^3/s to 295 m^3/s. (Cooke and Leach 2003). Following the rediversion, bluebacks did not concentrate below the dam and few were attracted into the fish lock during periods of zero discharge. Too much water flow also posed a problem, as bluebacks were found concentrating below the dam during periods of discharge, but were unable to locate the entrance to the fish lock due to high turbulence (Chappelear and Cooke 1994). As a result, blueback herring changed migration patterns, by abandoning the Santee River and followed the dredged canal to the higher flow of the St. Stephen Dam. Access to spawning grounds was increased, which contributed to increases in blueback herring populations. Although the importance of instream flow requirements has been previously recognized (Crecco and Savoy 1984; ASMFC 1985; Crecco et al. 1986; Ross et al. 1993), it has usually been with regard to spawning habitat requirements or recruitment potential (Moser and Ross 1994). Cooke and Leach concluded that the study of and possible adjustment of river flow may be an important consideration for restoring alosine habitat.

Bottom composition: In the sympatric range, adults often spawn in areas of rivers where there is gravel or clean sand substrates (Bigelow and Welsh 1925; Marcy 1976b; Loesch and Lund 1977; Johnston and Cheverie 1988). In the allopatric range, where water flow is more sluggish, there is more opportunity for detritus and silt to accumulate. Pardue (1983) considered substrates with 75% or more silt and other soft materials containing detritus and vegetation as optimal for spawning in these areas because it provides cover for eggs and larvae. Boger (2002) found that river herring spawning areas along the Rappahannock River, Virginia had substrates that consisted primarily of sand, pebbles, and cobbles (usually associated with higher-gradient streams), while areas with little or no spawning were dominated by organic matter and finer sediments (usually associated with lower-gradient streams and comparatively more agricultural land use).

Adult bluebacks captured in the Santee-Cooper River system, South Carolina, were always found within a range of pH 6.0-7.5 (Christie and Barwick 1985; Christie et al. 1981). Further north, within tributaries of the Delaware River, New Jersey spawning runs were found within a broader range of pH 4.7-7.1 (average 6.2) (Byrne 1988). Based on suggested ranges for eggs (cited in Klauda et al. 1991), Boger (2002) suggested a suitable range of 6-8 and an optimal range of 6.5-8 for spawning habitat. No other information could be found regarding tolerances or optima.

Adult bluebacks require a minimum of 5.0 mg/L of DO (Jones et al. 1978). Adults caught in the Cooper and Santee Rivers, South Carolina were always captured in areas that had a DO of 6 mg/L or higher (Christie et al. 1981).

Development, growth and movement patterns

Development

On average, eggs are hatched within 38-60 hours of being fertilized (Adams and Street 1969). Yolk-sac larvae drift passively downstream with the current to slower moving water, where they grow and develop into juveniles (Johnston and Cheverie 1988). Yolk-sac absorption occurs in 2-3 days after hatching, and soon thereafter, larvae will begin to feed exogenously (Cianci 1969). Larvae are sensitive to light, and abundance at the surface increases as dusk approaches and reaches a maximum by dawn (Meador 1982).

Eggs were found adhered to sticks, stones, gravel, and aquatic vegetation along the bottom of a fast-flowing stream in the Gulf of St. Lawrence. Initially they are demersal, but during the water-hardening stage, they are less adhesive and become pelagic (Johnston and Cheverie 1988). In general, blueback herring eggs are buoyant in flowing water, but settle along the bottom in still water (Ross and Biagi 1990).

Blueback herring eggs were collected in the upper Chesapeake Bay where temperatures ranged from 7-14°C; 90% were collected at 14°C (Dovel 1971). There was no reported significant reduction in hatching success for eggs acclimated at 15-18.3°C and exposed to temperatures of 22-28.3°C for 5-30 minutes in the laboratory (Schubel 1974), as well as those acclimated at 17.9-21.1°C and then exposed to 31.1°C for 30 minutes (Schubel and Koo 1976). Eggs acclimated at 32.9-36.1°C for 5-15 minutes experienced significant mortality, with total egg mortality occurring at 37.9°C. In their review of the literature, Klauda et al. (1991) concluded that suitable and optimal temperature ranges for eggs were 14-26° C and 20-24°C, respectively.

Incubation is complete after 80-94 hours at 20-21° C (Kuntz and Radcliffe 1917; Jones et al. 1978) and 55-58 hours at 22.2-23.7°C (Cianci 1969; Klauda et al. 1991). Typically, blueback herring eggs require 38-60 hours for hatching (Adams and Street 1969; Cianci 1969; Morgan and Prince 1976).

Larval blueback herring have been collected in the upper Chesapeake Bay where water temperatures ranged from 13-28°C; 96% were collected at 23-28°C (Dovel 1971). Blueback herring eggs and larvae collected from the Washademoak River, New Brunswick were acclimated at 19°C, then exposed to 29 and 34°C for 1-3 hours in the laboratory (Koo and Johnston 1978). While egg mortality and hatchability were deemed poor indicators of the effects of temperatures, larval deformity was considered a good indicator. Deformity rates were 0-25% at 29°C with a maximum exposure time of 3 hours, and 100% at 34°C (also 3 hours); such deformities were permanent and would have been lethal in the natural environment. In their review of the literature, Klauda et al. (1991) concluded that suitable temperature ranges for prolarvae and postlarvae were 14-26°C and 14-28°C, respectively; optimal ranges were not suggested.

Both Wang and Kernehan (1979) and Meador et al. (1984) observed that larval blueback herring achieved the greatest density at the surface during the night than at midday. This pattern of diel periodicity has also been described for the juvenile life stage (Loesch and Lund 1977; Loesch et al. 1982; Johnson et al. 1978).

Although spawning often occurs in freshwater, eggs and larvae can survive in salinities as high as 18-22 ppt (Johnston and Cheverie 1988). Klauda et al. (1991) suggested an optimal range of 0-2 ppt for eggs only.

Year-class size of blueback herring decreased with increasing discharge during May-June from the headpond at the Mactaquac Dam (Saint John River, New Brunswick) (Jessop 1990). Researchers speculated that this was due to low abundance of phyto- and zooplantkon that larvae rely on at first feeding, which can result when high discharges occur (Laberge 1975). This effect was not observed for alewife, which spawn 2-3 weeks earlier than alewife. Sismour (1994) also observed a rapid decline in abundance of early preflexion river herring larvae (includes both alewife and blueback herring) in the Pamunkey River, Virginia following high river flow in 1989. As with Jessop, he speculated that high flow led to increased turbidity, which reduced prey visibility, leading to starvation of larvae.

Dixon (1996) found that seasonally high river flow and low water temperature during one season in several Virginia rivers were associated with later larval emergence, reduced relative abundance, depressed growth rate and increased mortality compared with the previous season. He suggested that high river flow may be a forcing mechanism on another abiotic factor, perhaps turbidity, which directly affects larval growth and survival.

Bottom composition: As with spawning habitat, Pardue (1983) suggested that substrates with 75% silt or other soft materials containing detritus and vegetation were optimal for eggs and larval habitat.

Klauda (1989) conducted laboratory research on fertilized eggs and yolk-sac larvae, and suggested that critical acidity conditions (defined as laboratory and field test exposures associated with >50% direct mortality) for successful blueback herring reproduction in Maryland coastal plain streams occur during a single 8-96 hour pulse of acid, pH 5.5-6.2, with concomitant total monomeric aluminum concentrations of 15-137 µg/L. Eggs that were subjected to four treatments ranging from pH 5.7-7.5 and five aluminum treatments of 0-400 µg/L at a continuous exposure time between 96-120 h revealed the following results: four-hour old embryos were sensitive to aluminum in the test treatments of pH 5.7-6.7; 12-hour old embryos were most sensitive to pH 5.7 with no aluminum present; and 24-hour old embryos suffered no mortality at all pH and aluminum levels (Klauda and Palmer 1987a).

Laboratory tests by Klauda et al. (1987) found a pH-induced mortality threshold for yolk-sac larvae of pH 5.7-6.5, and a 96-hour LC50 pH of 6.37 (pH that induced 50% mortality); no aluminum was administered. At pH 6.7, the mortality rates were highly variable (3-75%).

Additional tests by Klauda and Palmer (1987b) found that as the exposure time was doubled (12 to 24 hours), mortality rates increased among yolk-sac larvae (25-49%) at a pH value of 5.5. When coupled with a concomitant exposure of total aluminum maxima of 100-150 µg/L, mortality increased to 19, 66, 98, and 100% after 4, 8, 12, and 24 hours exposure, respectively. Tests also revealed highly variable mortality rates (3-75%) for yolk-sac larvae at a pH of 6.7. In general, the data indicated that larvae were more sensitive to lower pH values (5.7 and 6.2) with no aluminum added, and were more tolerant of higher pH values (6.7 and 7.5). Yolk-sac larvae were more sensitive than four-hour old embryos to pH and aluminum treatments (Klauda and Palmer 1987a). Klauda et al. (1991) suggested overall suitable ranges for eggs and prolarvae of 5.7-8.5 and 6.2-8.5, respectively; optimal ranges were suggested to be 6.0-8.0 and 6.5-8.0, respectively.

Median pH values where bluebacks were spawning in the Rappahannock River, VA (6.27) reported by O'Connell and Angermeier were within the lethal range (5.7-6.5) and below a 96-h LC50 of 6.37 for larvae. Reduced pH levels may represent episodic events, such as acid precipitation, but additional study is required to determine what the effects of occasional pH depressions might be.

Larvae require a minimum of 5.0 mg/L of dissolved oxygen for survival (Jones et al. 1978). No further information was found for egg tolerances or optima.

As with alewife, blueback herring eggs have proven extremely tolerant to suspended solids, with no significant reduction in hatching success at concentrations up 1000 mg/L (Auld and Schubel 1972). Schubel and Wang (1973) demonstrated that high levels of suspended solids during and after spawning significantly increased the rate of egg infections from naturally occurring fungi in alewife, which caused delayed mortalities; thus, it may be likely that the same effects would be observed in blueback herring eggs (Klauda et al. 1991). Several in situ studies (Klauda and Palmer 1987b; Greening et al. 1989) noted that yolk-sac larvae appear to be more sensitive to suspended solids than eggs, but given that observations were made following storm events, which also resulted in changes to pH and current velocity, the effects of turbidity alone were inconclusive. Klauda et al. (1991) later noted a suitable range of <500 mg/L for the prolarva life stage.

An 80 h LC_{50} of 0.33 mg/L total residual chlorine (TRC) for blueback herring eggs incubated at 20.9° C in freshwater was reported. The LC_{50} for one-day old larvae exposed to TRC for 48 and 54 h ranged from 0.24-0.32 mg/L; LC_{50} for 2-day old larvae was between 0.25-0.32 mg/L (Morgan and Prince 1977). Concentrations that were greater than or equal to 0.30 mg/L increased the percentage of abnormally developed larvae (Morgan and Prince 1978).

Juveniles

Recruitment to the juvenile stage for blueback herring begins later in the year than for other alosines because they spawn later and have a shorter growing season (Hildebrand and Schroeder 1928; Schmidt et al. 1988). The juvenile stage is reached when fish are about 20 mm TL (Klauda et al. 1991), with growth occurring very rapidly (Bigelow and Schroeder 2002); typically this stage is reached in approximately 25-35 days post-hatch (Watson 1968).

Nursery areas of the Neuse River, North Carolina have been characterized as relatively deep, slow-flowing, black waters that drain hardwood swamps (Hawkins 1980). Massman (1953), Warriner et al. (1969), and Burbidge (1974) have reported that juveniles were most abundant upstream of spawning grounds in waters of Virginia. Burbidge noted a greater prey density at these locations, but was unsure if fish were actually moving upstream in large numbers, if survival rates upstream were higher compared to survival rates downstream, or if fish were simply moving out of tributaries and oxbows into these areas.

In Chesapeake Bay tributaries, juveniles (young-of-the-year) can be found throughout tidal freshwater nursery areas in spring and early summer, but subsequently head upstream in the summer when saline waters encroach on their nursery grounds (Warriner et al. 1970). Schmidt et al. (1988) reasoned that juvenile bluebacks in the Hudson River remained in the vicinity of their natal areas throughout the summer because they were relatively absent downriver until late September. In other studies, they were found to be most abundant in nearshore waters during the day (McFadden et al. 1978; Dey and Baumann 1978). In North Carolina waters, Street et al. (1975) found that juveniles typically reside in the lower ends of the rivers in which they were spawned. Odom (pers. comm. 2002) noted that juvenile bluebacks selected the pelagic main channel portion of tidal waters of the Potomac River, while American shad juveniles selected shallower nearshore flats adjacent to and within submerged aquatic vegetation (SAV) beds. Odom speculated that these species tend to partition this habitat.

Juveniles spend 3-9 months in their natal rivers before returning to the ocean (Kosa and Mather 2001). Observations by Stokesbury and Dadswell (1989) found that blueback herring remained in the offshore region of the Annapolis estuary (Nova Scotia) for almost a month before the correct migration cues triggered emigration. These waters are 25-30% seawater. Once water temperatures begin to drop in the late summer through early winter (depending on geographic area), juveniles start heading downstream, initiating their first phase of seaward migration (Pardue 1983; Loesch 1987). Migration downstream is also prompted by changes in water flow, water levels, precipitation, and light intensity (Kissil 1974; Pardue 1983). Other researchers have suggested that water flow plays little role in providing the migration cue under riverine conditions, but is more dependent on water temperature and new to quarter moon phases, which provide dark nights (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989).

In the Connecticut River, juveniles were found to move out rapidly, within a 24-hour period, peaking in the early evening at 1800 hours (O'Leary and Kynard 1986). Kosa and Mather (2001) studied juvenile river herring movement from 11 small, coastal systems in Massachusetts and found most emigrated between 1200 and 1600 hours. Emigration by juvenile bluebacks in the Annapolis River, Nova Scotia peaked at night, between 1800 and 2300 hours (Stokesbury and Dadswell 1989).

Juvenile blueback herring (age 1+) were found in the lower portion of the Connecticut River in early spring by Marcy (1969), which led him to speculate that many juveniles likely spend their first winter close to the mouth of the river. Some young-of-the-year may overwinter in deeper, higher salinity areas of the Chesapeake Bay (Hildebrand and Schroeder 1928). Dovel (1971) reported juvenile populations in the upper Chesapeake Bay that did not emigrate until early spring of their second year. Juveniles have also been reported overwintering in the Delaware

Bay (Jones et al. 1978). Since juvenile river herring do not survive temperatures of 3° C or less (Otto et al. 1976), they would not be expected to overwinter in coastal systems where such temperatures persist (Kosa and Mather 2001).

Juveniles have been collected throughout a broad range of temperatures from 11.5 to 32°C in the Cape Fear River, North Carolina (Davis and Cheek 1966), and a range of 6.7-32.5°C from a discharge canal along the Connecticut River (Marcy 1976b). In the upper Chesapeake Bay, juveniles have been collected in water temperatures of 13-28°C; 96% were collected at 23-28° C. Klauda et al. (1991) suggest that a suitable range for juveniles is 10-30°C.

Juveniles collected from the Delaware River, New Jersey, selected temperatures in the laboratory that were between 20 and 22°C, when acclimated at 15-20°C and 4-6 ppt salinity (Meldrim and Gift 1971). In laboratory studies, juvenile blueback herring acclimated to 25 and 26°C at 7-8 ppt salinity preferred a temperature range of 24-28°C; an avoidance temperature of 36°C was reported (PSE&G 1978). When juveniles were acclimated at 19 and 22.7°C, mortality was 100 and 61.7%, respectively, after exposure at 32-33°C for four to six minutes (Marcy and Jacobson 1976). Mortality was also 100% when acclimated at 15° C and exposed to 30.5°C for six minutes (PSE&G 1984). In saltwater, juveniles that were acclimated at 15°C in 29 ppt salinity had a 100% survival rate when exposed to 20 and 25°C, but total mortality occurred within six minutes when fish were exposed to 32°C (Terpin et al. 1977).

In the Connecticut River, emigration began when the water temperatures dropped to 21°C in September, peaking at 14-15°C, and ending when the temperature dropped to 10°C, in late October or early November (O'Leary and Kynard 1986). Milstein (1981) found juveniles overwintering in an offshore estuary of the coast of New Jersey where bottom temperatures ranged from 2.0-10.0°C. These waters were warmer and had a higher salinity than the cooler, lower salinity river-bay estuarine nurseries where they reside in the fall.

In minimum temperature tolerance studies, juveniles that were acclimated at 25°C in 6.5-7 ppt salinity survived exposure at 12-13°C, but suffered 100% mortality at 10° C (PSE&G 1978). Additionally, juveniles that were acclimated at 5°C in 8.5-10 ppt salinity survived exposure at 3° C, but total mortality occurred at 0.2°C. Pardue (1983) concluded that optimal surface water temperatures for juveniles over the range of their habitat was between 20-30°C.

Unlike alewife, juvenile bluebacks in the Potomac River remained at the surface or at mid-water depths during daylight hours from July through November, with almost no fish appearing at the bottom. At night, over half of them were taken in bottom trawls (Warinner et al. 1970). Burbidge (1974) also reported that juvenile blueback herring were more abundant in surface waters of the James River, Virginia during the day. Contrary to these results, Jessop (1990) found that abundance of juvenile bluebacks was greater in surface waters at night than during the day, but fish did not exhibit a strict negative phototropism. One explanation for these observed differences is the minimal sewage treatment that was required during the 1970's, which led to major phytoplankton and algal blooms in freshwater areas, reducing light penetration. Since then, water clarity has greatly improved (Dennison et al. 1993).

Dixon (1996) found that juvenile bluebacks were more available to surface sampling gear approximately 30 minutes after sunset and before sunrise, where there was a corresponding light intensity of 10-2 to 10-3 uE/m2/s. Because he did not detect a corresponding change in availability of primary zooplankton prey, he concluded that juveniles migrate to the surface water within a specific isolume with changes in incident light intensity, not as a response to prey movement. A light intensity of 10-2 to 10-3 uE/m2/s may be a threshold that controls retinomotor responses to support selective feeding and schooling behavior in this species. Dixon (1996) concluded that juveniles find a depth and isolume that optimizes schooling (for predation protection) and selective feeding during the day, balancing predation risks vs. preferred food availability. These results further support and refine Loesch et al.'s (1982) observations, who first reported the diel changes in movement of juveniles.

Juveniles are found most often in waters of 0-2 ppt prior to fall migration (Jones et al. 1988), but are tolerant of much higher salinities early in life. Pardue (1983) concluded that juveniles prefer low salinities in the spring and summer, with an optimal range between 0-5 ppt. Chittenden (1972) captured older juveniles in freshwater and subjected them to 28 ppt salinity at 22° C and all but one fish survived (mortality may have been due to handling stress). Klauda et al. (1991) suggested that 0-28 ppt was a suitable range for juveniles. Their ability to tolerate salinities as low as 0 ppt and as high as 28 ppt allows them to utilize both freshwater and marine nursery areas. Both Loesch (1968) and Kissil (1968) found that juvenile bluebacks remained in freshwater up to one month longer than juvenile alewife. In the Chowan River, North Carolina juvenile bluebacks became scarce in sampling areas following drought conditions during the summer of 1981, which resulted in saline waters encroaching further upriver into nursery areas. Researchers suggested that bluebacks had possibly moved further upstream to freshwater areas to avoid the saltwater intrusion (Winslow et al. 1983).

Discharge is an important factor influencing variability in relative abundance and emigration of juvenile river herring across smaller systems. Extremely high discharge may adversely affect juvenile emigration, and high or fluctuating discharge may decrease relative abundance of adult and juvenile bluebacks (Meador et al. 1984; West et al. 1988; Kosa and Mather 2001). In laboratory experiments, juvenile river herring avoided higher water velocities greater than 10 cm/s, especially in narrow channels (Gordon et al. 1992). In large rivers, where greater volumes of water can be transported per unit of time without substantial increases in velocity (Gordon et al. 1992), the effects of discharge may differ (Kosa and Mather 2001). Jessop (1994) found that the juvenile abundance index (JAI) of blueback herring decreased and daily instantaneous mortality increased with mean July-August river discharge from the Mactaquac Dam headpond on the Saint John River, New Brunswick, Canada. Impacts may have been the result of advection from the headpond, or from mortality as a result of reduced phytoplankton and zooplankton prey.

Juvenile blueback herring have been found among SAV beds of the lower Chesapeake Bay and it has been suggested that they may benefit from reduced predation in such areas (Olney and Boehlert 1988). It is important to note though, that no link has been made between the presence of SAV and abundance of alosines. Rather, SAV is known to improve the water quality, which may affect abundance of alosines (Sadzinski 2003). Juvenile blueback herring are a pelagic schooling fish, which likely do not rely on SAV to the extent that other anadromous fish do, such as striped bass (Dixon pers. comm.).

Juveniles have been collected in the Cape Fear River, North Carolina, where pH was between 5.2-6.8 (Davis and Cheek 1966), but the length of time spent within these areas was unknown. Abundance of juvenile river herring peaked at a pH of 8.2 in coastal systems in Massachusetts. Researchers speculated that between 7.2 and 8.2, increases in river herring abundance may be related to changes in system productivity (Kosa and Mather 2001). Although researchers were unable to determine the exact mechanism for the impact of pH on river herring, they suggested that pH does appear to contribute to variations in juvenile abundance.

Juveniles have been collected in waters of the Cape Fear River, North Carolina, where DO ranged from 2.4-10.0 mg/L (Davis and Cheek 1966). Juveniles that were exposed to DO of 2.0-3.0 mg/L for 16 hours experienced a 33% mortality rate (Dorfman and Westman 1970). Researchers determined that the juveniles were unable to detect and avoid waters with low DO. Mass mortalities of juveniles resulted from low DO in the Connecticut River over several years during June and July, most notably in the early morning hours when DO was below 3.6 mg/L and temperature was 27.6°C (Moss et al. 1976). Klauda et al. (1991) concluded that juveniles require a minimum of 4.0 mg/L of dissolved oxygen.

Dixon's study (1996) noted that the size and age of juveniles in the nursery zone increased in the downstream direction. Burbidge (1974) made similar observations that larger blueback herring juveniles were found in downstream reaches of the James River. Dixon (1996) noted that the relative age distribution and density of juveniles (center of abundance) persisted in the nursery zone throughout the sampling season, which precluded the hypothesis that cohorts move downriver as a function of age and size. Instead, Dixon referenced Sismour's (1994) theory that as river herring larvae hatch at different times and locations along the river, they will encounter varying concentrations and combinations of potential prey. It is these differences that will affect larval nutrition and survival. In early spring, larvae that are closer to the center of the chlorophyll maxima along the river (which likely support development and expansion of zooplankton assemblages [Dixon 1996]) are more likely to find suitable prey items. Early in the season, sufficient prey in upriver areas may be lacking. As the season progresses and the zooplankton prey field expands to upriver reaches, larvae in these areas may find suitable prey quantities and grow to the juvenile stage (Sismour 1994). Burbidge (1974) demonstrated a direct relationship between density of zooplankton and distribution and growth of blueback herring. This differential survival rate within the nursery zone over time may account for younger juveniles in upstream reaches (Dixon 1996).

Juveniles were captured in the Cape Fear River system, North Carolina, where the alkalinity ranged from 5-32 mg/L (Davis and Cheek 1966). This same study also found that juveniles selected areas where free carbon dioxide was between 4 and 22 ppm. Another study found that juveniles held in freshwater avoided 0.1 mg/L total residual chlorine (TRC) at 17.5°C (PSE&G 1978).

Juvenile river herring have been found overwintering in waters 0.6-7.4 km from the shore of New Jersey, at depths of 2.4-19.2 m (Milstein 1981), in what is considered an offshore estuary

(Cameron and Pritchard 1963). This area is warmer and has a higher salinity than the cooler, lower salinity river-bay estuarine nurseries that they reside in the fall. The majority of fish were present during the month of March, when bottom temperatures ranged from 4.4 to 6.5°C and salinity was between 29.0 and 32.0 ppt. Further south, young bluebacks have been found overwintering off the North Carolina coast from January to March, concentrated at depths of 5.5-18.3 m (Holland and Yelverton 1973; Street et al. 1975).

Adults

Sexual maturity is reached at age 3-6 for blueback herring. Information regarding life history of young-of-the-year and adult blueback herring after they emigrate to the sea, and before they return to freshwater to spawn, is incomplete (Klauda et al. 1991). It is assumed that most juveniles join the adult population at sea within the first year of their lives and follow a north-south seasonal migration along the Atlantic coast, similar to that of American shad. Changes in temperature likely drive oceanic migration (Neves 1981).

Despite conclusive evidence, it is speculated that bluebacks are similar to other anadromous clupeids, in that they may undergo seasonal migrations within preferred isotherms (Fay et al. 1983). Neves (1981) found that bluebacks were caught in the offshore area where surface water temperatures were between 2-20°C and bottom water temperatures ranged from 2-16°C, but almost all of the fish were caught in water temperatures <13°C. Catches were most frequent where bottom temperatures averaged between 4-7°C.

Stone and Jessop (1992) found that the presence of a cold (<5°C) intermediate water mass over warmer, deeper waters on the Scotian Shelf (Hatchey 1942), where the largest catches of river herring occurred, may have restricted the extent of vertical migration during the spring. Since few captures were made where bottom temperatures were <5°C during the spring, vertical migration may be confined by a water temperature inversion in this area at this time of the year.

It is unknown to what extent blueback herring overwinter in deepwaters off the continental shelf. Fish have been caught most frequently at 27-55 m throughout their offshore range from Cape Hatteras, North Carolina, to Nova Scotia. While at sea, blueback herring were more available to bottom trawling gear during the day, which led early researchers to conclude that they were aversive to light and followed the diel movement of plankton in the water column (Neves 1981). In the Gulf of Maine region, zooplankton concentrations are at depths <100m (Bigelow 1926). Since bluebacks are rarely found in waters greater than 100 m in this area, it was speculated that zooplankton influence the depth distribution of blueback herring at sea (Neves 1981). Dixon's more recent study (1996) of juveniles within the riverine environment (see Juvenile Depth section), found that they migrate to the surface within a specific isolume as light intensity changes.

Stone and Jessop (1992) found that blueback herring off Nova Scotia, the Bay of Fundy, and the Gulf of Maine were found offshore at middepths of 101-183 m in the spring, in shallower nearshore waters at 46-82 m in the summer, and in deeper offshore waters at 119-192 m in the fall. They also found differences in depth distribution, with smaller fish (sexually immature) occurring in shallow regions (<93 m) during spring and fall, while larger fish occurred in deeper areas (≤93 m) in all seasons. The semi-pelagic nature of juveniles may have provided them with protection from the effects of overfishing (Dadswell 1985).

Adults have been collected in salinities over the range of 0-35 ppt (Klauda et al. 1991). Chittenden (1972) subjected adults to gradual and abrupt changes in salinity, including direct transfers from fresh to salt water and vice versa, with no mortality. For non-spawning adults that do not ascend freshwater streams, they could be expected to be found mostly in seawater, and possibly brackish estuaries as they make their way up the coast to their summer feeding grounds.

Blueback herring from the southernmost range are capable of migrating long distances (over 2000 km) in ocean waters of the Atlantic seaboard and their patterns of migration may be similar to those of American shad (Neves 1981). They are most abundant from warmer waters of the Chesapeake Bay southward (Manooch 1988; Scott and Scott 1988), occurring in virtually all tributaries to the Chesapeake Bay, in the Delaware River, and in adjacent offshore waters (Jones et al. 1978). Although bluebacks and alewife co-occur throughout much of their range, bluebacks are more abundant by one or perhaps two orders of magnitude along the middle and southern parts of their ranges (Schmidt et al. 2003).

Ecological relationships

Larvae

First-feeding larvae in the Connecticut River fed primarily on rotifers, then shifted to cladocerans as they grew larger (Crecco and Blake 1983). In general, it has been suggested that clupeids evolved so as to synchronize the larval stage with the optimal phase of annual plankton production cycles (Blaxter et al. 1982).

Juveniles

Juveniles in nursery areas feed mostly on copepods, cladocerans (Domermuth and Reed 1980), and larval dipterans (Burbidge 1974; Grabe and Schmidt 1978). Burbidge (1974) found that juveniles selected highly for larger items in the James River, Virginia, such as adult copepods, rather than smaller prey, such as *Bosmina* sp., except where there was a high relative abundance of them. Juveniles fed primarily on small copepods and dipteran larvae in the Cape Fear River, North Carolina (Davis and Cheek 1966). As much as 40% of their diet may consist of benthic organisms (Watt and Duerden 1974).

Juveniles feed mostly at the surface, below the surface of the water, and to a much lesser degree, on benthic prey (Domermuth and Reed 1980; Bigelow and Schroeder 2002). Several researchers (Burbidge 1974; Jessop 1990) observed juveniles feeding at dawn and increasing throughout the day with a maximum at dusk, then declining overnight. It is suggested that during the day, juveniles will remain within or near their zone of preferred light intensity, and feed in a selective mode (Dixon 1996), such as a “particulate” feeding mode (Janssen 1982). Pardue (1983) considered habitats that contained 100 or more individuals of zooplankton per liter as optimum, which he suggested was critical for survival and growth at this stage. Several researchers (Vigerstad and Colb 1978; O’Neill 1980; Yako 1998) have hypothesized that a change in food availability may provide a cue for juvenile anadromous herring to begin emigrating seaward, but no causal link has been established.

Young-of-the-year bluebacks are fed upon by many freshwater and marine fishes, birds, amphibians, reptiles, and mammals. Eels, yellow perch, white perch, and bluefish, are among the fish species that prey on bluebacks (Loesch (1987; Juanes et al. 1993). It has been suggested that excessive predation by striped bass may be contributing to the decline of blueback herring stocks in the Connecticut River (Savoy and Crecco 1995). Juvenile blueback herring were found to be energetically valuable and a potentially key prey for largemouth bass in two Massachusetts rivers during the late summer once they reached a suitable size. Although largemouth bass do not consistently consume blueback herring, they are energy-rich prey, which provide the highest growth potential (Yako et al. 2000).

It is often noted throughout the literature, that alewife and blueback herring co-exist in the same geographic regions, yet interspecific competition is often reduced through several mechanisms. For example, juveniles of both species in the Connecticut River consume or select different sizes of prey, leading researchers to conclude that intraspecific competition may be greater than interspecific competition (Crecco and Blake 1983). This was also evident in a study in the Minas Basin, Nova Scotia, where juvenile bluebacks favored smaller and more planktonic prey (filter feeding strategy) than did juvenile alewife (particulate-feeding strategy) (Stone 1985; Stone and Daborn 1987). Alewife also spawn earlier than bluebacks, thereby giving juvenile alewife a relative size advantage over juvenile bluebacks, allowing them a larger selection of prey (Jessop 1990). Differences in juvenile diel feeding activity further reduces competition. One study noted diurnal feeding by juvenile alewife was bimodal, with peak consumption about one to three hours before sunset and a minor peak occurring about two hours after sunrise (Weaver 1975). Another study found that juvenile blueback herring began to feed actively at dawn, increasing throughout the day and maximizing at dusk, then diminishing from dusk until dawn (Burbidge 1974). Additionally, bluebacks were found closer to the surface at night than alewife, which were found at mid-water depths, which may further reduce interspecific competition for food between the species (Loesch 1987).

Blueback herring and American shad juveniles also occur in shallow nearshore waters during the day, but competition for prey is often reduced by: 1) more opportunistic feeding by shad; 2) differential selection for cladoceran prey; and 3) higher utilization of copepods by blueback herring (Domermuth and Reed 1980). Juvenile bluebacks are more planktivorous, feeding on copepods, larval dipterans, and cladocerans (Hirschfield et al. 1966, Burbidge 1974).

Adults

Blueback herring are size-selective zooplankton feeders (Bigelow and Schroeder 1953), whose diet at sea consists mainly of ctenophores, calanoid copepods, amphipods, mysids and other pelagic shrimps, and small fish (Brooks and Dodson 1965; Neves 1981; Stone 1985; Stone and Daborn 1987; Scott and Scott 1988; Bowman et al. 2000). In Minas Basin, Bay of Fundy, smaller blueback herring fed mostly on micrzooplankton, while larger fish consumed larger prey, including mysids and amphipods; feeding intensity also decreased with increasing age of fish (Stone 1985). Neves' (1981) analysis of offshore survey results led to the conclusion that blueback herring follow the diel movement of zooplankton while at sea. As discussed above (see Juvenile Depth section), Dixon's (1996) study in freshwater concluded that juvenile bluebacks followed diel movements in response to light intensity, not prey movement. Although direct evidence is lacking, catches of blueback herring in specific areas along Georges Bank, the perimeter of the Gulf of Maine, and south of Nantucket Shoals may be related to zooplankton abundance (Neves 1981).

Competition and Predation: Complete information on predation at sea is lacking for blueback herring (Scott and Scott 1988). Fish that are known to prey on bluebacks in the marine environment include spiny dogfish, American eel, cod, Atlantic salmon, silver hake, white hake, Atlantic halibut, as well as, larger schooling species including bluefish, weakfish, and striped bass (Dadswell 1985; Ross 1991; Rountree 1999; Bowman et al. 2000). Seals, gulls, and terns may also feed on bluebacks in the ocean.

In freshwater, information is lacking regarding which species prey on adults during their spawning runs, but it is assumed that they are consumed by other fish, reptiles (snakes and turtles), birds (i.e. ospreys, eagles, cormorants), and mammals (i.e. mink) (Loesch 1987; Scott and Scott 1988). Erkan (2002) notes that predation of alosines has increased dramatically in Rhode Island rivers in recent years, especially by the double-crested cormorant, which often takes advantage of fish staging near the entrance to fishways. Populations of nesting colonies have increased in size and have expanded into areas in which they have previously not been observed. Predation by otters and herons has also increased, but to a lesser extent (Erkan 2003).

Several researchers have found evidence of striped bass predation on blueback herring (Trent and Hassler 1966; Manooch 1973; Gardinier and Hoff 1982). A recent study strongly supports the hypothesis that striped bass predation in the Connecticut River on adult blueback herring has resulted in a dramatic and unexpected decline in blueback herring abundance since 1992 (Savoy and Crecco in press). Researchers further suggest that striped bass prey primarily on spawning adults because their predator avoidance capability may be compromised at this time, due to their strong drive to spawn during upstream migration. Rates of predation on ages 0 and 1 alosines was much lower than that of adults.

All life stages of blueback herring, including the egg and larval stages, are important prey for freshwater fishes, birds, amphibians, reptiles and mammals (Klauda et al. 1991). The bluebacks' ability to feed extensively on rotifers is offered as an explanation for their dominance over American shad in some rivers along the East Coast (Marcy 1976a; Loesch and Kriete 1980).

Blueback herring have also shown signs of being impacted by invasive species. There is strong evidences that juveniles in the Hudson River have experienced a reduced forage base as a result of zebra mussel colonization (Waldman and Limburg 2003).

Abundance and status of stocks

Several long-term data sets were recently analyzed to determine the current status of blueback herring in large river systems along the East Coast, including the Connecticut, Hudson, and Delaware rivers. Bluebacks show signs of overexploitation in all of these rivers, including reductions in mean age, decreases in percentage of returning spawners, and decreases in abundance. Although researchers did not include smaller drainages in the analysis, they did note that some runs in the northeastern U.S. and Atlantic Canada have been increasing recently (Schmidt et al. 2003).

Refer to Abundance and Status of Stocks in Section 4.2.3.

4.2.7 Hickory Shad

Description and Distribution

Hickory shad, *Alosa mediocris*, are anadromous fish that spend most of their adult lives at sea, entering brackish and freshwater only to spawn (Bigelow and Schroeder 2002). Little is known about their life history and specific habitat requirements; however, coastal migrations and habitat requirements are thought to be similar to that of other alosines, especially American shad (Klauda et al. 1991). Very few spawning studies have been conducted in recent years (O'Dell and Mowrer 1984; Odom, et al. 1988). This may be, in part, because of a lack of interest in studying this species relative to other alosines (Klauda et al., 1991), and also because finding evidence of spawning in the form of eggs and larvae has proven difficult to scientists (Mansueti 1962).

Hickory shad are thought to be currently distributed along the East Coast from Cape Cod, Massachusetts (Batsavage and Rulifson 1998), to Cape Canaveral; waters south of here are unsuitable due to rising water temperatures that become semi-tropical in nature (Williams and Grey 1975). Although it is known that hickory shad are a schooling species, almost nothing is known about their distribution and movements once they return to the ocean (Street 1970; Richkus and DiNardo 1984). They have been caught in fisheries along coastal southern New England in the summer and fall (Bigelow and Schroeder 1953) and off Long Island, New York (Schaefer 1967). Anglers report catching them in nearshore waters at Cape May, New Jersey from May to November, and then capturing them in inlets from November through December (W. Gordon, pers. comm.). Unlike American shad that migrate in large numbers to the Gulf of Maine/upper Bay of Fundy during the summer, hickory shad are very rarely found there (M. Dadswell, pers. comm.). It is speculated that they do not move far from land while at sea (Mansueti and Hardy 1967).

Reproduction

Spawning Habitat

Hickory shad ascend coastal rivers during spring migration. Although it is assumed that they return to their natal rivers to spawn like other alosines, there is no documented evidence of this (Batsavage and Rulifson 1998). Their distribution in the riverine environment is similar to that of American shad (Rulifson et al. 1982). In North Carolina, the freshwater reaches of coastal rivers are the major spawning sites for hickory shad. They have also been found in the Neuse River, North Carolina in flooded swamps, and sloughs off channels of tributary creeks, but not the mainstem river (Pate 1972). In Georgia, hickory shad apparently spawn in flooded areas off the channel of the Altamaha River, and not in the mainstem of the upper reaches (Adams 1970). Major spawning sites in Virginia have been found in mainstem rivers at the fall line, further downstream, and in tributaries (Davis et al. 1970). Mansueti (1962) found that hickory shad spawned approximately 6-10 km (3.7-6.2 miles) upriver of major spawning sites of American shad in the mainstem of the Patuxent River, Maryland. In contrast, hickory shad in the St. Johns River, Florida did not migrate as far upstream as American shad (Moody 1961).

Adult hickory shad have been found in the St. Johns River, Florida as early as December (possibly November) (McBride 2000) and were absent by late January to mid-February (FF&WCC 1973). Spawning in the Santee and Cooper rivers, South Carolina may occur between early March through mid-May (Bulak and Curtis 1979). In the Chesapeake Bay, spawning may begin in early April (Mansueti and Hardy 1967), typically peaks in early May (Mansueti 1962), but may occur as late as June in freshwaters of Virginia (Davis et al. 1970). A second run of spawners has been reported to occur in the Chesapeake Bay, albeit to a much lesser degree (Hildebrand and Schroeder 1928). It is unknown if the fish that spawn during the fall run also participate in the spring run (Schaeffer 1976). Although spawning has been documented as far north as the Connecticut River (ASMFC 1999), most hickory shad spawning occurs from Maryland south (Klauda et al. 1991). One angler has documented recent spawning events at the Fairmount Dam in Philadelphia (W. Gordon, pers. comm.).

Large variations in size of young fish have been reported at given spawning sites, which has led researchers to hypothesize that they have a protracted spawning period, with eggs being released in small numbers over a long period (Mansueti 1962; DesFosse et al. 1994). Mansueti (1962) found very few ripe-running or spawnable hickory shad on the spawning grounds in the Chesapeake Bay area, leading him to hypothesize that maturation of gonads occurs rapidly and spawning occurs at night. In the Albemarle Sound region of North Carolina, hickory shad are reported to have a prolonged and seasonally earlier spawning period than other alosines (Batsavage and Rulifson 1998). It is unknown how long adults remain in freshwater after they have spawned, but it is assumed that they move gradually downstream and return to the ocean by mid-summer (Street 1970). In the Potomac River, it is believed that adults may lag slightly behind American shad before returning to the Atlantic Ocean after spawning (Klauda et al. 1991). Anglers have reported catching spent hickory shad that are very thin and actively feeding on minnows, in the nearshore region off Cape May Point, New Jersey. The adults will typically appear the first week of May and stay until mid-June (W. Gordon, pers. comm.).

There are very few studies of spawning behavior (Klauda et al. 1991), but it is assumed that female hickory shad broadcast their eggs into the water between dusk and midnight, and are fertilized by one or more males, similar to spawning behavior of American shad (Mansueti 1962; Jones et al. 1978). Hickory shad are repeat spawners, with fish spawning on average between three and five times before dying; one male was found to have spawned seven times (Schaeffer 1976). In general, hickory shad are repeat spawners, but unlike American shad, there is no progressive increase in spawning frequency from south to north. Most river systems have high incidences of repeat spawners, with percentages as high as 70-80% (Street and Adams 1969; Loesch et al. 1979; Rulifson 1982; Richkus and DiNardo 1984). Recent data from Maryland rivers indicated that 72% of females and 62% of males had previously spawned (Richardson, pers. comm.). The Cape Fear River, North Carolina appears to be an exception, where 19% of the males and only 9% of the females were reported to be repeat spawners (Sholar 1977).

The age distribution of adult hickory shad in coastal rivers from Florida to North Carolina ranges from two to eight years (Rulifson et al. 1982). The majority (80%) of males in the Octoraro Creek, Maryland were found to be sexually mature at age II (Schaeffer 1976). Further south, in the Altamaha River, Georgia 75% of females and only 49% of males were sexually mature by age II (Street and Adams 1969). Recent data from Maryland rivers found that only 50% of males and 36% of females were sexually mature at age II; by age III, 89% of males and 90% of females had spawned (Richardson, pers. comm.). In general, the majority of females are likely to become sexually mature a year or more later than males (Klauda et al. 1991; Batsavage and Rulifson 1998).

Spawning activity has been reported when water temperatures range from 8-22°C, but typically peaks when it is between 15-19°C (Mansueti 1962; Street 1970; Pate 1972; Rulifson et al. 1982; Batsavage and Rulifson 1998). Several reported temperature ranges in the southeast include 13-21°C for the Albemarle area, North Carolina (Street et al. 1975), 14-19°C for the Tar River, North Carolina (Marshall 1976), and 15-22°C for the Altamaha River, Georgia (Street 1970). Spawning in Maryland waters has been reported to occur at 7.8-20.5°C (Richardson, pers. comm.).

Hawkins (1980) noted that hickory shad prefer deep and dark-water tributaries in the Neuse River, North Carolina for spawning. Moody (1961) found that hickory shad were more abundant (by frequency of occurrence and by weight) in deeper water than American shad in the St. Johns River, Florida.

In the St. Johns River, Florida, adult hickory shad were collected where salinities ranged from 2.0-10.7 ppt (McLane 1955). In Maryland waters, spawning was reported where water was 0 ppt (Richardson, pers. comm.).

Hawkins (1980) reported that hickory shad may prefer slow-flowing areas of the Neuse River, North Carolina for spawning. Conversely, hickory shad in Maryland have been reported to favor habitat with faster moving water than that of American shad (Richardson, pers. comm.).

Richardson (pers. comm.) reports catching adult hickory shad in waters of Maryland rivers, where structures, such as ledges and fallen trees are present. Bottom composition for spawning in these waters tends to be mud, sand, and gravel.

Adults were found spawning in Maryland waters where the DO was between 5.7-11.8 mg/l (Richardson, pers. comm.)

Development, growth and movement patterns

Abundance of hickory shad has historically been less than other alosines (Atran et al. 1983; Speir 1987). The historical range of hickory shad is thought to have occurred as far north as the Gulf of Maine (possibly to the mouth of the Bay of Fundy) and possibly as far as Campobello Island, New Brunswick (Hildebrand 1963). Their current northern range is Cape Cod, Massachusetts (Batsavage and Rulifson 1998), with abundance occurring mostly from New York southward. It appears that spawning does not occur north of Maryland with much frequency (Klauda et al. 1991). They are commonly reported to occur as far south as the St. Johns River, Florida (Hildebrand 1963), but Williams and Grey (1975) have reported them as far south as Tomoka River, a small freshwater tributary of the Halifax River (a brackish coastal lagoon). Waters south of Cape Canaveral are unsuitable due to rising water temperatures that become semi-tropical in nature (Williams and Grey 1975).

Development

Observations suggest that eggs are released in small quantities over a longer period of time than other alosines in response to unknown stimuli and may become ripe very quickly. Eggs are generally adhesive and will typically sink to the bottom in undisturbed or moderately agitated water, but are semi-demersal in slow moving currents and buoyant under turbulent conditions (Mansueti 1962).

Early efforts to artificially propagate fish in the laboratory were difficult and initial experiments failed. Mansueti (1962) was finally able to successfully hatch eggs in the laboratory at 18.3°C and 21.1°C, with hatching occurring 5-10 hours sooner under the latter conditions. Prolarvae hatching occurred 2-3 days after fertilization, with an average hatch time of 55 to 60 hours. No postlarvae were observed feeding in the laboratory after hatching and all postlarvae died within 10 days. More recent culture of hickory shad eggs by the state of Maryland reported successful incubation at 64°F (17.8°C), with hatching occurring in 5-6 days (Richardson, pers. comm.). Recently-developed tank-spawning methods have been highly successful and larvae and fingerlings have been transplanted in large quantities in the Chesapeake Bay tributaries (Hendricks 2003).

Prolarvae fully absorb the yolk sac after 4-5 days, and postlarvae will begin feeding exogenously at this point. The size range of postlarvae is 5.5-7.0 mm (Mansueti 1962).

Hickory shad eggs have been collected in water temperatures between 9.5-22° C in rivers of North Carolina (Street 1970; Pate 1972, Marshall 1976, Hawkins 1980). Eggs that were reared under laboratory conditions hatched in 48-72 hours at temperatures between 18-21° C (Mansueti 1962). The state of Maryland reports culturing hickory shad eggs at 64° F (17.8° C), which typically hatch in 5-6 days (Richardson, pers. comm.).

Mansueti (1962) noted that fish in the 9-20 mm range were taken 35-40 miles upstream from the mouth of the Patuxent River, at a depth of 20 feet.

Eggs have been found in the pH range of 6.4-6.6 in the Neuse River, North Carolina (Hawkins 1980).

Viable hickory shad eggs have been collected in the Neuse River, North Carolina, where dissolved oxygen (DO) concentrations were between 5-10 mg/L (Hawkins 1980).

Postlarval shad begin transforming into juveniles when they are 10-35 mm long (Ulrich et al. 1979; Krauthamer and Richkus 1987). The minimum size at which they are considered fully-developed juveniles is 35 mm (Mansueti and Hardy 1962). Captures of juveniles in Maryland rivers often occur at sharp dropoffs, in schools of several dozen, indicating strong schooling behavior (Richardson, pers. comm.). Several studies suggest that most young hickory shad leave their freshwater and brackish habitats in early summer and migrate to estuarine nursery areas at an earlier age than other anadromous alosines (Mansueti 1962; Adams 1970; Pate 1972; Sholar 1977). Catches of juveniles that have been reported in the surf zone off Long Island, New York from April to November also support this hypothesis (Schaefer 1967). In the Altamaha River, Georgia, juveniles drift downstream and reach the estuary by late spring (Street 1970), which may be their nursery area (Smith 1968). Juveniles also drift down the Pee Dee and Waccamaw rivers, South Carolina earlier than young American shad, and enter Winyah Bay by July, remaining there throughout the first summer. By early fall, they have moved into oceanic waters (Crochet et al. 1976). Almost no juvenile fish could be found in rivers of Virginia, except for a few in the Rappahannock and York River systems collected in the 1970's (Klauda et al. 1991).

Other juvenile hickory shad may forego estuarine waters altogether and move directly into saltwater, unlike other alosines that use freshwater nurseries before moving into marine waters (Pate 1972; Sholar 1977). This ability to move directly into saltwater is believed to occur at an earlier age than for other anadromous alosines (Mansueti 1962; Schaefer 1967; Adams 1970; Pate 1972; Sholar 1977). Juvenile hickory shad from Albemarle Sound, North Carolina region did not use estuarine waters as a nursery ground, but instead, migrated to the ocean much earlier than other juvenile alosines (Batsavage and Rulifson 1998). Several researchers suggested that juvenile hickory shad move to shallow offshore areas off Georgia near the mouth of the Altamaha River and then disperse further by August and September (Godwin and Adams 1969; Street 1970). Anglers that catch spent adults in early May through mid-June at Cape May Point, New Jersey have reported that juveniles begin replacing adults as the summer progresses (W. Gordon, pers. comm.).

Juvenile hickory shad that are larger than average compared to other alosines have been captured in Maryland (Mansueti 1962; Virginia (Atran et al. 1983) and Georgia rivers (Adams 1970). These findings suggest that juvenile hickory shad are larger in size due to an earlier spawning period and have a faster growth rate (Godwin and Adams 1969).

Although no temperature optima or tolerances could be found in the literature, juveniles were found in the Roanoke River, North Carolina in temperatures ranging from 22.6 –28.0°C (Batsavage and Rulifson 1998). Richardson (pers. comm.) has reported catching juveniles in Maryland rivers at temperatures between 16-31°C from early July through early October. They have been reported to remain in freshwater until temperatures drop in October and November in Virginia, then move downstream as temperatures continue to decrease (Davis 1973).

Juveniles in Maryland were captured where salinities ranged from 0-7.2 ppt (Richardson, pers. comm.). Juveniles were found in estuarine waters of the Altamaha River, Georgia, in the summer, where salinities reached 10 ppt in the summer, and August and December, where salinities ranged from 10-20 ppt (Street 1970). As noted above, juveniles may forego the oligohaline portion of the estuary in favor of a more saline nursery environment (Pate 1972).

Juveniles in Maryland waters have been captured where DO ranges from 4.1-10.9 mg/l (Richardson, pers. comm.).

Ecological relationships

Pate (1972) could find no stomach contents in over 400 adult migrating hickory shad that he examined from the Neuse River, North Carolina. However, adults in the St. Johns River, Florida were found actively feeding, with 62.4% of the food items consisting of fish, and to a lesser extent, crustaceans (Williams et al. 1975) (see discussion under American shad by Walter and Olney, 2003)

Although no information was found in the literature, striped bass have been reported preying heavily on hickory shad beginning in early April at Deer Creek, Maryland (W. Gordon, pers. comm., Richardson, pers. comm.).

Adults are piscivorous, feeding on sand lance, anchovies, cunner, herring, scup, and silversides. They may also feed on squid, fish eggs, small crabs, and pelagic crustaceans (Hildebrand and Schroeder 1928; Williams et al. 1975; Bigelow and Schroeder 2002).

Abundance and status of stocks

This species has supported minor commercial fisheries because the meat is bony and regarded as inferior to American shad (Whitehead 1985); however, their roe is considered by some to be more delectable than any of the other river herrings (Nichols 1959). Hickory shad is highly sought after by sport fishermen when adults ascend rivers and tributaries during their spawning run (Mansueti 1962; Pate 1972). Although there is a lack of accurate monitoring of hickory shad, there is information that indicates some stocks are healthy. Since 1989, the Albemarle Sound, North Carolina population has experienced a surge in numbers, which supports a growing sport fishery on the Roanoke River and increased commercial fishing in Albemarle Sound. A short life span and low fecundity makes this population vulnerable to overharvest (Batsavage and Rulifson 1998). It should be noted that in other areas of its range, the hickory shad is considered highly fecund, with egg production estimated to be as high as 509,749 eggs per female in the Altamaha River, Georgia (Street 1970). Since the mid-1990's, hickory shad numbers have increased in the upper Chesapeake Bay and its tributaries (ASMFC 1999), including the lower Susquehanna, Potomac near Washington, D.C., upper Rappahannock, and James rivers (R. St. Pierre, pers. comm.). The National Marine Fisheries Service estimated that 5.6 metric tons of hickory shad were landed in 1990, and by 1999, estimated landings dramatically increased to 61.9 metric tons (Waldman and Limburg 2003).

Refer to Abundance and Status of Stocks in Section 4.2.3.

4.2.8 American eel

Description and Distribution

American eel are found in fresh, brackish, and coastal waters from the southern tip of Greenland to northeastern South America. They are ubiquitous in many habitats, and can contribute up to more than 25% of the total fish biomass in some individual systems (Smith and Sauders 1955; Ogden 1970; Jacobs et al. 2003; James McCleave, personal communication). In Connecticut rivers, the American eel was 4 times more abundant than any other species (Jacobs et al. 2003). American eel habitats include the open ocean, estuaries, large coastal tributaries, rivers, small freshwater streams, lakes, and ponds. They utilize habitats from the entire east coast of North America and the northern portion of South America, into the inland areas of the Mississippi River, the Great Lake drainages (Primarily Lake Ontario), and north into the Canadian province tributaries. American eels are also sometimes found in land locked lakes, particularly in the northeastern United States (Facey and Van den Avyle 1987). The latitudinal range for the American eel has been documented as 5° to 62°N (Bertin 1956), and their range covers more than 10,000 km of coastline (Boëtius and Harding 1985). American eels are thought to occupy the broadest array of habitats of any fish in the world (Helfman et al. 1987).

Americans eel are catadromous; they reproduce in salt water, and after an oceanic larval stage, migrate to brackish or fresh water where they grow to maturity. Upon reaching maturity, the eels migrate back to the ocean to spawn. Spawning occurs in the early winter and spring in the Sargasso Sea, and the newly hatched larvae (pre-leptocephalus and leptocephalus stages) passively drift and swim toward the continental shelf where they metamorphose into glass eels (Kleckner et al. 1983; Kleckner and McCleave 1985; McCleave et al. 1987).

The transformation into a glass eel includes a decrease in length and weight due to a reduction of water content, changes in the shape of the head and jaw, and accelerated development of the digestive system (Fahay 1978). Glass eels are miniature transparent eels and are morphologically similar to elvers (the next life stage), but they are unpigmented. As American eels develop pigment, they begin to migrate into freshwater. These young pigmented eels are termed elvers. Some elvers remain in coastal rivers and estuaries, while others may continue movements upstream in the winter and the spring (Facey and Van den Avyle 1987).

The next life stage is the yellow eel. This growth stage is characterized by a lack of sexual maturity and may last many years. Towards the end of this life stage, some of the eels become sexually differentiated. The maturation process into an adult, or silver eel, involves gradual changes, including a color change to metallic bronze black sheen, color change of the pectoral fins from yellow-green to black, fattening of the body, thickening of the skin, enlargement of the eyes and changes in visual pigments in the eye, (Vladykov 1973; Beatty 1975), increased length of capillaries in the rete of the swim bladder (Kleckner and Kruger 1981), and degeneration of the digestive tract. These changes make the eel more suited for migration at deeper depths (Vladykov 1973; Beatty 1975; Kleckner and Kruger 1981). During maturation, American eels migrate downriver to marine waters, then to the Sargasso Sea, where they spawn once and die.

American eels represent one panmictic population, meaning that they are a single breeding population that exhibits random mating. Thus, for example, an eel from the northern portion of their range could mate with an eel from the southern portion of their range, and the offspring could inhabit any portion of that range. As a result, recruits to a particular system are likely not the offspring of the adults from that system (ASMFC 2000).

Life history information for American eels remains incomplete, and for some life stages, habitat specific information is lacking. There is much uncertainty regarding how much variation in life history traits occurs across the whole population. Knowledge is lacking on the silver eel's migration from freshwater to the sea, as well as the egg, leptocephali, and glass eel life stages while in marine waters. Furthermore, while a potential spawning area of the eel has been identified in the Sargasso Sea, the specific location remains unknown (ASMFC 2000).

Reproduction

Silver eel (spawning habitat)

American eel spawn in the Sargasso Sea; a large portion of the western North Atlantic Ocean east of the Bahamas and south of Bermuda. Spawning occurs during the winter and the spring, from February to April, and possibly beyond April (Kleckner et al. 1983; McCleave et al. 1987). No other information exists on the spawning requirements, behavior, or exact location of spawning in the Sargasso Sea. Tesch (1977), who reviewed work by Schmidt (1923), and Vladykov and March (1975) determined that a spawning area existed south of Bermuda and north of the Bahamas. This zone is centered at about 25°N and 69°W. McCleave et al. (1987) reported spawning in the area from 52° to 79°W longitude and 19° to 29°N latitude.

Kleckner et al. (1983) and Kleckner and McCleave (1988) note that within this area, breeding occurs in the subtropical front systems of the oligotrophic subtropical gyres. This frontal zone, which is located within the North Atlantic Subtropical Convergence, occurs yearly during the suspected spawning season. The area is marked by abrupt horizontal temperature changes, and its position varies annually, seasonally, or even daily due to mesoscale eddies. This front is a shallow water phenomenon that occurs in the upper 500 m. It separates the permanently stratified, warm saline water mass in the southern Sargasso Sea from a cooler, less saline, seasonally stratified surface water mass in the northern Sargasso Sea. It is thought that spawning occurs on the warm side of this front (McCleave and Kleckner 1985; McCleave et al. 1987). However, no direct spawning of American eels has been observed and no adult American eels have been captured in the Sargasso Sea. Thus, the exact location of spawning area has only been inferred from the collection of leptocephali, or larvae, less than 7mm in size (Kleckner et al. 1983; Klekner and McCleave 1985).

The northern limit of the spawning area for American eel appears to be the thermal fronts that separate the northern and southern water masses of the Sargasso Sea (Kleckner et al. 1983). Kleckner et al. (1983) found that the smallest leptocephali collected during their study (3.9-5.5mm) were located on the warm side of these fronts. Kleckner and McCleave (1985) suggest that the northern limit for spawning occurs at 24-29°N, and the Bahamas/ Antilles Arc form the southern and western borders. So far, the eastern limit of American eel spawning has not been defined (Kleckner and McCleave 1985). Kleckner and McCleave (1985) suggest that this limit may be controlled by a directional orientation mechanism used by American eel adult to locate the spawning area.

It remains unknown to biologists how American eel locate the spawning area in the Sargasso Sea and what cues cause them to cease migrating. McCleave and Kleckner (1985) offer three hypotheses relating to how American eel migrate in the open ocean. The first is that swimming in one general compass direction (south), in addition to oceanic circulation, allows the eels to reach the spawning area. The second is that only a moderate directional orientation will result in successful migrations. The final hypothesis is that migration occurs within the upper three hundred meters of water, which McCleave and Kleckner (1985) speculate is significant with regard to the mechanism of migration. Stasko and Rommel (1977) suggest that the eels orient themselves using geoelectrical fields generated by ocean currents.

Kleckner et al. (1983) suggest that American eel cease migrating when they cross the frontal zone located at 24-29°N, which meanders from east to west for hundreds of kilometers. They believe that some feature of the surface water south of the front cues the American eel to cease migrating. It has been suggested that temperature and odor might be that cue (Ekman 1932, McCleave and Kleckner 1985). The temperature between the zones may vary as much as 2°C, and the northern and the southern zones exhibit differing species compositions of phytoplankton, zooplankton, and mesopelagic fishes, which could account for a change in odor (McCleave and Kleckner 1985). Furthermore, the upper layers in the pycnocline in the Sargasso Sea may contain dissolved amino acids, which are known to be potent to American eel (Liebezeit et al. 1980; Silver 1979). McCleave and Kleckner (1985) suggest it is possible that the leptocephali larvae imprint to this area in the same way that salmon imprint to a home stream.

American eel are thought to be semelparous, meaning that they die after spawning. Evidence for this includes no observations of adult eels migrating upriver, and no spent eels reported in the literature (Facey and Van den Avyle 1987).

Bottom composition is not known to be important to spawning adults, as spawning is thought to occur in the mid-upper water column (Kleckner et al. 1983; Kleckner and McCleave 1985).

Kleckner et al. (1983) and Kleckner and McCleave (1985) suggest that morphological and physiological evidence indicate that spawning occurs in the upper few hundred meters of the water column. This is based on the fact that larval American eel (less than 5mm long) have been found in water 50-350 m deep.

Temperatures may be important to spawning adults, as they spawn on the warmer side of the front in the Sargasso Sea (Kleckner et al. 1983; Kleckner and McCleave 1985). Spawning is thought to occur in the warm waters of the Sargasso Sea in an area where water temperatures are characterized by 18-19°C isotherms between 200-300m (Kleckner et al. 1983). Kleckner and McCleave (1985) describe the hypothesized spawning area as having temperatures greater than 18.2°C.

Salinity might be a key habitat parameter for spawning adults, as spawning occurs on the side of the front in the Sargasso Sea that has warmer temperatures and more saline waters (Kleckner et al. 1983; Kleckner and McCleave 1985). The spawning grounds of the American eel occur in a high salinity region of the Sargasso Sea where the salinity reaches a maximum of 36.6 ppt (Kleckner and McCleave 1985).

Development, growth and movement patterns

Eggs and leptocephali

There is little information existing on the environmental requirements or the incubation period of American eel eggs. It is assumed that the eggs hatch in the same area as they are spawned in the Sargasso Sea (See discussion in above section). Hatching is thought to occur from February through April in the Sargasso Sea, with a peak occurring in February (Kleckner et al. 1983).

After hatching, American eel undergo a brief pre-larval stage, and then enter the larval leptocephali life stage. Lepocephali are flattened from side to side and resemble a willow leaf (ASMFC 2000). They grow to about 55-65 mm before metamorphosis to the glass eel stage (Kleckner and McCleave 1985). While growing, the leptocephali drift and swim in the upper water column for up to a year (Kleckner and McCleave 1985). Their distribution is a result of the oceanic circulation patterns and the swimming behavior of the larvae (ASMFC 2000).

Kleckner and McCleave (1985) reported on the spatial and temporal distribution of leptocephali by collecting specimens and analyzing data collected by Schmidt in the 1920s. They found that leptocephali 7-10mm in length were caught from mid-February to the end of April. Specimens >45 mm were taken during all months. Kleckner and McCleave (1985) identified two year classes that occurred from February to mid-June as indicated by a bimodal distribution in length. Kleckner and McCleave (1985) collected the majority of leptocephali between 11°00'N to 42° 33.5'N latitude and 43°50'W longitude. One leptocephalus was collected at 49°43'N, 20°45'W and measured 70 mm TL. Kleckner and McCleave (1985) stated that all leptocephali 10 mm TL or less and all 0-group leptocephali collected were found within a 550 km arc east of the Bahaman Islands and north of Hispanola Islands. These specimens were found from February to March. From April to May, only one 0-group leptocephali was collected in the eastern Sargasso Sea from 23° to 28°N and 51° and 63°W (Kleckner and McCleave 1985).

Kleckner and McCleave (1985) found 0-group American eel in the Carribean Current along the west shore of the Yucatan Channel, in the Straits of Florida, and in the Gulf Stream to the east of Cape Hatteras in April and May. Through June and July, specimens were taken in the Caribbean, Gulf Loop, Florida, and Gulf Stream currents (Kleckner and McCleave 1985).

By August, larvae 40-67 mm occupy the entire Gulf Stream area up to the Gulf of Maine. From August through October, only a few large leptocephali, or newly metamorphosed glass eels remain far out in the Western Atlantic coast. Kleckner and McCleave (1985) report that during August and September, they collected leptocephali from stations in the southern Caribbean sea, Gulf Loop Current, Florida Current, Gulf Stream, and North Atlantic Current. From this time onward, eels approach the North American continent and Greenland as glass eels (Kleckner and McCleave 1980; Kract and Tesch 1981). Kleckner and McCleave (1985) found that American eel leptocephali were found in collections in the Caribbean Sea from south of Puerto Rico to the Yucatan Channel in October and November. They were also collected at this time south of the northeastern United States and in the Canadian Maritime Provinces.

Kleckner and McCleave (1985) found that 1-group American eels were scattered widely in collections taken in the Caribbean Sea and western North Atlantic Ocean during February and March and April and May. Many specimens were taken near the Bahama Islands and near the Florida Current off the Southeastern United States (Kleckner and McCleave 1985). They also found that metamorphosing American eel leptocephali were found north of the Gulf Stream between 65°42'W and 73°30'W. Additionally, metamorphosing leptocephali were taken 55 km southwest of Bermuda and approximately 45 km southeast of Cape Hatteras. One specimen was taken 110km North of Campeche Bank in the Gulf of Mexico.

Larvae are transported northwest from the spawning grounds to the eastern seaboard by the Antilles current, Florida current, and the Gulf Stream (Facey and Van den Avyle 1987). The proposed route of American eel larvae is a westward drift from the spawning grounds in the Sargasso Sea via the Antilles Current, and then North with the Florida Current to join the Gulf Stream north of Bermuda (Kleckner and McCleave 1985; McCleave 1993; McCleave et al. 1998; Reviewed in Knights 2003).

A small portion of leptocephali reach the Caribbean, Gulf of Mexico, and the Straits of Florida. The proposed route of these larvae occur to the west and southwest of the spawning grounds via the Windward Passage and Mona Passages, which transport the American eel leptocephali to the Caribbean Sea. From here, eddies could carry them along the Caribbean coast, or the Caribbean current could convey them through the Yucatan Channel into the Gulf of Mexico and the Gulf loop current (Nof and Olsen 1983; Olsen et al. 1984; Kleckner and McCleave 1985 and sources within; McCleave and Kleckner 1987 and sources within). Leptocephali entering the Straits of Florida likely were carried by the Gulf Loop Current, which flows out of the Gulf of Mexico as the Florida Current. Additionally, they may be conveyed into the Straits of Florida from the Bahamas/Antilles archipelago by currents through the Old Bahama Channel, then the Nicholas and Santaren Channels north of Cuba, or through the Northwest Providence Channel south of Grand Bahaman Island (Kleckner and McCleave 1985 and sources within).

It is possible that some eel larvae become trapped in the Sargasso Sea for over a year by recirculating currents (Knights 2003). This occurs when the larvae become trapped in the sub-gyre where the Florida and Antilles Currents interact, thus causing the larvae to drift north, or recirculate back into the oligotrophic Sargasso Sea from the Gulf Stream (Boëtius and Harding 1985).

As the larvae approach the edge of the continental shelf, they metamorphose into miniature transparent eel, called glass eels (ASMFC 2000).

Bottom substrate is not important to this lifestage, as American eel larvae are planktonic and float and drift in the water column. Thus, no bottom substrate is used during this life stage (Kleckner and McCleave 1985).

The importance of depth to the American eel egg and larval life stage is not stated in the literature. No information exists on the depth that eel eggs are found, as eggs have ever been collected in the Sargasso Sea (ASMFC 2000).

Once American eel enter the leptocephalus stage, they are found in the upper 250 m of the water column (Castonguay and McCleave 1987). Larvae less than 5mm long have been captured at depths between 50 and 350 m. Larvae between 5-10 mm appear to vertically migrate, as they are found between 100m and 150m during the day, and between 50 m and 100 m during the night (Castonguay and McCleave 1987; McCleave et al. 1987).

No studies have concluded the temperature requirements of American eel in the wild. However, the Japanese eel (*Anguilla japonica*) eggs hatch in 38-45 hours at 23°C (Yamamoto and Yamauchi 1974).

The salinity requirements of eggs and larvae have not been documented in literature. Facey and Van den Avyle (1987) state that postlarval American eels are tolerant of a broad range of salinities because postlarval American eel occur both in freshwater and in marine habitats. Leptocephali are in near-ionic equilibrium with seawater (Hulet et al. 1972).

Glass eels and elvers

American eel metamorphose into glass eels over the Continental Shelf. Shortly after, the unpigmented glass eels enter estuaries and eventually migrate to freshwater and ascend rivers during the late winter and early spring. It is thought that glass eels and elvers use olfaction to locate freshwater (Sheldon 1974; Sorensen 1986; Sorensen and Bianchini 1986); however, the specifics of this theory are mostly unknown. Creutzberg (1959, 1961) demonstrated that European eels were able to detect the odor of freshwater, and alter their behavior accordingly. Sorensen (1986) reported that American eels were attracted to the smell of brook water, as well as the smell of decaying leaf detritus.

Vladykov (1966) stated that the migration upriver occurs earlier in the southern portion of the range and later in the north. However, other studies show variations and overlaps in migration timing (Facey and Van den Avyle 1987). Migrating eels in the Southeastern states and the Mid-Atlantic have been collected from January through May (Jeffries 1960; Smith 1968, Fahay 1978; Hornberger 1978; Sykes 1981; Helfman et al. 1984). In the northern states, migrating elvers reach estuaries as early as late winter (Jeffries 1960), although the main migration occurs in the spring. In the East River, Chester, Nova Scotia, Jessop (2000) reported eel recruitment in the river mouth from May through June, and upstream migrations occurring from July through September. Dutil et al. (1987a) reported that the glass eel and elver migration to the St. Lawrence estuary occurred in the second half of June and was over by the end of July. American eels in Maine have been documented arriving upstream from the end of March to the beginning of May (Facey and Van den Avyle 1987). Ricker and Squires (1974) and Sheldon (1974) report that the run in Maine is from late April to June. In Rhode Island, migrations peak during April and May (Facey and Van den Avyle 1987). In North Carolina, Rulifson et al (2004) found that recruitment of elvers occurred from January through April, with the highest density of eels occurring from March to April.

Glass eels enter estuaries by drifting on flood tides and holding position near the bottom of ebb tides, and by actively swimming along shore in estuaries above tidal influence (Barbin and Krueger 1994). Movements are primarily nocturnal (Dutil et al. 1987a). Glass eels in estuaries eventually change into pigmented elvers (Haro 1991).

During the elver life stage, American eels are active mostly at night. During the day they either burrow or remain in deepwaters (Deelder 1958). Elvers move back up into the water column on flood tides and return to the bottom during ebb tides (Pacheco and Grant 1973; McCleave and Kleckner 1985; McCleave and Wippelhauser 1986).

Eels have been documented stalling their inward migration before they enter freshwater (McCleave and Kleckner 1985). Cues that trigger this behavior are unknown. It is thought that eels may be able to detect the odor of freshwater (Creutzberg 1959, 1961; Sorensen 1986). Stalling at the freshwater interface may allow the eels to adjust physiologically and behaviorally before entering the new environment (Sorensen and Bianchini 1986). This upstream migration is possibly triggered by water chemistry changes caused by the intrusion of estuarine water during the high spring tides (Sorensen and Bianchini 1986). Elvers eventually begin their upstream migration and become more active during the day (Sorensen and Bianchini 1986). Tesch (1977) reported that European elvers oriented themselves with river currents for upstream movement. If the current was too weak or strong, the eels moved into backwater areas and delayed their migration. Since American eels and European eels have similar behaviors, it is possible that fast or slow currents also affect American eels.

Factors that are thought to influence the daily abundance of migrating elvers include nightly tidal height, river water temperature and discharge, and difference between bay and river temperature (McCleave and Kleckner 1985; Sorensen and Bianchini 1986; Ciccotti et al. 1995; McCleave and Wipplehauser 1987; Wipplehauser and McCleave 1987; Martin 1995; Jessop 2003). Migration occurs in waves and is initially triggered by an increase in temperature to about 12-14°C. After initiating migration, temperature does not appear to have an effect on migrating elvers (Jellyman and Ryan 1983; Martin 1995; Jessop 2003). River discharge appears to control the daily abundance of upstream migrants, with decreases in abundance occurring with increases in river discharge. Jessop (2003) states that increased tidal height acts to deliver an increasing abundance of elvers to the river mouth. Temperature then acts to initiate upstream migration, while discharge controls the rate of movement upstream.

While most American eel elvers migrate into freshwater, some may cease migration in coastal waters and estuaries and remain there from the time they are a year of age until they reach the mature silver eel stage and begin the spawning migration (Morrison et al. 2003). In addition to the upriver migration, fall and spring migrations have been documented (Smith and Saunders 1955; Medcof 1969).

Substrate may be an important habitat parameter for American eel, as elvers are noted burrowing during the day and in between movements upstream. American eels appear to use many different types of substrates. Facey and Van den Avyle (1987) stated that migrating elvers make use of soft undisturbed bottom sediments as shelter. A study by Edel (1976) demonstrated that American eel are less active when there is shelter present. Fahay (1978) stated that postlarval eels are benthic and utilize burrows, tubes, snags plant masses, other types of shelter, and the substrate itself. Eels have been documented burrowing in both mud and sand (P. Geer, Pers Comm).

Creutzberg (1961) reported that at night, unpigmented European eels in coastal waters are found in a variety of depths throughout the water column during incoming tides. During the day, elvers move to the bottom and bury themselves in the substrate (Deedler 1958).

Temperature is important to elvers because it is thought to trigger upstream migration. Migrations of eels begin when temperature increases above 10°C, with the majority of the movement taking place at temperatures greater than 20°C (Moriarty 1986; Haro and Krueger 1991; Hartley 1992; Thibault and Verreault 1995; Richkus and Whalen 1999; Bernard and Desrochers 2002; Jessop 2003). Jessop (2003) found that elvers in the East River, Chester, Nova Scotia, actively moved upstream when river temperatures reached 10-12°C, and the first wave of migrants peaked at 11-16°C. Water temperatures of less than 10-12°C had a gating effect on the elvers (Jessop 2003). Other researchers have found similar results. Helfman et al (1984) noted migrations in Georgia at 11°C, Soreson and Bianchini (1986) found a range of 10-15°C in Rhode Island, with a peak at 14°C, and Smith (1955) and Groom (1975) found a temperature range of 10-12°C for migrating eels in New Brunswick. Bernard and Desrochers (2002) found that most of the eels were caught in the St. Lawrence River, Quebec in July and August when the water temperature was above 20°C. While temperature is thought to play an active role in stimulating migration, other factors also play a role in the abundance of eels migrating upstream (Jessop 2003).

Other than stimulating migration, temperature does not appear to play a key role in the elver life cycle. Juvenile American eels utilize a broad range of habitats and are likely to have flexible temperature requirements. Glass eels were documented in Penobscot, Maine in temperatures ranging from 3.9°C to 13.8°C (Sheldon and McCleave 1985). Elvers have been documented in a wide variety of temperatures, including cold freshwater streams and lakes, to warm brackish coastal bays and lakes. They have been found at temperatures as low as -0.8°C (Jeffries 1960).

Little is known about the salinity requirements of juvenile American eels. Sheldon and McCleave (1985) document glass eels in Penobscot, Maine, in salinities ranging from 0-25.2 ppt.

Sheldon and McCleave noted that in Penobscot, Maine, glass eels accumulated on the surface when surface currents on the ebb tide decreased below 15 cm/s. River discharge and its effects on water velocity were found to be the primary factor influencing the rate of elver upstream migrations (Jessop 2000). In velocities exceeding 35-40 cm/s, elvers had difficulty swimming and maintaining their position (McCleave 1980; Barbin and Krueger 1994). Jessop (2000) found that most elvers will not swim at water velocities exceeding 25 cm/s, and instead will remain resting in the substrate. Delays or prevention of upstream elver migration can be caused by high flows (Lowe 1951; Jessop and Harvie 2003). Lowe (1951) noted that high flows on the Bann River, Ireland, delayed European eel (*A. Anguilla*) elver migrations for many weeks.

<u>Yellow eels</u>
Some yellow eels continue migrating upstream until they reach maturity, while others remain in the lower portions of coastal estuaries and rivers (Haro 1986; Richkus and Whalen 1999; ASMFC 2000; Morrison et al. 2003). Morrison et al. (2003) studied the migration histories of yellow eels using otolith microchemistry. Yellow eels in the Hudson River, New York showed three modes of habitat use: 1) Those eels captured in freshwater, utilized only freshwater during their elver and yellow life stages; 2) over half of those captured in brackish water resided in freshwater for at least 2 years before migrating back to brackish water; and 3) the rest of the eels captured in brackish water habitats either resided entirely in brackish water, without ever utilizing fresh water environments (Morrison et al. 2003).

Few young eels are found in inland lakes (Hurley 1972; Facey and LaBar 1981; Kolenosky and Hendry 1982), as upstream migrants tend to be older, larger, more mature eels. Upstream migrations occur primarily at night from dusk to dawn. However, migrations do sometimes occur during the day (Helfman 1986; Dutil et al. 1988; Facey and Van Den Avyle 1987; McGrath et al. 2003; Verdon et al. 2003). Some studies have indicated that American eels migrate in response to the lunar cycle, with eels being less active during moonlit periods (Winn et al. 1975; Tesch 1977; Sorensen and Bianchini 1986; Cairns and Hooley 2003). Yellow eels remain in freshwater and brackish systems up to 20 years before maturing into silver eels and migrating to the sea to spawn (Tesch 1977; Helfman et al. 1987).

Migrations upstream occur from March through October, and peak in May and July depending on location (Richkus and Whalen 1999). In the St. Lawrence River, migration peaks between mid-July and mid-August. McGrath et al. (2003a) found that the numbers of American eels in the St. Lawrence River, New York approaching the Moses-Saunders Power Dam peaked in early July and early October. Verdon et al (2003) found that American eels in the Richelieu River, Quebec began upstream migrations as early as June 11th and ended late September.

Some yellow eels cease migrating in the brackish portions of rivers, while others continue into the upper rivers (Hardy 1978; Fahay 1978). There is some evidence that some American eels establish a home range (Gunning and Shoop 1962; Vladykov 1971; Helfman et al. 1983; LaBar and Facey 1983; Bozeman et al. 1985; Ford and Mercer 1986; Dutil et al. 1988; Parker 1995). A home range is defined as the area in which the animal normally travels (Gerking 1953). Ford and Mercer (1986) found some evidence of a home range and territoriality, and found that larger eels were located primarily in large creeks, while smaller eels were found in narrow creeks at the back of the marsh, in the Great Sippewisset Marsh, Massachusetts. They estimated a home range of <100m (Ford and Mercer 1986). Other home range estimates include 28 ha in Lake Champlain, Vermont (LaBar and Facey 1983), 0.1-2 ha in a Georgia tidal creek (Helfman et al 1983; Bozeman et al. 1986) and 0.5-2 ha in a tributary of the St. Lawrence River (Dutil et al. 1988).

Parker (1995) found that homing in yellow phase American eels in the Penobscot Estuary, Maine was precise. More than half of the displaced eels returned to within 50m of the capture site and remained there for several days. He also found that 9 of the 16 eels displaced returned to within 300 m of their capture site, and 3 eels moved towards their capture sites, but did not arrive there while under observation. Parker (1995) found a home range of 300 ha. The size of the home range can be influenced by food availability, competition, and predator densities (Bozeman et al. 1985; Parker 1995). Displaced eels use selective stream transport to return to their prior sites (Parker and McCleave 1997).

Many studies indicate that sex ratios within individual rivers are highly skewed (Facey and LaBar 1981; Helfman et al. 1987; McCleave 1996; Krueger and Oliveira 1997; Oliveira et al. 2001; Goodwin and Angermeier 2003). Sex ratios have shown varied results regarding sex demographic patterns in American eels. Some studies state that males are more prevalent in estuaries, while females dominate in the freshwater portions of rivers (Vladykov 1966; Helfman et al. 1984; McCleave 1996; Bigelow and Schroeder 2002). Helfman et al. (1984) reported that 64% of the eels found in a Georgia estuary were male, while 94% of the eels found in freshwater were female. Hansen and Eversole (1984) reported that in South Carolina, females were about twenty times more abundant than males. Many studies found that eels in St. Lawrence River and Lake Ontario are mostly female (Vladykov 1966; Dutil 1987b). Oliveira et al. (2001) found that 52-98% of American eels in the Chandler, East Machias, and Sheepscot Rivers, Maine were male. Females have been reported as dominant in most Canadian habitats (Hurley 1972; Dolan and Power 1977; Jessop 1987.) Age, size, and sex patterns are unknown for most of the species range.

Recently, evidence suggests that density plays the key role in determining the sex of American eel; males are produced in high density areas, and females in low density areas. Thus, females are more common in upper reaches of rivers where eel density is lowest (Krueger and Oliveira 1999). Oliveira (1999) and Oliveira et al. (2001) hypothesize that males are produced in areas where crowding is occurring. Males favor areas closer to the sea and spawning ground in more productive habitats, where they can grow and mature faster (Helfman et al. 1987). On the other hand, females tend to disperse widely within their range and utilize all suitable habitats. They favor slower growth and greater size, thus increasing fecundity and swimming ability (Krueger and Oliveira 1999; Goodwin and Angermeier 2003). In upper reaches of rivers, American eels tend to mature at older ages and larger sizes (Helfman et al. 1987).

Yellow phase American eels are bottom/substrate oriented and may show little movement (Eales 1968; Ogden 1970; LaBar and Facey 1983). The substrate preference of American eel is not documented in literature. Geer (2003) found that in the Chesapeake Bay, Virginia, eels were mostly found over detritus, hydroid, or shell bottoms. Chaput et al. (1997) state that American eels in the St. Lawrence River use soft sediments to burrow during the winter. Krause (1961) also found that European eels in Germany burrowed themselves in the mud.

Little information exists regarding the depths at which American eels are found. Due to the diverse range of habitats that American eel utilize, depth range probably varies greatly. Geer (2003) found that the majority of yellow eels were caught in the upper tributaries of the Chesapeake Bay. In these areas, the depth ranged from 4 to 10m.

The onset of upstream migration in yellow eels is thought to be linked to water temperature (Moriarty 1986; Haro and Krueger 1991; Hartley 1992; Thibault and Verreault 1995; EPRI 1999). Knights and White (1998) found that European eels are stimulated to migrate by temperatures greater than 14-16°C and increases in migrations occur at temperatures greater than 20°C. Verdon et al. (2003) found similar results in the Richelieu River, Quebec. They found that migration occurs earlier in this river than in the upper St. Lawrence River, and hypothesize that in larger systems, like the St. Lawrence, temperature increases are more gradual and less variable, causing a later upstream migration. In the upper St. Lawrence River, upstream migration begins in late June and peak at the end of July (Verdon and Desrochers 2003). Verdon and Desrochers (2003) found that eels captured in the St. Lawrence River peaked when the temperatures reached 22-23°C, and a decrease in captures coincided with a decrease in water temperature from 24°C to 21°C. Once the temperatures fell below 21°C, captures of American eels became scarce (Verdon and Desrochers 2003). McGrath et al. (2003a) noted a decrease in migrant yellow eels at the Moses-Saunders Power Dam in the St. Lawrence River, when temperatures declined to 10°C in the fall. Geer (2003) reported that eels in the Chesapeake Bay, Virginia were found between 13°C and 27°C. They were most abundant in waters where the temperature was 26-28°C and least abundant in waters less than 8°C. Low catch rates at these temperatures suggests inactivity.

Yellow eels live in a variety of habitats, including, cold, high-elevation or high-latitude freshwater streams and lakes, to warm, brackish coastal bays and estuaries in the Gulf of Mexico (Facey and Van den Avyle 1987). Walsh et al. (1983) documented that yellow eel were held at 5°C for over five weeks. Also, American eels have been reported to survive passage through a nuclear power plant, where they were exposed to elevated temperatures for 1 to 1.5 hours (Marcy 1973).

It is likely that salinity is not a key habitat parameter, as American eel are found in a wide variety of salinities. The importance of salinity to the yellow phase of American eel was not found in the literature. Geer (2003) reported that in the Chesapeake Bay, Virginia, more American eels were present in the upper tributaries near or above the freshwater interface. Eighty-nine percent of the catch was in salinities below 12 ppt, and 27% of the catch occurred in waters less than 2 ppt.

Yellow eels are likely not velocity dependent, as high densities of eels have been found in lakes and ponds where velocity is low or nonexistent (Kevin McGrath, Personnel Communication). However, in their study of physical habitat relationship for American eel, Wiley et al (2004) found that in Maryland, velocity-depth diversity was the only important stream habitat variable in relation to eel density. The highest densities of eel occurred in sites that had 4 velocity-depth regimes; slow (<0.3m/s)-deep (>0.5m), slow-shallow (<0.5m), fast (>0.3m/s)-deep, and fast-shallow. Sites with only one of two velocity-depth regimes had significantly lower eel densities (Wiley et al. 2004).

Rulifson et al. (2004) found that catch was affected by dissolved oxygen rates in North Carolina. They found that dissolved oxygen was a strong predictor in the distribution of American eels. High catches of eels were almost always in waters with dissolved oxygen levels above 4mg/L (Rulifson et al. 2004). Geer (2003) found that 82% of the American eels caught in the Chesapeake Bay, Virginia were found in waters with dissolved oxygen levels between 5 and 9mg/L. However, no association was found between dissolved oxygen and catch (Geer 2003). This could be due to the fact that sampling was conducted only in the areas with dissolved oxygen levels above 5 mg/L (Rulifson et al. 2004).

Silver eels

Geographic and temporal patterns: Once American eel enter the final life stage, termed silver eel, they are sexually mature and begin migrating out to sea. In New England tributaries, spawning migrations begin in the late summer and continue through fall. Eels migrate later in the southeastern states and in the Middle Atlantic than in the northern states. It is hypothesized that this delay helps to synchronize the arrival of the eels at the spawning grounds in the Sargasso Sea (Wenner 1973; Facey and Halfman 1985; Helfman et al. 1987).

Yellow eels transform into silver eels before migrating out to sea. Little is known about this phase of their life (ASMFC 2000). Downstream migrations occur in spurts with long periods of no movement and peaks of intensive movements (Barbin et al. 1998). The rate of migration varies, with stalls in migrations occurring while the silver eels wait for specific environmental cues (Reviewed in Richkus and Whalen 1999). Migration begins at different times depending on location, and occurs primarily in the fall, although winter migrations have been documented (Facey and Helfman 1985; Euston et al. 1997, 1998). In Newfoundland, the largest eel migrations occur in late September, and early October (Bouillon and Haedrich 1985). McGrath et al. (2003b) found that American eels in the upper portion of the St. Lawrence River migrated downstream from the end of June to the beginning of October, and that the primary migration in the lower estuarine portion of the River occurred in October.

Migration of eels is thought to occur mostly at night (Haro and Castro-Santos 2000; McGrath et al. 2003c). Haro and Castro-Santos (2000) stated that silver eels in the Connecticut River, Massachusetts, migrated primarily at night, within several hours after sunset. The eels remained inactive during the day (Haro and Castro-Santos 2000). The variables thought to influence downstream migration in silver eels include water temperature, river and stream discharge, odor, and light-intensity, including moon phase (Hain 1975; Westin 1990; Haro 1991; Richkus and Whalen 1999; Richkus and Dixon 2003). Research has indicated that catch rates of American eels are higher during the dark phases of the moon and when cloud cover is highest (Winn et al. 1975; Tesch 1977; Cairns and Hooley 2003; McGrath et al. 2003c). Cairns and Hooley (2003) found that in tidal bays and estuaries in Prince Edward Island, Canada, catch per unit effort (CPUE) for silver and yellow eels decreased at full moon. CPUE was negatively correlated with the proportion of moon fullness and was negatively correlated with the illuminance index (Cairns and Hooley 2003). Cairns and Hooley (2003) suggest that this is a mechanism to avoid predation. Some studies indicate that eels exhibit an endogenous lunar cycle of activity (Boëtius 1967; Hain 1975; Edel 1976).

Rainfall, which leads to increased river discharge, may also have an impact on migrations (Lowe 1952; Winn et al. 1975; Mitchell 1995; Euston et al. 1997, 1998). Winn et al. (1975) noted increased migrations after rains, as well as during the third and forth lunar quarter. Haro et al. (2003) found in Maine that more eels were captured on days with rain, then on days without rain.

Age and size at which migration begins varies geographically. American eels in the northern part of the range exhibit slower growth and remain longer in freshwater and estuarine systems before beginning migration back to sea (Facey and LaBar 1981). Various studies in Newfoundland, Lake Ontario, and Lake Champlain have shown that American eels migrate back to sea after about 12 to 13 years, and at a mean size of 69cm (Gary and Andrews 1971; Hurley 1972; Facey and LaBar 1981; McGrath 2003b). In the southern part of their range, American eels begin migrating earlier than in the north (Hansen and Eversole 1984; Helfman et al. 1984; Owens and Greer 2003). Hansen and Eversole (1984) found that in the Cooper River, South Carolina, American eels older than 7 years old and greater than 65cm in length were sparse, suggesting that eels migrate at a younger age and smaller size. Helfman et al. (1984) found similar results in the Altamaha River, Georgia, and more recently Owens and Greer (2003) found that populations in Virginia tidal rivers were made up mostly of eels less than 7 years old.

There is little information documented in the literature on the substrate requirements of American eel. One study by Valdykov (1955) reported that silver American eels in the northern habitats utilize muddy substrates during the winter months. Goodwin and Angermeier (2003) found that the highest catch of eels in the Shenandoah River drainage streams appeared to be associated with site characteristics including leaf packs, rootwads, woody debris, and flowing water.

Depth does not appear to be an important habitat characteristic for American eels, as many authors have documented them using a wide range of depths during their migrations. Haro and Castro-Santos (2000) found that silver eels in the Connecticut River, Massachusetts used all depths. They were unable to quantify the shallow depth range used by American eels, but in deeper waters, they found that silver eel depths ranged between 6.6 and 10m. The tagged eels tended to occupy the deepest third of the study site. However, eels were also observed swimming at night near the surface of the water (Haro and Castro-Santos 2000). McGrath et al (2003c) found similar results. They found during their surface and midwater trawling study that American eels were caught at the highest rates between 6 and 10 m. However, they state that they are unsure if these findings are significant since sampling was limited near the bottom (18-24m). Haro and Carlos-Santos (1997) recorded eels in the Connecticut River at depths greater than 16ft (5 m), and at least one specimen near the bottom at 32ft (10m) deep. Barbin et al. (1998) documented the same thing in the Penobscot Estuary, Maine. They found that American eels moved freely from between surface waters and the bottom, and that when movement occurred, the eels were near the surface on ebbing tides.

Upon entering the ocean, American eel appear to migrate in the upper water column. Evidence for this includes physiological changes, including the color change to a countershaded silver eel, changes to the visual system, and morphological changes to the swimbladder (McCleave and Kleckner 1985). The color change from yellow to silver provides the American eel with a darker dorsal area and a lighter ventral area. This countershading is only useful in the photic zone of the ocean, possibly only in the upper 600 m (McCleave and Klekcner 1985). Fishes found below 600 m are often dark and not countershaded (Marshall 1971, 1972). American eels also undergo changes in vision, including an increased eye diameter, increase in retinal surface area, addition of new rod cells, increase of convergence of rods on each neural pathway, decreases in cone density, and changes in vision pigments (Winn et al. 1975; Beatty 1975; Pankhurst 1982; Pankhurst and Lythgoe 1982; Pankhurst and Lythgoe 1983). These changes allow the American eel to adapt to dim, monochromic, blue light, conditions which are found in the mesopelagic zone during the day and in the epipelagic zone at night (Jerlov 1976; McCleave and Kleckner 1985). Lastly, the swimbladder changes during metamorphosis, allowing eels to maintain an inflated swim bladder at greater depths (Kleckner 1980).

Tesch (1978a, 1978b) tracked European silver eels (Anguilla anguilla) over the European continental slope and found that eels swam at depths between 50 and 400 m; the maximum depth in this area was 2000 m. However, the tracking was terminated prematurely due to pressure-transmitter failure. Wenner (1973) documented American eels at depths ranging from 15-68 m in the Chesapeake Bay, MD and Cape Cod, MA.

Temperature may be an important trigger for migrating silver eels. Commercial fishermen in the Elbe estuary have noted that lingering summer temperatures into the fall cause a delay in migration (Tesch 2003). Vollestad et al. (1986) documented that migrating European eels in Norwegian streams showed the most activity in a temperature range of 9-18°C (see comment in draft ASMFC doc). Like juveniles, mature silver eels utilize a broad range of habitats, and thus are likely to tolerate a wide range of temperatures (Facey and Van den Avyle 1987).

A few studies have been done to determine the preferred temperatures of American eels. Barila and Stauffer (1980) reported a temperature preference of 16.7°C, while Karlsson et al. (1984) found that American eels preferred temperature of 17.4 + 2.0°C. Activity in eels increases at temperatures above 13°C (Van den Avyle 1982). Haro and Castro-Santos (2000) caught downstream migrating eels on the Connecticut River, Massachusetts, where the temperature ranged from 9.5°C to 9.7°C.

American eels migrate during the fall and winter months. Barbin et al. (1998) documented American eels migrating in September and October in the Penobscot Estuary, Maine in water temperatures ranging from 9.6°C to 17.6°C.

The importance of salinity to silver American eels has not been documented in the literature. As a habitat generalist, the American eel utilize a wide variety of salinities from freshwater to saltwater, thus migrations occur through a broad range of salinities. Barbin et al. (1998) suggest that salinity structure (see comment in draft ASMFC doc).could be used as a mechanism to help orient eels out of estuaries. They documented American eels in the Souadabscook stream (tributary to the mouth of the estuary) and the Penobscot Estuary, Maine in salinities ranging from 0-30 ppt.

Ecological relationships

Once the spawning migration begins, American eel cease feeding and their digestive systems atrophies. Lipid is stored and used to provide the energy required for downstream migration, production of gametes, and the actual act of spawning (Fontaine and Olivereau 1962).

Both American eels and European eels (*Anguilla anguilla*) use the Sargasso Sea for spawning grounds (McCleave et al. 1987). However, McCleave et al. (1987) speculate that American eel spawn from February to April from approximately 19° to 29°N latitude and 52° to 79°W longitude, while European eels spawn from March to June from approximately 23° to 30°N latitude and 48° and 74°W longitude. Thus, their overlap area is not very large.

One study by Appelbaum (1982) suggests that predation on American eel larvae in the Sargasso Sea may be minimal. Appelbaum (1982) found that of 1,000 pelagic fish representing 25 species, only the myctophid, *Ceratoscopelus warmingii*, had American eel larvae in its stomach. More research is needed in this area.

Dutil et al. (1987a) found that the stomachs of elvers contained 90% Chironomidae and 8% Simuliidae. No food remains were found in the stomachs or intestines of glass eels (Dutil et al. 1987a).

Yellow phase American eels are preyed upon by many fish species including striped bass. Eel were found in 20% of striped bass stomachs in the Merrimack River, New Hampshire. Additionally, migrations of striped bass coincide with upstream elver migrations (Reviewed in Richkus and Whalen 1999). Jessop (2000) found that a major source of predation on American eel elvers in the East River, Chester, Nova Scotia, was cannibalism by larger American eels. Other authors have also reported cannibalism on younger eels (Tesch 1991; Barker 1997).

Yellow phase American eel are thought to be opportunistic feeders; preying upon whatever is available in their habitat (Bigelow and Schroeder 2002). Mature eels have been documented feeding on invertebrates including insects, crayfish, snails, worms, and small fish (Ogden 1970; Scott and Crossman 1973; Facey and LaBar 1981). They have also been documented consuming plant material (Moriarity 1978) and carrion (Ogden 1970). Cannabalism on smaller eels has also been documented extensively in the literature (Tesch 1991; Barker 1997).

Godfrey (1957) found that 90% of the eel's diet consisted of insects, while 10% consumed whole fish. Facey and LaBar (1981) reported that eel feed heavily upon benthic organisms. They found that 43% of the eels examined contained insects, and 26% contained fish. Smaller eels have been reported feeding on mayflies, magalopterans, and cassisflies (Smith 1985). Rulifson et al. (2004) found that in North Carolina, large eels consumed crayfish and fish (mullet and centrarchids). Smaller eels fed on arthropods, small mullet and minnows, polychaetes, unidentifiable matter, and plant. Fish, crustaceans, and arthropods were the most important prey items (Rulifson et al. 2004).

Wenner and Musick (1975) state that yellow eels fed on fish during the winter and spring, and on insects and molluscs in the spring and fall. Smaller eels (less than 40cm) in New Jersey streams mostly fed on aquatic insects larvae, including ephemeroptera, megaloptera, and trichoptera, while the larger eels consumed fish and crustaceans (Ogden 1970). Sorensen et al. (1986) report that in Rhode Island eels feed primarily at night, and that activity peaks at nightfall. Yellow eels have also been reported feeding on crustaceans, like the blue crab, and bivalves, such as soft-shelled clams and polychaetes (Wenner and Musick 1975).

Lookabaugh and Angermeier (2003) also found that prey size increased with eel size. In the piedmont regions of the James River drainage, Virginia, small eels fed primarily on aquatic insects, whereas larger eels consumed fish and crayfish. In the coastal plain, microcrustaceans and aquatic insects were preyed upon by small and medium sized eels, while large eels fed on crayfish.

Silver phase American eels do not feed during their migration to the Sargasso Sea.

Silver phase American eels are preyed upon by many different species, including fish, aquatic mammals, birds, and mammals (mink) (Sinha and Jones 1967; Seymour 1974). However, the importance of American eel as a food source for other animals has not been well documented in literature (ASMFC 2000).

Abundance and status of stocks

(from the 2006 Adendum to the ASMFC 1999 FMP)
Current stock status for American eel is poorly understood due to limited and non-uniform stock assessment efforts and protocols across the range of this species. Reliable indices of abundance of this species are scarce. Limited data from indirect measurements (harvest by various gear types and locations) and localized stock assessment information are currently collected.

Although eel have been continuously harvested, consistent data on harvest are often unavailable. Harvest data are often a poor indicator of abundance because harvest is dependent on demand and may consist of annually changing mixes of year classes. Most of the data collections were of short duration and were not standardized between management agencies. Harvest data from the Atlantic coastal states (Maine to Florida) indicate that harvest has declined after a peak in the mid-1970s. Annual eel catch ranged from 913,251 pounds to 3,626,936 pounds between 1970 and 2000. The lowest harvest (between 1970 and 2001) was 898,459 pounds and occurred in 2001.

Because fishing effort data is unavailable, finding a correlation between population numbers and landings data is problematic. In 2003, declarations from the International Eel Symposium (AFS 2003, Quebec City, Quebec, Canada) and the Great Lakes Fishery Commission (GLFC) highlighted concerns regarding the health of American eel stock. Available data point to decreasing recruitment combined with localized declines in abundance. This information is cause for concern and represents an opportunity for cooperation with other entities such as the GLFC to preserve the American eel stock.

In 2005, the ASMFC American Eel Stock Assessment Subcommittee (SASC) conducted a stock assessment for American eel. This assessment was reviewed by the ASMFC American Eel Technical Committee and underwent an independent peer review in December 2005. The results of the peer review can be found on the Atlantic States Marine Fisheries Commission website, www.asmfc.org.

4.2.9 Red Drum

Description and Distribution

Red drum are members of the family Sciaenidae which inhabit tropical and temperate waters worldwide (Johnson 1978). Chao (1976) reviewed the sciaenids of the western Atlantic, and determined that they encompassed 56 species in 21 genera. Sciaenids are commonly known as drums because many of them, including red drum, produce characteristic drumming sounds by contracting muscles on either side of their swimbladder (Jordan and Evermann 1896; Bigelow and Schroeder 1953; Fish and Mowbray 1970; Guest and Laswell 1978).

The accepted scientific name for red rum is *Sciaenops ocellatus*. The preferred common name for *Sciaenops ocellatus*, according to the American Fisheries Society's *A List of Common and Scientific Names of Fishes from the United States and Canada* (Robins et al. 1980) is red drum. Other common names include: channel bass, spottail bass, red bass, bass, sea bass, spotted bass, redfish, bull redfish, spottail, rat red, pescado colorado, drum, banded drum, puppy drum (Hildebrand and Schroeder 1928), sweet William and billy bass (Wenner 1988).

Along the Atlantic coast, red drum range from the Chesapeake Bay to Key West, Florida. Historically, red drum were found as far north as Massachusetts in large enough numbers to support a moderate commercial fishery in New Jersey in the early 1930s (Lux and Mahoney 1969; Ross et al. 1995). On the Gulf of Mexico coast, they are found from extreme southwest Florida to Tuxpan, Mexico (Simmons and Breuer 1962; Matlock 1987). Red drum are distributed in oceanic waters and estuarine areas in relation to their maturity stage.

Reproduction

Red drum spawn primarily during late summer and fall throughout its range along the Atlantic and Gulf coasts. Early studies indicated that spawning occurs from July through December with a peak in late September/October along the Atlantic coast (Hildebrand and Schroeder 1928; Mansueti 1960; Yokel 1966; Spitsbergen and Wolff 1974; Wolff 1976; Weinstein 1979). There is some evidence that within-season spawning peaks tend to coincide with the full moon (Peters and McMichael 1987; Comyns et al. 1991; Johnson and Funicelli 1991).

Early studies led investigators to conclude that red drum spawned in nearshore areas in the vicinity of inlets and passes throughout their range (Pearson 1929; Miles 1950; Simmons and Breuer 1962; Yokel 1966; Jannke 1971; Setzler 1977; Music and Pafford 1984; Holt et al.1985). However, evidence now suggests that red drum also utilize high-salinity estuarine areas along the south Atlantic coast (Murphy and Taylor 1990; Johnson and Funicelli 1991; Nicholson and Jordan 1994; Woodward 1994). Presumably, these expansive areas offer adequate conditions for survival of eggs and larvae and favorable circulation patterns that help transport larvae to suitable nursery areas (Ross and Stevens 1992). In the South Atlantic, red drum spawning has been documented from nearshore waters, in the vicinity of passes and inlets and inside estuaries such as Pamlico Sound and Mosquito Lagoon (Murphy and Taylor 1990; Wenner et al. 1990; Johnson and Funicelli 1991; Ross and Stevens 1992; Ross et al. 1995).

North Carolina

Nelson et al. (1991) summarized data on the spatial distribution and relative abundance of all life stages of red drum in southeastern estuaries. In North Carolina, spawning adults were reported to be common in salinities above 25 ppt in Bogue Sound and the Cape Fear River. Spawning adults were present but not frequently encountered in Pamlico Sound and the New River.

Ross and Stevens (1992) cited reports of red drum schooling over shoal and channel areas in Pamlico Sound near Hatteras, Ocracoke and Drum inlets, and near the mouths of bays and rivers on the western side of the Sound from August through early October. Red drum gather in these areas every year, presumably to spawn, since all fish landed from these schools have been in spawning condition. Marks and DiDomenico (1996) investigated movements, maturity and spawning seasonality of red drum in North Carolina coastal and estuarine waters. They report capturing the majority of spawning red drum (60%) in inlets and around shoals 2 - 5 km inside Oregon, Hatteras, Ocracoke and Drum inlets. In addition, 30% of reproductively active fish were captured in several areas of western Pamlico Sound between the Neuse and Pamlico rivers. Luczkovich et. al (1999) recently confirmed suspected spawning areas using hydrophone equipment to detect drumming sounds associated with spawning activity. Ichthyoplankton surveys were also used to corroborate spawning activity. Red drum spawning aggregations were identified in Pamlico Sound near Ocracoke and Hatteras inlets, and in the Bay River during August, September and October with peak activity in September. The authors deemed the mouth of the Bay River to be particularly critical for red drum spawning within the study area.

South Carolina

Nelson et al. (1991) reported spawning red drum to be common in Winyah Bay, Charleston Harbor, St. Helena Sound and the Broad River in salinities above 25 ppt in South Carolina. However, drumming activity, indicative of active spawning, (Holt et al. 1985) has not been detected in all of these estuaries. Hydrophone surveys were conducted along coastal South Carolina, from Winyah Bay to Calibogue Sound in 1994 (Roumillat and Tyree, unpubl.). Drumming activity was only recorded in two areas: a 40 m deep hole in the main channel leading to Charleston Harbor and two shallower areas (~ 12 m deep) off Morgan Island, near the mouth of the Coosaw River in St. Helena Sound. The latter two areas were located approximately 10 km inshore of ocean beaches. The occurrence of spawning aggregations of red drum at the mouth of Charleston Harbor has been further confirmed by the collection of viable eggs. The latter were positively identified as red drum eggs using a genetic analysis technique (Knott III 1998).

Wenner (2000) concluded that spawning activity in Charleston Harbor and in St. Helena Sound would explain recruitment of red drum to estuaries in the central and southern portion of the South Carolina coast. However, this does not explain the abundance of young red drum found in areas to the north of Charleston Harbor. Spawning in nearshore waters between Charleston Harbor and Georgetown, such as shoal areas around the Cape Romain Wildlife Refuge, would be a source of recruits to estuarine areas north of Charleston. However, this has not yet been investigated.

Georgia

Music and Pafford (1984) cited information obtained from anglers who target large red drum as evidence for spawning activity taking place in Georgia offshore waters. Anglers reported no fish in spawning condition from inshore waters. In addition, the study failed to obtain red drum larvae or postlarvae in ichthyoplankton samples. At the time, adult red drum occurred in low numbers off the Georgia coast; their greatest concentration was at the mouth of the Altamaha River in the central portion of the coast.

Nelson et al. (1991) reported spawning adults to be rare in all of Georgia's estuaries. However, more recent investigations (Woodward 1994) reported capturing reproductively active fish (based on external examination and the extrusion of oocytes from females) inside the Altamaha River estuary. Many of the females captured contained hydrated oocytes or were spent. Similarly, Nicholson and Jordan (1994) reported capturing females in pre-spawn condition as far as 20 km up the Altamaha River delta. Fish remained in these “pre-spawn staging areas” for up to 13 days, moved down to the ocean inlets for several days and then returned to the upriver sites.

Florida

Along the Atlantic coast of Florida, red drum also spawn in nearshore waters and inside estuaries. Nelson et al. (1991) reported spawning red drum to be abundant in salinities above 25 ppt in the St. Johns River and the Indian River. Murphy and Taylor (1990) reported capturing female red drum in spawning condition 35 km south of Ponce de Leon Inlet and 90 km north of Sebastian inlet. Johnson and Funicelli (1991) corroborated estuarine spawning inside Mosquito Lagoon using hydrophone surveys conducted at dusk (when red drum courtship behavior and drumming presumably take place) and surface plankton tows to collect recently spawned eggs. Mosquito Lagoon extends over 54 km long and 4 km wide and is separated from the Atlantic Ocean by a narrow barrier beach. Ponce de Leon Inlet connects the lagoon to the Atlantic Ocean at its northern end and Haulover Canal (a manmade structure) links it to the Indian River at its southern end. Depth ranges from 0.1 - 5 m and salinity averages 32 ppt. Tidal fluctuations are minimal (less than 15 cm seasonally) and water movements result from wind-driven circulation (Dubbleday 1975; Smith 1987). Eggs collected within Mosquito Lagoon and Ponce de Leon Inlet were successfully hatched in the laboratory thus confirming spawning of red drum in these locations. Sites where drumming activity was recorded yielded the largest number of viable eggs; however, eggs were also collected in areas where drumming activity was not detected.

In North Carolina, Ross and Stevens (1992) reported that juvenile red drum (10-30 mm) recruited to nurseries during September-October. More recently, Ross et al. (1995) determined that spawning took place from August through early October. In South Carolina, Wenner et al. (1990) examined histological sections of red drum ovaries and determined that spawning activity lasted from early August through September. Music and Pafford (1984) collected six juvenile red drum in mid-July and mid-November in Georgia waters. Based on this, the authors stated that red drum in Georgia probably spawn from as early as June to as late as December. Woodward (1994) maintained that spawning in coastal Georgia occurs from as early as August and into October. Spawning on both coasts of Florida peaked from September through October (Murphy and Taylor 1990). Spawning red drum in Florida have been reported as early as July (Peters and McMichael 1987) and as late as November (Johnson and Funicelli 1991) and there is evidence that some spawning may also occur during early spring (Yokel 1966; Jannke 1971).

In the northern Gulf of Mexico, Fitzhugh et al. (1988) reported evidence for a spawning season extending from August through October. More recently, Wilson and Nieland (1994) used mean monthly gonosomatic index (GSI) values and histological data to establish the spawning season. They determined that the latter extends from mid August through October. Similarly, Comyns et al. (1991) reported that spawning in the north-central portion of the Gulf of Mexico took place from August through late October or early November with a peak in September. Perret et al. (1980) reported that spawning along the Gulf side of the Florida coast probably begins in September and peaks in October. Similarly, spawning in Alabama begins in mid-August, peaks in mid-September through October, and extends through December. In Louisiana, red drum are reported to spawn from August through November.

Red drum are reportedly only second to the most fecund species among sciaenids (Wilson and Nieland 1994). However, estimates of fecundity among wild red drum are few due to difficulty in sampling the spawning population. Estimates of red drum fecundity in the wild range from 0.5 to 15.8 million oocytes per season (Pearson 1929; Miles 1950; Holt et al. 1983a). Overstreet (1983) reported fecundity estimates for Mississippi red drum of 62 million and 95 million oocytes using gravimetric and volumetric methods, respectively. Fecundity estimates obtained through laboratory experiments have ranged from 2.9 to 60 million ova per season (Colura 1974; Arnold et al. 1977; Roberts et al. 1978; Arnold 1988). Batch fecundity estimates for wild red drum in the Gulf of Mexico were initially provided by Fitzhugh et al. (1988). The authors provided the first evidence of group-synchrony among red drum and described ovarian development based on histological samples. Mean batch fecundity for red drum caught off Louisiana in the month of September was 1.7 million eggs, whereas that for October was 0.7 million. The authors used the hydrated oocyte method (Hunter and Macewicz 1985) to determine the mean number of oocytes per gram of ovarian weight. Significant differences in oocyte densities were reported between left and right ovarian lobes and among anterior, mid and posterior locations within each lobe. It was suggested that differences could have resulted from variations in the rate of hydration among locations. Wilson and Nieland (1994) expanded on the work begun by Fitzhugh et al. (1988) and estimated batch fecundity of wild red drum in the northern Gulf of Mexico. Analysis of 51 specimens yielded batch fecundity estimates ranging from 0.16 million to 3.27 million oocytes per batch with a mean batch fecundity of 1.54 million ova. Murphy and Crabtree (1999) recently provided batch fecundity estimates for red drum sampled offshore west-central Florida in 1996-1998. Their estimates were based upon examination of 77 females and ranged from 114,934 to 2,318,315 oocytes.

Spawning frequency is probably not constant over the duration of the spawning season for red drum and other group-synchronous spawners (Wilson and Nieland 1994). There is evidence that spawning peaks of red drum may coincide with new and full moons (Peters and McMichael 1987; Comyns et al. 1991). Hence, ideally, spawning frequencies should be estimated on a monthly basis for the duration of the spawning season. Wilson and Nieland (1994) calculated spawning frequency using two different methods. The postovulatory follicle method yielded variable estimates of spawning frequency between once every 3 days to once every 80 days. The average spawning frequency for the seven-season duration of the study was 8.8 days. The time-calibrated method (takes into account the proportion of day-0 females -- imminent spawners -- and day-1 females -- those showing evidence of a previous night's spawn) yielded frequencies of one spawn every 2-4 days. Given the above estimates of batch fecundity and spawning frequency, annual fecundity was estimated at 20-40 million ova for the average red drum female in the northern Gulf of Mexico. Comyns et al. (1991), used a mean batch fecundity of 2.128 million ova (obtained from data provided by Wilson and Nieland during September 1986, 1987 and 1988) and daily egg production estimates (derived from larval densities) to arrive at adult red drum biomass in the north-central Gulf of Mexico. However, the authors cautioned that the batch fecundity fraction was probably an underestimate since data were obtained from animals sampled with purse seines which are fished only during daylight hours. The mean spawning fraction, was reported as 0.20, indicating a spawning frequency of once every 5 days during the month of September.

Development, growth and movement patterns

Throughout their range, red drum exhibit differential maturity between the sexes. Males generally mature at younger ages and smaller sizes than females. Studies carried out to determine age and size at maturity of red drum have generally shown differences among them due mainly to the use of different maturity schedules. Wilson and Nieland (1994) noted that discrepancies in maturity schedules could result not only from geographical variation, but also from lack of consistency in the methodologies used to assess reproductive status. It is crucial that assessments of ovarian development be established using histological criteria (West 1990). However, it was not until relatively recently that histological techniques have been utilized to reliably establish sex and maturity.

Recent studies have reported discrepancies in size at maturity for red drum (Table 4.2-3). Differences may result not only from natural variations over the species geographical range, but also from misinterpretation of reproductive states. The latter can in turn be due to inappropriate methodology or sampling at a time when it becomes difficult to differentiate between an immature individual from one that is in between spawning events. Furthermore, sizes appear in the literature as total length (TL) as well as fork length (FL) thus obscuring direct comparisons among studies. In order to provide comparable sizes, therefore, the following length conversions (Wenner 2000) were used:

$FL = 0.921\ TL + 17.573 \qquad r^2 = 0.999 \qquad N = 3374$

$TL = 1.084\ FL - 18.425 \qquad r^2 = 0.999 \qquad N = 3374$

Table 4.2-3. Published estimates of age and size at first maturity (since 1990) and age and size at 50% maturity for male and female red drum in the South Atlantic and Gulf of Mexico. Fork lengths were converted to mm TL using the above relationships.

Source	First Maturity				P_{50} Maturity			
	Males		Females		Males		Females	
	TL	Age	TL	Age	TL	Age	TL	Age
Ross *et al*. (1995)	523	1	742	3	656	2	847	3
Marks and DiDomenico (1996)	--	--	--	--	722	--	885	--
Wenner *et al*. (1990)	545	3	825	4	--	--	--	--
Wenner (2000)	573	2	691	3	713	3.5	792	4.3
Woodward (1994)	777	--	805	--	824	--	825	--
Murphy and Taylor (1990) - FL east coast	397	1 or 2	614	3	571	2	993	5
Murphy and Taylor (1990) - FL gulf coast	451	1 or 2	665	3	591	2	911	5
Wilson and Nieland (1994)	660	2	665	3	733	--	766	--

Eggs and larvae

Information on the distribution of red drum eggs along the South Atlantic coast is very limited. Nelson et al. (1991) reported red drum eggs to be commonly encountered in several southeastern estuaries, in salinities above 25 ppt. Laboratory experiments in Texas (Neill 1987; Holt et al. 1981) established that optimum temperature and salinity for hatching and survival of red drum larvae are 25°C and 30 ppt, respectively. The spatial distribution and relative abundance of eggs in southeastern estuaries, as expected, mirrors that of spawning adults (Nelson et. al. 1991). Hence, eggs and early larvae utilize high salinity waters inside inlets and passes and in the estuary proper.

In Florida, Johnson and Funicelli (1991) collected viable red drum eggs in Mosquito Lagoon, Florida, with average daily water temperatures of 20 - 25°C and average salinities of 30 to 32 ppt. The largest number of eggs collected during the study was in depths ranging from 1.5 to 2.1 m with the highest concentrations of eggs found at the edge of the channel.

Upon hatching, red drum larvae are pelagic (Johnson 1978) and evidence from laboratory studies indicates that development is temperature-dependent (Holt et al. 1981). They make the transition between pelagic and demersal habitats upon reaching the nursery grounds when they are approximately 5 to 8 mm in length (Pearson 1929; Peters and McMichael 1987; Comyns et al. 1991; Rooker and Holt 1997). During this portion of their life cycle, they may utilize tidal currents (Setzler 1977; Holt et al. 1989) or density-driven currents (Mansueti 1960) for transport to low-salinity nurseries in the upper reaches of estuaries (Bass and Avault 1975; Setzler 1977; Weinstein 1979; Holt et al. 1983b; Holt et al. 1989; Peters and McMichael 1987; McGovern 1986; Daniel III 1988). Once in the nurseries, red drum larvae grow rapidly. Evidence suggests that red drum may select nursery areas based on the presence of environmental conditions that contribute to rapid growth (Baltz et al. 1998).

Limited information exists on the distribution of red drum larvae along the Atlantic coast. They are reportedly common in most major southeastern estuaries, with the exception of Albemarle Sound, and they are abundant in the St. Johns and Indian River estuaries, Florida (Nelson et al. 1991). Data on the spatial distribution of red drum larvae in the Gulf of Mexico has been summarized by Mercer (1984). More recently, Lyczkowski-Shultz and Steen (1991) investigated the distribution of red drum larvae in offshore and nearshore waters in the north central Gulf of Mexico east of the Mississippi River delta and south of the Mississippi barrier islands over the east Louisiana-Mississippi-Alabama shelf. They reported evidence of diel vertical stratification among red drum larvae found in depths < 25 m at both offshore and nearshore locations. Larvae (1.7 - 5.0 mm mean length) were found at depth during the night and higher in the water column during the day. At the time of this study, water was well mixed and temperature ranged between approximately 26 and 28°C. No consistent relationship between the distribution of larvae and tidal stage was detected.

In the Gulf of Mexico, red drum larvae (<7 mm) have been collected in nearshore oceanic waters, passes and inlets to estuarine waters, and within estuaries (Mercer 1984). Peters and McMichael (1987) collected red drum larvae mostly from the lower reaches of Tampa Bay although some were collected on shallow water grass beds near the middle of the Bay. There was a general increase in size of larvae from the mouth of Tampa Bay up the bay toward its headwaters. In smaller estuaries, e.g. in South Florida, red drum may spawn further offshore and larvae are transported by currents to the mouth of the estuaries where, as small juveniles, they become concentrated on their way to nursery areas in the estuary. Red drum larvae have been collected within Mosquito Lagoon along Florida's Atlantic coast where adults readily spawn far from any estuarine inlet (Johnson and Finucane 1991). Surface water temperatures and salinities for collections containing larvae in Tampa Bay were 18.3-29.7° C and 16-34 ppt, respectively (Peters and McMichael 1987).

Juveniles and subadults

Estuarine distribution of juvenile red drum varies seasonally as the fish grow and begin to disperse. Along the South Atlantic coast, they utilize a variety of inshore habitats. Included are tidal freshwater habitats and the low-salinity reaches of estuaries, estuarine emergent vegetated wetlands (flooded salt marshes, brackish marsh and tidal creeks), estuarine scrub/shrub (mangrove fringe), submerged aquatic vegetation (SAV), oyster reefs and shell banks, and unconsolidated bottom (soft sediments) (SAFMC 1998b).

In general, juvenile red drum are found throughout South Atlantic estuaries in all of the habitat types described above. In the Chesapeake Bay, juveniles (20-90 mm TL) were collected in shallow waters from September to November, but no indication as to the characteristics of the habitat was given (Mansueti 1960). According to Nelson et al. (1991), South Atlantic estuaries where juveniles (including subadults) are abundant are Bogue Sound, North Carolina; Winyah Bay, South Carolina; Ossabaw Sound, and St. Catherine/Sapelo Sound, Georgia; and the St. Johns River, Florida. They are highly abundant in the Altamaha River and St. Andrew/St. Simon Sound, Georgia, and the Indian River, Florida.

Red drum begin the subadult phase of their life cycle upon leaving the shallow nursery habitat at approximately 200 mm TL (10 months of age). They are considered subadults until they reach sexual maturity at 3-5 years (C. Wenner, pers. comm.). It is at this stage in their life cycle that red drum utilize a variety of habitats within the estuary and when they are most vulnerable to exploitation (Pafford et al. 1990; Wenner 1992). Tagging studies conducted throughout the species' range indicate that most subadult red drum tend to remain in the vicinity of a given area (Beaumarriage 1969; Osburn et al. 1982; Music and Pafford 1984; Wenner, et al. 1990; Pafford et al. 1990; Ross and Stevens 1992; Woodward 1994; Marks and DiDomenico 1996). Movement within the estuary is most likely related to changes in temperature and food availability (Pafford et al. 1990; Woodward 1994).

North Carolina

The state of North Carolina has 147,000 acres of designated Primary Nursery Areas (PNA) and Secondary Nursery Areas (SNA) that generally comprise the upper reaches of tidal creeks and rivers and may include coastal wetlands, shell-bottom and soft sub-tidal bottom habitats (NCDMF 2001). The North Carolina Division of Marine Fisheries (NCDMF) surveys of juvenile red drum have documented their presence from the Cape Fear River, north through Buzzards Bay in Dare County (Ross and Stevens 1992). Juvenile red drum were consistently abundant in shallow waters (< 5 feet) near the mouths of the Pamlico and Neuse Rivers and in smaller bays and rivers between them. In general, habitats supporting juvenile red drum in North Carolina can be characterized as detritus or mud-bottom tidal creeks in western Pamlico Sound, and mud or sand bottom habitat in other areas (Ross and Stevens 1992).

North Carolina, unlike South Carolina and Georgia, possesses SAV beds that red drum presumably utilize as nursery areas as their current range overlaps SAV distribution (Laney 1997). The NC DMF has documented high abundance of late age-0 red drum in shallow, high salinity seagrass beds behind the Outer Banks (NC DMF 2000). However, investigations have shown juveniles to prefer areas with patchy grass coverage over sites with homogeneous vegetation (Mercer 1984; Ross and Stevens 1992; Rooker and Holt 1997). The extent to which red drum utilize SAV beds in North Carolina is unclear. This habitat does constitute important foraging grounds for 1 and 2-year old fish (SAFMC 1998). The NMFS recently identified approximately 200,000 acres of seagrass beds in coastal North Carolina. Expanses of seagrass are concentrated in the shallow areas of Core Sound and Pamlico Sound along the backside of the barrier islands. Seagrass extends south to the New River and is distributed patchily in Albemarle and Currituck Sounds, in western Pamlico Sound, and along the shores of the Pamlico and Neuse Rivers and their tributaries (NC DMF 2000).

Tagging studies indicate that late age-0 and 1 year-old red drum are common throughout the shallow portions of the estuaries and are particularly abundant along the shorelines of rivers and bays, in creeks, and over grass flats and shoals of the sounds. During the fall, those subadult fish inhabiting the rivers move to higher salinity areas such as the grass flats and shoals of the barrier islands and the front beaches. Fish that reside near inlets and along the barrier islands during the summer are more likely to enter the surf in the fall. During the winter, most subadults are recaptured in the estuaries, although some are taken in the surf and inlets. During spring and summer, recaptures are common along the barrier islands, near coastal inlets, and in the surf zone, with a large number of the subadults continuing to frequent the rivers. By their second and third year of growth, red drum are less common in rivers. Instead, they are found along the barrier islands, inhabiting the shallow water areas around the outer bars and shoals of the surf and in coastal inlets over inshore grass flats, creeks or bays.

South Carolina

In South Carolina estuaries, juvenile red drum have been collected over a range of salinities in shallow tidal creeks and in tidal impoundments. Daniel (1988) collected post-larval and juvenile red drum (6-13 mm SL) in the upper reaches of the Wando River estuary and off the Intracoastal Waterway from August through December. Collection sites were characterized by shell hash, sand and mud bottom. Juveniles were rare in the tidal creeks throughout the winter and they reappeared in the collections again in the spring. Similarly, Wenner et al. (1990) collected post-larval and juvenile red drum from June 1986 through July 1988 in shallow tidal creeks in temperatures from 9 to 30o C and salinities from 0.8 to 33.7 ppt. Smallest juveniles were observed in the creeks from August through October, indicating that this is the time when red drum recruit to nursery areas in South Carolina. With the onset of winter temperatures, juveniles left the shallow creeks for deeper water in the main channels of rivers (9-15 m) and returned again to the shallows in the spring. Juveniles are also present in areas where low-salinities do not occur, i.e. behind the barrier islands on the Isle of Palms, Capers Island, Bulls Island (C. Wenner, pers. comm.). Thus, the shallow areas of tidal creeks that run through Spartina alterniflora dominated marshes throughout the coast are the primary nursery areas for red drum in South Carolina.

Subadult red drum have been observed in larger tidal creeks and rivers, near inlets, jetties, sandbars, and even nearshore artificial reefs (Wenner 1992). Some of the subadult red drum in South Carolina also temporarily inhabit the front beaches of barrier islands. During winter months, schools of subadult red drum have been sighted in sheltered, shallow inshore areas. During 1994 and 1995, the Inshore Fisheries Section of the South Carolina DNR conducted several aerial surveys to attempt to evaluate abundance and habitat utilization of subadult red drum along the South Carolina coast. Aerial surveys were generally deemed inefficient at estimating the number of fish inhabiting particular areas, especially inlets and beachfront areas because the visibility of schools from the air depends on the interplay of temporal, climactic, topographic and behavioral factors. On the occasions when red drum schools were reliably located, they were found in flats at the confluence of rivers, inside inlets, creeks, sounds and bays. Aerial surveys proved useful to characterize the general topography of subadult red drum habitat in the intertidal and shallow-subtidal portions of the coast. It appears that typical habitats where subadult red drum are found in South Carolina are of two general types. In the northern portion of the coast, typical subadult habitat consists of broad (up to 200 m or more in width), gently sloping flats often leading to the main channel of a river or sound. Along the southern portion of the coast, subadult red drum habitat consists of more narrow (50 m or less), fairly level flats traversed by numerous small channels, typically 5-10 m wide by less than 2 m deep at low tide).

Georgia

Dahlberg (1972) collected juvenile red drum along beaches, in tidal canals, and low- and high-salinity tidal pools of the Sapelo Sound and St. Catherine's Sound estuarine systems in Georgia.

A telemetry study conducted more recently on subadult and young adult red drum in Georgia (Nicholson et al. 1996) found that subadults co-occurred with adult fish in schools along beaches and shoals during fall months, and at natural and artificial reefs in offshore waters during the winter.

Florida

Along the east coast of Florida, juvenile red drum probably utilize similar habitats as those used by their west coast counterparts. Peters and McMichael (1987) collected more juveniles in quiet backwater areas of Tampa Bay than at other sampling locales, but caught a significant number of small juveniles (10-20 mm SL) in seagrass beds.

Juvenile red drum (>6 and <75 mm SL) are found along estuary margins where they move into protected backwater areas as they grow (Peters and McMichael 1987). There is a wide range of acceptable habitat for juveniles: protected coves and lagoons with seagrass over sand or mud bottoms (Pearson 1929; Miles 1950), unvegetated, "open water" shores (Kilby 1955), and unvegetated muddy bottom (Springer and Woodburn 1960). Juveniles were usually collected in the shallow shore zones of the Indian River Lagoon (Snelson 1983).

Pre-recruit red drum (>70 and <450 mm TL) aggregate in the rivers, bays, canals, tidal creeks, boat basins, and passes within an estuary (Peters and McMichael 1987). They also move into shallow nearshore waters and seagrass beds. In colder areas, juveniles may move into passes or to nearshore continental shelf waters during the winter (Mercer 1984). At this size they usually occur in large aggregations and their voracious appetites make them vulnerable to fishing pressure (Peters and McMichael 1987). Red drum are euryhaline and have been collected on the east coast of Florida at salinities from 0-22.3 ppt (Springer 1960; Tagatz 1967). Springer (1960) collected red drum from 2-29o C in the St. Lucie and Indian Rivers, Florida.

Fully recruited red drum (>449 mm TL) include large, immature "subadults" and sexually mature adults. Subadults frequent many of the same habitats preferred by pre-recruits and can be found in large aggregations on seagrass beds, over oyster bars, mudflats and sand bottom. Adults are also found within the estuary as well as nearshore continental shelf waters (Mercer 1984; Murphy and Taylor 1990). Adults appear to remain in the Mosquito/Indian River Lagoon throughout their lives (Johnson and Finucane 1991). Along the Florida Atlantic coast red drum are common in the benthic-open shelf habitat and occur in the surf zone, inlets, and lagoons (Gilmore et al. 1981; Snelson 1983). Tagging studies in Florida indicate that most subadult red drum remain close to the tag-release location for several years. However, Creek habitat was utilized by 10-26 month old red drum in the northern Indian River, Florida (Adams and Tremain 2000). Some fish repeatedly used this important habitat for up to 18 months.

Adults

Adult red drum migrate inshore and/or north and offshore and/or south in spring and fall, respectively, throughout their range along the Atlantic coast. Overall, adults tend to spend more time in coastal waters after reaching sexual maturity; however, they continue to frequent inshore waters on a seasonal basis.

North Carolina

In North Carolina, large schools of adult red drum have been observed in offshore waters south of Cape Hatteras in April and north of Cape Hatteras in May and June. Adult red drum are caught in large numbers in the Outter Banks region from late March through May and from October through November. Movements of adult red drum in coastal North Carolina have been documented based on the presence of adult fish in recreational and commercial landings, as well as information obtained from North Carolina's Adult Drum Volunteer Tagging Program. In the spring, around the month of April, adult fish move from offshore wintering grounds to North Carolina beaches. Large aggregations have been observed around Ocracoke, Hatteras and Oregon Inlets. They occur along the beaches near inlets for one to two months, with a large portion of the population moving inside Pamlico Sound during the summer months. Schools of adult fish are common in coastal inlets and in Pamlico Sound, particularly in the mouth of the Pamlico and Neuse rivers in August and September. During this time, spawning takes place. By late September most adult drum are found around the coastal inlets and along the beaches where they remain through November before moving offshore for winter. Anglers have reported catches of large red drum around the shoals and outer bars of the barrier islands, as well as around submerged structure up to a couple of kilometers offshore during December. Mercer (1984) reported schools of large red drum moving down from Virginia waters and along the coastal beaches of the Outer Banks during the fall. By late December, most large red drum have moved offshore where they are no longer available to nearshore fishing activity. The movement is reversed in spring, with large schools of adult red drum moving inshore and along the beaches from Cape Lookout to Cape Hatteras. Fish then proceed north with many of them utilizing coastal inlets to enter Pamlico Sound where they spend the summer. Other schools are reported to continue moving north to the Chesapeake Bay and the Virginia barrier islands.

South Carolina

The South Carolina Department of Natural Resources' Finfish Management Section initiated a study in 1994 to develop techniques for sampling adult red drum in the coastal ocean habitat. Initial sampling was conducted in spring 1994 near barrier island beaches in the vicinity of Charleston Harbor. Bottom longline sets were made perpendicular or parallel to the beach. However, the gear and platform that were used proved unsuitable and no fish were collected. Nonetheless, adult red drum are successfully captured by surf fishermen off South Carolina barrier island beaches during spring months.

Adult red drum have been collected in the Morgan River (St. Helena Sound), in the channel adjacent to Pelican Bank in late spring-early summer. SC DNR personnel have also documented adult red drum congregations at the tip of the north Charleston Harbor jetty. This is a high current area with patchy live-bottom along the edge of the drop-off into the main navigation channel. It is rich in food availability and attracts large concentrations of other species such as sandbar and finetooth sharks. Adult red drum have been collected in the area as early as May and as late as December.

Most sampling for adult red drum in South Carolina has concentrated on live-bottom habitats located 5-8 nm off beaches to the southeast and east of Charleston Harbor. These areas are characterized by scattered, low-relief (<1.5 m) limestone outcrops encrusted with sessile invertebrates that attract large aggregations of bait fish and portunid crabs. The current plume extending from Charleston Harbor creates considerable variations in turbidity in these areas.

Resident species of finfish include black seabass, pinfish, spottail pinfish and toadfish. Offshore migrating red drum utilize these areas heavily during the fall. However, schools do not appear to spend much time in these areas, as evidenced by the lack of recaptures of tagged fish on subsequent days sampling in the same location. Rather, schools seem to "pulse" through these areas to feed as they move offshore.

In addition to natural live-bottom areas off South Carolina, adult red drum also utilize “created live-bottom” areas and artificial reefs during their fall migration. Created live-bottom exists in an area southeast of Charleston Harbor referred to as “The Humps.” This area is located to the south and west of the offshore dredge disposal area for Charleston Harbor. A substantial berm of large chunks of marl 2-3 m above the surrounding bottom was created by spoil disposal barges. These marl lumps are heavily colonized with anemones and other sessile invertebrates. Crabs are abundant and the bottom profile also attracts schools of bait fish and high numbers of resident black seabass. Catches of adult red drum are sometimes high in this area albeit not as consistently as over natural live bottom.

Charter boat captains and private boat anglers report nearshore artificial reefs to be productive areas for large adult red drum, particularly in the fall. Anglers have reported large schools of red drum at the Capers and 4KI reefs. The Fish America and Whitewater reefs in the southern part of the state are also productive areas for large red drum according to charterboat logbooks.

The Inshore Fisheries Section of the SC DNR has been conducting routine sampling of the shallow areas of several South Carolina estuaries since 1985. Trammel nets have been the predominant gear used. Although the sampling design of this particular project does not target adult red drum, they are usually captured inshore throughout the year, but greatest catches have typically occurred in July-September in 20-25 ppt salinity. The area around Fort Johnson and the mouth of Charleston Harbor have yielded the greatest catches of adult red drum over the years (SC DNR unpublished data).

Georgia

Studies conducted in Georgia have revealed the importance of the Altamaha River estuary to adult red drum for spawning activity (Woodward 1994; Nicholson and Jordan 1994). After the spawning season ends, adult red drum leave the delta and move to shoal and sandbar areas near inlets. They remain in these areas until mid-November, when a drop in temperature (below 20°C) prompts them to move to nearshore waters.

Nicholson and Jordan (1994) found adult red drum from late November until the following May at natural and artificial reefs along tide rips or associated with the plume of major rivers. Data from this study suggested high seasonal fidelity to a specific area. Fish that were tagged in the fall along shoals and beaches were relocated 9-22 km offshore during winter months and back at the original capture site in the spring. In the summer, fish moved up the Altamaha River as far as 20 km to what the authors refer to as “pre-spawn staging areas” and returned to the same shoal or beach again in the fall.

Florida

In eastern Florida, adult red drum are found mostly in nearshore waters and within the Mosquito/Indian River Lagoon system (Muller 1999). Extensive tagging in the northern Gulf also has shown only limited movement, although fish tagged off Louisiana have been captured as far east as Cape San Blas, Florida. Along Florida's Atlantic coast adults tagged during an age-validation study showed very little movement in the Mosquito or northern Indian River Lagoons (Murphy and Taylor 1991). Carr and Chaney (1976) tracked a large red drum in this area and observed it entering almost every estuarine creek that it encountered, moving 140 m up one of the creeks at night. However, some mature adults appear to move between adjacent estuarine systems, but without any apparent seasonal pattern (M. Murphy, Florida Fish and Wildlife Conservation Commission unpublished data).

Age and Growth

Larvae and juveniles

Growth and mortality in early life dictate recruitment success and subsequent year-class strength among marine fishes. These parameters are in turn affected by both biotic and abiotic factors that can be highly variable. Growth of red drum larvae and juveniles has been shown to be affected by temperature (Holt et al. 1981; Lee et al. 1984; Holt 1987; Baltz et al. 1998) and prey availability (G. J. Holt, unpubl. data in Rooker et al. 1999). Rooker and Holt (1997) found that recent growth of newly settled red drum in the Aransas Estuary, Texas, was positively related to temperature with a 2% increase in growth rate per oC increase. However, the authors point out that the observed difference in recent otolith growth may not be directly related to somatic growth since there is evidence for a lapse in the former compared to the growth of the animal (Neilson and Geen 1984). Long-term growth rates, however, did not exhibit a significant relationship to water temperature in the Aransas Estuary. Comyns et al. (1989), showed a strong positive relationship between growth and water temperature among red drum larvae sampled in the north-central Gulf of Mexico. Growth rates were substantially higher than those reported for laboratory reared animals (Lee et al. 1984).

Early publications (Pearson 1929; Miles 1950; Simmons and Breuer 1962; Bass and Avault 1975; Theiling and Loyacano 1976; Wakeman and Ramsey 1985) reported growth rates for larval and juvenile red drum based on analyses of the temporal sequence of length frequency distributions. Estimates of growth obtained in this manner, however, may be biased by factors such as gear avoidance, recruitment, emigration and mortality. More reliable estimates of age and growth can be established through examination of daily growth rings on otoliths. Peters and McMichael (1987) reported similar growth rates between juvenile red drum in Tampa Bay, Florida, and juvenile red drum in other areas of the Gulf of Mexico (Pearson 1929; Miles 1950; Simmons and Breuer 1962; Bass and Avault 1975) and the Chesapeake Bay (Hildebrand and Schroeder 1928; Mansueti 1960). However, their growth equations yielded higher growth estimates than those resulting from length-frequencies. The authors used growth increments on otoliths to establish age-at-size and size-at-age relationships and verified daily growth ring formation on otoliths of red drum larvae using laboratory reared specimens. The resulting relationship between observed number of rings and fish age indicated that rings were laid down once per day beginning on the day of hatch. Daily growth ring deposition on otoliths of young red drum has also been validated in the laboratory with the use of chemical marks on otoliths of known-age individuals (S. A. Holt, unpubl. data as referenced in Rooker et al. 1999). Comyns et al. (1989) investigated growth rates of wild red drum larvae in the north-central Gulf of Mexico in September and October of 1983 and 1984, and in September of 1985. Growth of red drum larvae < 4 mm was slower than that of larger larvae. Length estimates derived from growth equations in this study were similar to those obtained by Peters and McMichael (1987) for red drum larvae in Tampa Bay, Florida. Similarly, Rooker and Holt (1997), examined growth rates among cohorts of newly settled red drum in the Aransas Estuary during the recruitment period (September to December) of 1994. They found that fish exhibited rapid growth rates ranging from 0.5 to 0.8 mm d-1. Growth rates were considerably variable among cohorts and were highest for mid-season cohorts and lowest for early and late cohorts. More recently, Rooker et al. (1999) reported instantaneous growth coefficients of newly settled red drum ranging from 0.049 in 1994 to 0.051 in 1995 in the Aransas Estuary.

Subadults and adults

Age determination in this species is typically carried out through analysis of thin sections of sagittal otoliths. Analysis of checkmarks on scales only offers reliable ages for subadult red drum ages 0-4 (C. Wenner, pers. comm.). Early published reports agree that the first annular mark in this species does not appear until the second year, when fish are from 14 to 18 months old (Pearson 1929; Rohr 1964; Theiling and Loyacano 1976; Hysmith et al. 1983; Wakefield and Colura 1983; Matlock 1984, referenced in Murphy and Taylor 1990). More recently, it has been maintained that the first annular mark forms during the second winter or spring when the animal is between 18 and 21 months old, depending on the hatch date used (Wenner et al. 1990; Murphy and Taylor 1990; Pafford et al. 1990; Ross et al. 1995).

Marginal increment analysis is used to establish the time of annulus formation on both scales and otoliths. Among red drum, annulus formation occurs during spring months (Beckman et al. 1989; Murphy and Taylor 1990; Wenner et al. 1990; Pafford et al. 1990; Ross et al. 1995). The frequency of ring deposition can be validated by mark-recapture studies and/or analysis of otoliths from fish injected with a chemical marker such as oxytetracycline (OTC). In red drum, growth ring deposition has been established to occur only once per year (Beckman et al. 1988, 1989; Murphy and Taylor 1990; Pafford et al. 1990; Murphy and Taylor 1991; Ross et al. 1995).

Red drum is a long-lived species. The oldest and largest red drum have historically been reported from waters between Cape Lookout and the Virginia barrier islands (Ross et al. 1995). Among fish, the potential to attain maximum growth may be inversely related to the length of the spawning season (Conover 1990). Hence, it is not surprising that the oldest and largest individuals inhabit the high latitude fringes of their range. Along the Atlantic coast of the United States, individuals as old as 57 years (Foster, unpublished, as referenced in Ross et al. 1995) have been reported off North Carolina. In South Carolina, the oldest fish captured was 41 years old (Wenner et al. unpublished data), whereas Georgia (Woodward 1994) and eastern Florida (Murphy and Taylor 1990) have reported individuals as old as 51 years and 33 years, respectively. Along the Gulf coast, red drum have been aged up to 24 years in Florida (Murphy and Taylor 1990) and 37 years in the northern Gulf of Mexico (Beckman et al. 1989).

Growth in fishes has historically been described by means of the von Bertalanffy (1938) growth model. This model was utilized by early investigators to describe growth in red drum until Condrey et al. (1988) introduced the double von Bertalanffy growth curve. The latter combines growth for fish younger and older than a transitional age that separates two distinct growth phases in the life history of the species: rapid growth during the subadult period and diminishing growth as individuals attain and live beyond sexual maturity. The transitional age, tx, is equal to (K2 t2 - K1 t1) / (K2 - K1) where K1 and t1 correspond to individuals younger than tx and K2 and t2 are for individuals older than tx. Estimates of double von Bertalanffy parameters were summarized in the 1989 red drum stock assessment report (Vaughan and Helser 1990) for the South Atlantic states (Table 4.2-4).

Table 4.2-4. Estimates of double von Bertalanffy parameters for red drum by state. Data from Vaughan and Helser (1990).

State	L_{max}	K 1	K 2	t 1	t 2	t x
North Carolina	1,168.2	0.26	0.07	-0.80	-15.9	4.7
South Carolina	1,041.9	0.29	0.07	-0.61	-18.1	5.7
Georgia	1,148.9	0.24	0.03	-1.88	-44.6	3.9
Florida	1,037.0	0.30	0.14	-1.15	-7.5	4.7

Additional parameter estimates have appeared in the literature since then. Ross et al. (1995) used a double von Bertalanffy model to describe growth of red drum sampled in North Carolina from October 1987 through December 1990. The following parameter estimates were reported: Lmax = 1,163 mm FL, K1 = 0.30/year, K2 = 0.07/year, t1 = -0.33 year, t2 = -15.4 years, tx = 4.4 years.

The 1992 red drum stock assessment report (Vaughan 1993) introduced a different model to describe growth in this species. In this model (developed by Geaghan at LSU and referenced in Hoese et al. 1991) Lmax is not constant as it is assumed to be in the regular von Bertalanffy model. Instead, it is a linear function of age: Lmax = b0 + b1 * t where Lmax and b0 are total lengths, b1 is total length per year, and t is age. The linear von Bertalanffy curve has been found appropriate for describing the rapid growth of red drum at early ages and their slower growth in later years (Vaughan 1996). Table 4.2-5 (adapted from Vaughan 1996) summarizes estimates of single and linear von Bertalanffy parameters for the north and south regions of the Atlantic coast from 1986 through 1994.

Few studies describing the growth of red drum have been published since 1990. Murphy and Taylor (1990) sampled commercial and recreational catches of red drum from the east (Mosquito/Upper Indian River Lagoon) and west (Tampa Bay) coasts of Florida between 1981-1983. They reported rapid growth until ages 4 or 5 and a marked decline in growth rate thereafter. Growth rates did not differ between male and female subadult red drum (ages 1-3) nor was there a difference for von Bertalanffy growth parameters K and t0. However, asymptotic length, L4, was greater for Atlantic coast red drum. Estimates of von Bertalanffy parameters for the Atlantic coast were Lmax = 978.8 mm FL, K = 0.148/year, t0 = -0.149. Estimates for Gulf coast red drum were Lmax = 934.1 mm FL, K = 0.460/year, t0 = 0.029. Maximum observed lengths for Atlantic and Gulf coast fish were 1,110 mm FL and 980 mm FL, respectively.

Table 4.2-5. Red drum growth described by single and linear von Bertalanffy models weighting inversely by number of fish at age. Lmax and b0 are total lengths in millimeters, K is the growth coefficient, and t0 is years. Data are for the period 1986 - 1994 (Numbers in parentheses are standard errors). Data from Vaughan (1996).

Single von Bertalanffy parameters

Type	**n**	L_{max}	K	t0
North region	1969	1,186.4	0.18 (0.004)	-1.47 (0.009)
South region	19,383	1,055.8	0.283 (0.001)	-0.23 (0.01)

Linear von Bertalanffy parameters

Type	**b0**	**b1**	**K**	**t0**
North region	1,043.4	0.15 (0.03)	0.363 (0.009)	-0.12 (0.05)
South region	992.9	0.09 (0.01)	0.344 (0.002)	-0.04 (0.01)

Wenner et al. (1990) reported single von Bertalanffy parameter estimates derived from analysis of otolith sections, scales, and tag-recapture for subadult red drum sampled in estuarine areas of South Carolina. Estimates derived from otolith analysis were as follows: Lmax = 979 mm TL, K = 0.035/year, t0 = 1.095. Lengths-at-age for the models were similar to mean observed lengths at age and were in agreement with those reported earlier by Music and Pafford (1984) for subadult red drum sampled in Georgia.

Ross et al. (1995) sampled red drum from October 1987 through December 1990 in North Carolina waters. Growth was rapid until fish reached 5 years of age and was described by means of single and double von Bertalanffy models. Parameters for the single growth curve were Lmax = 1,114 mm FL, K = 0.19/year, t0 = -1.48. As reported by Murphy and Taylor (1990) and Vaughan and Helser (1990), growth rates did not differ between the sexes. Maximum observed lengths for male and female red drum were 1,250 mm FL and 1,343 mm FL, respectively.

Movements/Migration Patterns

North Carolina

The movements of juvenile and adult red drum in North Carolina have been summarized by Mercer (1984) and described from tagging studies conducted by NC DMF from 1986 through 1995 (Ross and Stevens 1992; Marks and DiDomenico 1996). Tagging studies in North Carolina, which are currently ongoing, have consisted of two segments: tagging of primarily subadult red drum by Division staff and tagging of larger adult red drum by anglers participating in a state-sponsored volunteer tagging program. Since the mid-1980s greater than 25,000 red drum have been tagged (Figure 4.2-1). Overall, both adult and subadult red drum tagged in North Carolina's estuaries have shown limited movement, with greater than 99% of all recaptures occurring within coastal waters.

Figure 4.2-1. Length frequency of red drum tagged in North Carolina (all gears combined), 1983-1998. Data are divided into fish tagged by Division staff and those tagged by recreational anglers through cooperative volunteer tagging program (Source: NC DMF unpublished data).

The NC DMF has focused on tagging subadult (primarily one-year old) red drum. While most of the effort has been concentrated in the Pamlico River and over the grass flats located behind the barrier islands of Pamlico Sound during the months of June through October, tagging efforts have occurred year round throughout state coastal waters. Late age-0 and age-1 red drum have consistently shown limited movement. During the study period 1991-1995 over 65% of the 1,197 tagged red drum <18 inches were captured within 10 km of the release site. Late age-0 and age-1 red drum are common throughout the shallow portions of North Carolina's estuaries and are particularly abundant along the shorelines of rivers and bays, in creeks, and over grass flats and shoals common in many of the sounds. During the fall, increased tag returns indicate that a portion of the subadult fish residing in the rivers move toward higher salinity areas such as the grass flats and shoals of the barrier islands and inlets and the surf. Those subadults that reside near the coastal inlets and along the barrier islands during the summer are more likely to enter the surf in the fall. During the winter, tag return rates are low with most subadults recaptured in the estuaries, although some are taken in the surf and inlets. During spring and summer, recaptures are common along the barrier islands, near coastal inlets, and in the surf zone, with a large number of the subadults continuing to be recaptured in the rivers.

Movements of adult red drum have been documented based on the presence of adult fish in recreational and commercial landings, as well as by information obtained from North Carolina's Adult Drum Volunteer Tagging Program. In the spring, around the month of April, adult fish move from offshore wintering grounds towards North Carolina beaches. Large aggregations have been observed around Ocracoke, Hatteras and Oregon Inlets. They occur along the beaches near inlets for one to two months, with a large portion of the population moving inside Pamlico Sound during the summer months. In August and September schools of adult fish are common in coastal inlets and in Pamlico Sound, particularly in the mouth of the Pamlico and Neuse rivers. During this time, spawning activity takes place. By late September most adult drum are found around the coastal inlets and along the beaches where they remain through November before moving offshore for winter. Anglers have reported catches of large red drum around the shoals and outer bars of the barrier islands, as well as around submerged structures up to a couple of kilometers offshore during December. Mercer (1984) reported schools of large red drum moving down from Virginia waters and along the coastal beaches of the Outer Banks during the fall. By late December, most large red drum have moved offshore where they are no longer available to nearshore fishing activity. During the spring the movement is reversed with large schools of adult red drum moving inshore and along the beaches from Cape Lookout to Cape Hatteras. Fish then proceed north with many of them utilizing coastal inlets to enter Pamlico Sound where they will spend the summer. Other schools of fish are reported to continue moving north to the Chesapeake Bay and the Virginia barrier islands.

South Carolina

The Marine Resources Division of the South Carolina Department of Natural Resources (SC DNR) has conducted fishery-independent tagging of red drum in inshore waters along the coast since 1986. A total of 27,881 red drum have been tagged since then with close to 4,000 individuals tagged in 1996 alone

Project personnel recaptured over 7,500 fish whereas anglers recaptured 5,600. Among angler recaptures, 90% occurred within 9 nautical miles from the site of release whereas 99.4% of red drum recaptured by DNR personnel have remained within 9 nautical miles of the release site. The longest distance traveled by an individual was 233 nautical miles.

Of the animals that have been recaptured over 150 nautical miles from the site of release (7 in all), 4 were recaptured in Florida, one in Georgia and 2 in North Carolina. Interestingly, all long-distance travelers were 2 years old or younger. Tagged red drum have remained at large up to 2,350 days. Slightly over 45% of the animals reported by anglers have remained at large from 1 to 149 days. Similarly, about 46% of those recaptured by DNR personnel have been at large less than 150 days.

Wenner (1999) summarized data for 1994 through 1997 as part of a fishery-independent assessment of subadult red drum in the South Atlantic Bight. A total of 3,610 red drum were tagged in South Carolina waters in three strata: Charleston Harbor, Cape Romain, and lower Stono - Kiawah Rivers. Over 50% of the red drum tagged during the study were recaptured near the mark-and-release site. Approximately 20% were recaptured less than one nautical mile away from the release site. Anglers recaptured over 87% of the tagged fish 5 nautical miles or less from the point of marking. Approximately 5% of the total number of fish recaptured by anglers (n = 593) moved more than 25 nautical miles and only 2 individuals moved over 100 nautical miles. Marked red drum were at large from 1 to 1,076 days. As can be expected, the number of days at liberty was a function of the distribution of fishing effort throughout the year.

In addition to employing fishery-independent surveys to provide life-history information and assess the status of the red drum population in South Carolina, the Marine Division has also conducted a Marine Gamefish Tagging Program since 1974 as a vehicle for promoting conservation through catch-and-release. The latter is the largest state-sponsored public gamefish tagging program in the Southeastern United States. Since its inception, over 12,000 anglers have participated in the program.

Close to 45,000 red drum have been tagged by anglers since 1989 with a recapture rate of about 13%. Trends in the seasonality of the fishery are evident. Most tagging and recapture activity takes place in the fall, resulting mostly from a "fair weather fishermen" effect rather than an increase in the availability of fish during this time. Recapture data from the tagging program shows that movement of red drum, in particular sub-adults, is minimal. The majority of recaptures have occurred less than 3 nautical miles from the release site. In instances where fish moved more than 30 nautical miles, approximately one third were adult fish.

The Inshore Fisheries Section of the Marine Division also conducts a fishery-dependent program to obtain harvest data and supplement life-history information on several target species, including red drum. Anglers are asked to donate their filleted fish carcasses by placing them in chest freezers located in several locations along coastal South Carolina. Data from the South Carolina freezer program, which was initiated in 1995, indicate that most of the harvest of red drum occurs during the fall of the year, specifically during October and November.

Georgia

Woodward (1994) conducted a tagging and population dynamics study in coastal Georgia. Movement of subadult red drum was limited to within 5 km of the site of release. Only 4% of the immature fish that were tagged and released were recovered more than 30 km from the release site. Music and Pafford (1984) and Pafford et al. (1990) report a similar pattern for subadult red drum. Adults leave shoal and sandbar areas around mid-November and enter nearshore waters of the Atlantic Ocean were they form large aggregations entering estuaries on a seasonal basis. One such aggregation was sampled for age composition, and was found to comprise individuals from 5 to 35 years of age (Woodward 1994).

Based on relocations of telemetered subadult and young adult red drum in coastal Georgia, Nicholson et al. (1996) determined that young adult red drum exhibit a similar movement pattern and seasonal distribution to that observed among adults. Their use of biotelemetry tracking methods revealed the importance of the Altamaha River delta to adult red drum in Georgia. Adults in pre-spawning condition were found in inshore waters (6-12 m deep) during the summer months and offshore from late November through the following May.

Florida

To be added.

Mortality

Natural mortality (M) is estimated from the relationship to size at age in Boudreau and Dickie (1989). Separate estimates were made of M for subadults (mean of 0.20 for the northern region and 0.23 for the southern region from ages 1-5) and adults (mean of 0.12 for the northern region and 0.13 for the southern region from ages 6 and older).

Salinity

Red drum are euryhaline, tolerating salinities between 0 to 35 ppt (Peters and McMichael 1987; Daniel 1988). In Florida, red drum have been collected in salinities ranging from 0 to 35 ppt (Tagatz 1967; Jannke 1971; Funicelli et al. 1988; Johnson and Funicelli 1991). Daniel (1988) collected 2,716 red drum (4-450 mm SL) in salinities from 7 to 36 ppt in the Charleston Harbor estuary, South Carolina. Also in South Carolina, tagged subadult red drum have been captured in fresh water up the Ashley and Cooper rivers and recreational anglers commonly fish for red drum in those areas (J. Archambault, pers. comm.). In North Carolina estuaries, red drum (10-391 mm TL) were collected over a salinity range of 0 to 33 ppt (Ross et al. 1987). Neill (1987), in a review of environmental requirements for red drum, noted that adult and subadult red drum are most often found in salinities of 20 to 40 ppt and rarely above 50 ppt while juveniles ranged into the freshest parts of estuaries. The author stated that eggs and newly hatched larvae required salinities above 25 ppt, but salinities between 5 and 10 ppt were optimum for juveniles 1-10 cm SL. Crocker et al. (1981) evaluated growth and survival of red drum larvae and juveniles in fresh and salt water. They found that tolerance to freshwater was size-dependent. Red drum larvae (23 days old, 6.2 mm SL) showed 5% survival, postlarvae (34 days old, 16.2-19.7 mm SL) had 70% survival and juveniles (57 days old, 56.9 mm SL) showed 95% survival when subjected to dechlorinated freshwater for 96 hours. Survival in control salinities of 10 ppt was 90% or greater. Similarly, Yokel (1966) suggested a direct relationship between size and salinity preference, with juveniles preferring lower salinities and larger individuals more common at higher salinities. However, both larval and juvenile red drum are present in areas where low salinities do not generally occur, i.e. behind barrier islands along the South Carolina coast (C. Wenner, pers. comm.). Wakeman and Wolschlag (1983) studied osmotic adaptation with respect to blood serum osmolality and oxygen uptake in hatchery-reared (1.3-3.8 g) and wild, juvenile red drum. They observed rapid stabilization of serum osmolalities and standard metabolic rates suggesting that red drum are well adapted to rapid salinity changes.

Temperature

Red drum are eurythermal and have been collected over a temperature range of 2-33°C, although they tend to move to deeper water at extreme temperatures (Simmons and Breuer 1962). In Florida, Funicelli et al. (1988) collected red drum in water temperatures ranging from 2-31°C, and Peters and McMichael (1987) collected juveniles in 8.9-33°C water in Tampa Bay. In North Carolina, red drum (10-415 mm FL) were collected in temperatures ranging from 7.5-30°C (Ross, pers. comm.; as cited in SAFMC 1990b).

Daniel (1988) collected red drum (4-450 mm TL) with a low surface temperature of 7.3°C in January 1987 and a high of 32°C in July 1986, in a South Carolina estuary. Neill (1987) noted that the optimum temperature for survival of red drum larvae and hatching of red drum eggs was 25°C (at 30 ppt salinity) and suggested that this temperature may be the overall optimum for the species. Similarly, Holt et al. (1987) found that red drum larvae developed optimally in water temperatures between 25-30°C in salinities between 25-30 ppt. More recently, Rooker et al. (1999) conducted a study on post-settlement red drum in the Aransas Estuary, Texas, and reported that growth and survival are enhanced in temperatures ranging around 26°C.

Estuarine animals such as red drum can typically tolerate rapid changes in environmental variables. However, red drum have exhibited marked susceptibility to cold temperatures as indicated by periodic fish kills in coastal areas during severe winters. Gunter (1947) reported that larger juveniles and adults were more susceptible to the effects of winter cold waves than were small fish. High red drum mortality in Texas during freezes was documented by Gunter (1941) and Gunter and Hildebrand (1951). Red drum were killed in three out of nine severe cold spells at Sanibel Island, Florida, but mortality was not severe (Storey and Gudger 1936). In South Carolina, dead red drum were found in Hamlin Sound, Clark Sound, and on the front beach of Dewees Island after the Christmas 1989 freeze (C. Wenner, pers. comm.). Red drum were found dead or dying in the power plant intake canal and on shoals that had iced over in the lower Cape Fear River estuary, North Carolina during the severe winters of 1976 and 1977 (Schwartz et al. 1981).

Experiments conducted by Neill (1987) suggested that juvenile red drum (10-40 mm SL) can survive a gradual decrease in temperature to values as low as 8-10o C in 5-10 ppt water with high hardness (> 100 ppm Ca++). More recently, Whitehurst and Robinette (1994) found no mortality of juveniles (131-158 mm TL) subjected to gradual temperature declines to below 4o C at 9 ppt salinity. The authors attributed the high survival rates in part to salinities close to 11 ppt, a value that Wakeman and Wolschlag (1983) determined to be isosmotic to red drum blood. When the ambient salinity is isosmotic with the blood, red drum presumably experience less physiological stresses (Craig et al. 1995) thus improving their ability to withstand environmental challenges. Whitehurst and Robinette (1994) also speculated that the quality of the water used in their bioassay helped to increase tolerance of juvenile red drum to cold temperatures since some opportunistic pathogens were probably removed by their filtering mechanism.

Ward et al. (1993) conducted experiments to compare critical thermal maxima (CTMax) and minima (CTMin) between juvenile red rum from Texas and North Carolina. CTMax and CTMin are the mean of the upper and lower temperatures at which an organism is so affected as to be unable to escape lethal conditions. The CTMax for Texas juveniles (29.84°C) was slightly greater than that for North Carolina fish (29.23°C), although this difference was considered to lack biological significance. However, the authors noted that juveniles acclimated to sublethal low temperatures had higher survival rates when exposed to low temperature stress than fish acclimated to higher temperatures. In a similar study, Procarione and King (1993) found that juvenile red drum from South Carolina did not resist low water temperatures better than Texas fish at any acclimation temperature.

Ecological relationships

Red drum larvae begin feeding exogenously at 4 days post hatch, once food reserves in the yolk-sac are exhausted (Johnson 1978). As larvae, red drum feed mainly on copepods (Simmons and Breuer 1962; Bass and Avault 1975; Holt et al. 1983b; Steen and Laroche 1983; Baltz et al. 1998) and mysids, the latter comprising up to 97% of the diet by number and 86% by volume (Peters and McMichael 1987). Other important items in the diet of larval red drum are copepod nauplii and eggs (Steen and Laroche 1983). Generally, red drum larvae have been found to have little dietary overlap with other size classes (Peters and McMichael 1987).

Red drum utilize the entire water column when feeding. However, they concentrate on locating prey on the bottom (Yokel 1966). When feeding in shallow estuarine waters, it is not uncommon to observe the fish “tailing,” a feeding behavior whereby the fish's caudal and dorsal fins protrude outside the water as the animal searches the bottom for prey items (Gunter 1945;

Simmons and Breuer 1962; Yokel 1966; Overstreet and Heard 1978). Red drum may also occasionally feed at the surface when preying on fish such as menhaden (Matlock 1987).

Upon reaching the juvenile stage, red drum prey mainly on amphipods, mysids, and palaemonetid shrimp. However, the importance of these prey items in the diet of juveniles can vary among regions. Daniel (1988) performed stomach content analysis on red drum 30-500 mm SL in Charleston Harbor, South Carolina. Mysids were not found to be an important prey item except among red drum 16-30 mm SL (34% by volume). Amphipods were also prey to juvenile red drum, but were not a significant item in their diet. Peters and McMichael (1987) found mysids to be present in the diet of all size classes examined > 8 mm, although total volumes were small, especially among larger juveniles (> 75 mm). Amphipods were found in stomachs of juvenile red drum, becoming the dominant prey item for fish 30-60 mm. Juvenile red drum also consumed shrimp (*Palaemonetes pugio*, *Hippolite zostericola* and one species of Alphaeidae), but they were not an important item in the diet except for juveniles 75-90 mm, where shrimp comprised 56% of the food volume. Llanso et al. (1998) found non-decapod crustaceans, mainly amphipods and mysids, to be the most abundant prey item in the diet of red drum < 200 mm living in an impounded area of Tampa Bay, Florida. Similarly, Bass and Avault (1975) found that red drum 10-49 mm preyed on mysid shrimp almost exclusively. Mysids were found in stomachs of juvenile drum from 10-169 mm. Other items commonly reported in the diet of juvenile red drum are polychaetes and decapod post-larvae (Steen and Laroche 1983; Llanso et al. 1998).

Decapod crustaceans become an increasingly important part of the diet of red drum as they grow (Bass and Avault 1975; Music and Pafford 1984). Daniel (1988) found decapod crustaceans, primarily mud crabs, *Panopeus herbstii*, and fiddler crabs, *Uca* spp. to be the predominant component in the diet of red drum 200-300 mm SL making up almost 96% of the total prey volume. Llanso et al. (1998) reported that as red drum grew over 200 mm, crabs (*Rithropanopeus harisii*, *Pinnixia* spp., *Uca* spp., *Upogebia affinis*) were added to the diet. Wenner et al. (1990) noted that red drum in South Carolina consume all three species of fiddler crabs, *Uca minax*, *U. pugilator,* and *U. pugnax*, whereas these species are not as important in the diet of fish inhabiting the Gulf of Mexico. Apparently, this difference in resource utilization is due partly to differential abundances of fiddler crab species between the two regions and partly to decreased accessibility to the habitats of fiddler crabs in the Gulf of Mexico. Bass and Avault (1975) maintain that, in the Gulf of Mexico, decapod crustaceans begin forming part of the diet when red drum are approximately 20 mm. Decapods that are consumed, in order of appearance, are grass shrimp, penaeid shrimp, and crabs, with the blue crab, *Callinectes sapidus* being the predominant prey species. Boothby and Avault (1971) and Overstreet and Heard (1978) found that blue crabs and penaeid shrimp were predominant in the diet of red drum in Mississippi Sound and Louisiana, respectively. Fish also make up an important part of the red drum diet; their importance also increases among larger red drum. Daniel (1988) found that fishes -- mostly juveniles of the spot, *Leiostomus xanthurus*, and mummichog, *Fundulus heteroclitus* -- were most significant in the diet of larger red drum in Charleston Harbor, South Carolina. Wenner et al. (1990) and Music and Pafford (1984) found that red drum in South Carolina and Georgia preyed on the same fish species, with the exception of the ophicthid eel, *Ophicthus ophis*, which was prey to red drum in Georgia but not in South Carolina. Menhaden are one of the predominant species consumed by red drum in the Gulf of Mexico (Boothby and Avault 1971; Matlock 1987).

Juvenile red drum may spend the first four or five years of life within estuaries (Pearson 1929) where they compete with other estuarine species for food. Young-of-the-year red drum (15-245 mm TL) in North Carolina estuaries were frequently collected with bay anchovy, inland silverside, Atlantic silverside, sheepshead minnow, striped mullet, menhaden, spot, Atlantic croaker, mojarras, gobies, summer flounder, and southern flounder (ASMFC 1984). Red drum may compete with other sciaenid species for benthic resources.

Adult red drum occur offshore, often under schools of blue runner and little tunny in the Gulf of Mexico. When nearshore, schools of red drum often occur near black drum Atlantic tarpon, and pompano (Overstreet 1983).

Abundance and status of stocks

Gold and Richardson (1991) identified weakly differentiated subpopulations occurring in the northeast Gulf of Mexico, Mosquito Lagoon, Florida, and along the North and South Carolina coast. Seyoum et al. (2000) also found genetic evidence for separate populations on the Atlantic and Gulf of Mexico coasts of Florida, but found no evidence of a separate population in Mosquito Lagoon. Red drum along the Gulf of Mexico side of the Florida peninsula may be somewhat isolated from red drum in the northern and western Gulf of Mexico. Tagging studies conducted by SC DNR revealed a high fidelity of returns to state waters where subadult red drum were tagged and released (C. Wenner, pers. comm). Less than 5% of the returns came from adjacent state waters. No adults tagged and released in South Carolina have been recaptured in other states.

Stock Assessment Summary

An assessment of the status of the Atlantic stock of red drum was conducted using recreational and commercial fishery data from 1986 through 1998 (Vaughan and Carmichael 2000). This assessment updated data and analyses from the 1989, 1991, 1992 and 1995 stock assessments (Vaughan and Helser 1990; Vaughan 1992, 1993, 1996).

It is important to remember that the population models used in the coast wide assessments (specifically yield per recruit and static SPR) are based on equilibrium assumptions. Previous estimates of escapement rates (relative survival of red drum from age at entry to fishery to age 4) for 1992-94 ranged from 10.4% for the northern region and 17.2% for the southern region (Vaughan 1996). Escapement rate estimates for Florida Atlantic coast red drum (through age 4) during 1992-94 ranged from 51-69% assuming the size structure of released fish was the same then as it is now (Murphy 2005). This may mean that rates in Georgia and South Carolina are lower than the regional estimate. Estimates of static SPR (the ratio of spawning stock biomass per recruit with and without fishing mortality) ranged from 9% for the northern region to 14% for the southern region. This may be an overestimate because during this period most states north of North Carolina allowed a fishery for adults and the analysis assumes no adult fishing mortality or any discard mortality from commercial fishing operations and recreational use of commercial (gillnet) gear.

Based on the most recent full assessment (Vaughan and Carmichael 2000), results for the northern region indicated that escapement rates were on the order of 18%, but may be overestimated due to the lack of discard data from both the commercial fishery and recreational netting practices. Also, the estimate for the southern region (15%) may not be reflective of escapement rates throughout the region, where there appears to be significant regional differences between Florida and Georgia/South Carolina. Estimates of escapement rates on Florida's Atlantic coast have shown a slow decline since peaking during 1988 at 94% following two years of near-complete moratoria on fishing (Murphy 2005). After fishing for red drum reopened in 1989, escapement began to decline reaching 51-69% during 1992-1994 and 32-43% during 2001-2003.

As summarized in Vaughan and Carmichael (2000) available length-frequency distributions and age-length keys were used to convert recreational and commercial catches to catch in numbers at age. Separable and tuned virtual population analyses were conducted on the catch in numbers at age to obtain estimates of fishing mortality rates and population size (including recruitment to age-1). In turn, these estimates of fishing mortality rates combined with estimates of growth (length and weight), sex ratios, sexual maturity and fecundity were used to estimate yield per recruit, escapement to age-4, and static (or equilibrium) spawning potential ratio (static SPR, based on both female biomass and egg production).

Population models used in this assessment (specifically yield per recruit and static spawning potential ratio) are based on equilibrium assumptions: because no direct estimates are available as to the current status of the adult stock, model results imply potential longer term, equilibrium effects. Because current status of the adult stock is unknown, a specific rebuilding schedule cannot be determined. However, the duration of a rebuilding schedule should reflect, in part, a measure of the generation time of the fish species under consideration. For a long-lived, but relatively early spawning species such as red drum, mean generation time would be on the order of 15 to 20 years based on age-specific egg production. Maximum age is 50 to 60 years for the northern region, and about 40 years for the southern region.

The next stock assessment is scheduled for the spring of 2009 through the full Southeast Data Assessment and Review (SEDAR) process. In 2005, additional funds were provided from Congress to theASMFC to address a number of research priorities. One of these priorities was to determine stock status of red drum. With these additional funds, NC, SC and GA are developing statespecific sampling protocols to provide a fisheries-independent index of abundance for adult red drum. This adult index will be used in the red drum assessment process, and will aid managers in determining biological reference points.

North Carolina

Red drum in North Carolina are classified as overfished (SPR <30%) due to high fishing mortality rates and low recruitment of juvenile fish to the adult stock (NCDMF 2001). Information necessary to estimate abundance at age for adult red drum and calculate spawning stock biomass (SSB) are lacking because slot limits restrict the age classes that may be harvested, and fishery-independent survey data are not available for the adult fish. Therefore, the primary benchmarks used in determining the status of red drum are spawning potential ratio (SPR) and escapement or survivability to age-4. Although early assessments evaluated the

Atlantic Coastal red drum population as a single stock, recent assessments are divided into northern and southern components to better account for the limited migration of the species (Vaughan 1996). Northern region assessment results are largely representative of the North Carolina stock, since North Carolina accounts for an average of 96% of the commercial landings, an average of 85% of the recreational landings, and the only fishery-independent data that are available for the region.

The most recent estimates of SPR for the northern region are based on data from 1992 through 1997. This period represents the changes adopted by North Carolina as a result of Amendment 1. Regulations in the period were a recreational bag limit of 5 fish, an 18-27" slot limit, including one fish which could exceed 27"; commercial regulations included an 18-27" slot limit on the sale of red drum and one red drum exceeding 27" was allowed for personal consumption per day. In addition to changes implemented through Amendment 1, North Carolina also imposed a 250,000 pound quota on the commercial fishery to prevent this fishery from expanding beyond historical harvest levels. The best estimate of SPR for the North Carolina stock is 18% for 1992-1997, still well below the overfishing definition of 30%, but significantly improved over the 1.3% for 1986-1991. Escapement increased from 1.2% in the early period to 18% in the later period, while fully recruited fishing mortality declined from F=1.67 for 1986-1991 to F=0.71 for 1992-1997. In addition, the selectivity of age classes 3 to 5 also declined between the early and late period, indicating that older fish were subjected to less fishing pressure in the later period, likely the result of a reduced bag limit on red drum >27" total length.

Although the red drum stock in North Carolina is currently considered to be overfished, it should be noted that this designation is based on data through 1997 and does not reflect the full impacts of the harvest restrictions implemented by the NCDMF and NCMFC late in the 1998 fishing season as part of the development of a state level red drum FMP. There are two primary goals of the recent regulatory changes: 1) reduce the recreational and commercial harvest rates to levels which prevent overfishing and 2) reduce unnecessary and unquantifiable bycatch of red drum in the gill net fishery. Actions taken include a reduction in the recreational bag limit from 5 to 1 fish, an 18-27"slot limit on all harvest, no possession of red drum >27", a daily commercial trip limit which has ranged from 100 lbs. to five fish and a requirement to attend small mesh gill nets (<5" stretch mesh) from May 1 through October 31 in areas known to be critical juvenile red drum habitat. Additionally, in the last year, the NCDMF has maintained a daily commercial trip limit ranging from 5 to 10 fish and also requires that at least 50% of the landings by weight for an individual trip consist of edible finfish other than red drum making this exclusively a bycatch fishery. This most recent action is intended to prevent any directed effort in the commercial fishery, while still allowing unavoidable bycatch to be landed and therefore accounted for in future assessments.

South Carolina

A stratified-random, fishery independent trammel net survey in South Carolina estuaries has shown a steady decline in the abundance of sub-adult red drum (ages <1 to age 4+). The mean CPUE has dropped from ~8 fish in 1991 to less than 2 fish in 2000. The abundance of age-1 fish in the survey has also decreased. The survey catch data are correlated with the recreational harvest indicating that the fisheries independent survey tracks the MRFSS. Along with declining mean catches, the research survey demonstrated a declining trend in the frequency of occurrence of red drum in net sets as well as the frequency of occurrence of "pods" of red drum larger than 10 fish. In summary, these data show that:

(1) the abundance of sub-adults inside the estuary has declined over time;
(2) recruitment of age-1 fish to the fishery has shown a decline over the decade with the exception of the brief upward tick in the time series in 1995 which resulted from the abundance of the 1994 yearclass;
(3) frequency of encounter of red drum in the survey has declined which suggests that the spatial distribution of the fish has contracted with decreasing abundance;
(4) the occurrence of larger aggregations of red drum in the estuaries has declined as overall abundance has declined;
(5) the trend in the survey catches is reflected in the recreational estimates of the harvest from the MRFSS;
(6) declining trends in abundance of sub-adult red drum was similar in all estuarine systems sampled.

South Carolina initiated a statewide, fishery-independent survey of its recreational fishery in 1986 (State Finfish Survey). Standardized annual data sets for length composition are available from 1988 to the present and for CPUE data from 1990 to the present, based on the private boat fishery in inland waters. South Carolina has also had a mandatory, universal trip logbook system for the charterboat fishery in place since July, 1992 that provides a CPUE database. The state uses these sources of fishery-dependent data in addition to the MRFSS, due in part to concerns about the accuracy of the MRFSS in regards to South Carolina's recreational fishery. Specific problems are the allocation of MRFSS private boat effort between inland and nearshore (0-3 miles) ocean areas since 1995 and estimation of effort in the charterboat mode. State personnel believe that the allocation of private boat effort to inland waters has been disproportionately low in recent years versus the historical pattern, resulting in underestimation of the red drum catch. State personnel also believe that the MRFSS has attributed excess effort to the charterboat mode, resulting in significant overestimation of the red drum catch for this mode in some years. There is also concern about the relatively small sample sizes and geographic distribution of the length composition and CPUE data for red drum in the MRFSS.

The interpretation of the data from the state's fishery-dependent sources is somewhat contradictory to the conclusions drawn from the trammel net survey. The private boat CPUE data suggest increasing recruitment from 1990-1996, followed by a moderate decline in 1997. Since then, CPUE has remained rather stable in the central and northern parts of the state, but a continuing decline in recruitment is indicated in the southern part of the state. The charterboat CPUE data, based on somewhat larger fish, suggest that the population of that component is either stable or increasing slightly.

The state has also conducted two statewide opinion polls of saltwater recreational fisheries license holders regarding their perceptions of the status of the red drum stocks in South Carolina. In 1996, 72% of the survey respondents thought that the population had either increased or showed no change during the previous five years. In the 2001 survey, a smaller majority (59%) of the respondents were in this category.

Georgia

According to the most recent assessment (Vaughan and Carmichael 2000), red drum in the southern region are overfished, and it can then be inferred that red drum in Georgia are overfished. However, the southern region includes both South Carolina and Florida, and there is no separate analysis of data for Georgia. Therefore, the assessment may not accurately represent the situation in Georgia with regard to escapement and SPR within the populations found in that state's waters. Consequently, the results of the southern region assessment must be carefully interpreted when discussing the status of red drum in Georgia.

Mark-recapture studies and trammel net surveys conducted from 1994-1997 showed high mortality within the population resident in the St. Simons estuary, particularly for red drum less than age-2. However, estimates of instantaneous total mortality determined from catch curves based on trammel net data were significantly less that those estimated from fishery-dependent data (MRFSS) for all of coastal Georgia. This suggests that survival to age-5 may have been greater than indicated in regional stock assessments completed in the early 1990s. However, the aforementioned trammel net and tagging surveys were terminated in 1997, so there is no recent fishery-independent information from which to estimate either fishing or total mortality.

Pafford et al. (1990) reported on the age composition and relative abundance of cohorts within a sample of approximately 300 adult red drum collected from the Altamaha River delta. This sample showed a spawning biomass comprised of fish from age 5 to age 40. Young adults (<age-10) were a much smaller portion of the sample than expected, suggesting that recent recruitment had been low. However, there have been no surveys of the age composition of the adult stock in Georgia since that time. Therefore, nothing is known about the current status of the adult portion of the stock, either in terms of age composition or absolute abundance.

The estimated catch of red drum within the recreational fishery as determined from the MRFSS shows no evident trends during the 1990s or since the implementation of current harvest regulations. The total catch declined in the late 1990s only to rebound in 2000 to a level similar to that estimated in the years of the early 1990s. It is unclear whether the reduced catches of the late 1990s are attributable to inadequacies within the MRFSS or to low abundance of red drum. In either case, it is impossible to draw strong conclusions from fishery-dependent data in the absence of an index of juvenile or sub-adult abundance.

Florida

Fishing mortality rates for red drum appeared to increase on the Atlantic coast during the late 1990s. The harvest of red drum increased sharply in 2000. The number of fishing trips made by anglers catching or seeking red drum had varied without trend for much of the latter half of the 1990s but increased to peak or near peak levels in 2000. Total-catch rates for anglers were steady during the late 1990's before dropping in 2000.

A precise analysis of the condition of the red drum stocks in Florida is not possible because there is no information on the size of red drum that make up a large portion of the harvest. Creel clerks measure some of the harvested red drum they encounter on their surveys and while they can ask anglers the number of red drum disposed of or released dead or alive, they do not gather information on the size of these fish. Since 1998, 19-34% of the harvest has been attributable to these unseen fish. In Murphy (2002) the size of red drum in this unseen harvest were assumed; 1) the same as the size in the examined harvest, 2) the same as scientific samples of red drum from haul seines, 3) distributed as 95% undersized, 5% legal, and 5% over-sized, or 4) distributed as 40% undersized, 30% legal, and 30% over-sized.

The abundance of young newly recruited age-0 red drum declined during the latter half of the 1980s but has since increased. The estimates of absolute abundance of red drum ages 1-3 depended heavily on the assumed lengths of the unseen harvest but had a midpoint of about 0.55 million fish on the Atlantic coast of Florida. Since the mid 1990s the model estimates of total abundance for ages1-3 have not changed significantly.

Estimates of equilibrium (year-specific) escapement rates were highly dependent on the scenario chosen for the length structure of the unseen harvest. Florida Atlantic coast estimates ranged from 24% if the unseen harvested was mostly under-sized red drum (scenario #3 above) to 48% if the unseen harvest was mostly legal and over-sized fish (scenario #4 above). Year-class-specific escapement rates indicate that the level of escapement in 2000 is clearly higher than the Florida Fish and Wildlife Commission's target if the unseen red drum harvest is mostly legal and over-sized fish or is distributed the same as the lengths of red drum sampled by FWC-FMRI scientists using haul seines (scenario #2 above). However, if the unseen harvest is distributed as mostly under-sized fish, then it is unlikely that escapement rates are meeting the 30% target.

4.2.10 Weakfish

Description and Distribution

(information from the ASMFC’s Weakfish FMP, 2002)
The weakfish is a moderately-lived (at least up to 17 – 18 years of age but larger fish have not been aged; Mercer 1985, 1989) species that normally spends the majority of its adult life in coastal estuaries and the ocean, migrating north and south and onshore/offshore seasonally.

The larvae and post-larvae begin feeding on microscopic animals during their journey from spawning areas to coastal nursery areas and continue to feed on these small animals after their arrival in the nursery areas, located in the deeper portions of coastal rivers, bays, sounds and estuaries. Here they grow into juveniles. Studies in North Carolina sounds indicated that juvenile weakfish were most abundant in shallow bays or navigational channels characterized by moderate depths, slightly higher salinity’s, and presence of sand and /or sand-seagrass bottom. Juveniles remain in coastal sounds and estuarine until October through December of their first year, after which they migrate to the coast. Weakfish in the northern end of the range leave the inshore areas earlier than weakfish in the southern end of the range.

In the ocean, weakfish appear to move north and inshore during the summer, and to the south and offshore during the winter. Important wintering grounds for the stock are located on the Continental Shelf from Chesapeake Bay to Cape Lookout, North Carolina. With warmer water temperatures in the spring, the mature adult fish migrate to the spawning areas to complete their life cycle.

Reproduction

Mature female weakfish (ages 1 and older) produce large quantities of eggs, that are fertilized by mature males (ages 1 and older) as they are released into waters of nearshore and estuarine spawning areas. Length at maturity is less for southern fish than for northern fish. Southern fish are suggested to produce more eggs at smaller sizes than northern fish do. Work on weakfish fecundity indicated that weakfish, like other sciaenids, are batch rather than total spawners. In other words, females release their eggs over a period of time rather than all at once. Weakfish are indeterminate batch spawners meaning one cannot count all the eggs they will produce in a year in the ovaries at the beginning of spawning season because they continuously produce eggs during spawning season. This may mean that annual fecundity varies for the same fish. However, the relative amount of eggs produced appears proportional to female weight in a given year for both spotted seatrout *Cynoscion nebulosus* (W. Roumillat, SC DNR, personal communication) and weakfish (J. Nye, University of Delaware, personal communication). In the case of weakfish, spawning stock biomass and percent maximum spawning potential based on female weight are assessed. The fertilized eggs hatch into larvae in 36 – 40 hours at temperatures of 20-21°C. Spawning occurs in nearshore and estuarine areas from March through September, with a peak during April to June.

Development, growth and movement patterns

Spawning

Weakfish spawn in estuarine and nearshore habitats throughout the species range. The principal spawning area is from North Carolina to Montauk, NY (Hogarth et al. 1995b), although extensive spawning and presence of juveniles has been observed in the bays and inlets of Georgia and South Carolina (pers. Comm, D. Whitaker, SCDNR). Spawning occurs after the spring inshore migration. Timing of spawning is variable, beginning as early as March in North Carolina, and as late as May to the north. Peak spawning occurs from April to June in North Carolina. Peaks in the New York Bight estuarine occur in May and June.

Eggs and Larvae

Nursery habitats are those areas in which larval weakfish reside or migrate after hatching until they reach sexual maturity (90% by age 1, 100% by age 2). These areas include the nearshore waters as well as the bays, estuaries, and sounds to which they are transported by currents or in which they hatch.

Juveniles

Juvenile weakfish inhabit the deeper waters of bays, estuaries, and sounds, including their tributary rivers. They also use the nearshore Atlantic Ocean as a nursery area. In North Carolina and other states, they are associated with sand or sand/seagreass bottom. They feed initially on zooplankton, switching to mysid shrimp and anchovies as they grow. In Chesapeake and Delaware Bays, they migrate to the Atlantic Ocean by December.

Adults

Adult weakfish reside in both estuarine and nearshore Atlantic Ocean habitats. Warming of coastal waters in the spring keys migration inshore and northward from the wintering grounds to bays, estuaries and sounds. Larger fish move inshore first and tend to congregate in the northern part of the range. Catch data from commercial fisheries in Chesapeake and Delaware Bays and

Pamlico Sound indicate that the larger fish are followed by smaller weakfish in summer. Shortly after their initial spring appearance, weakfish return to the larger bays and nearshore ocean to spawn. In northern areas, a greater portion of the adults spends the summer in the ocean rather than estuaries.

Weakfish form aggregations and move offshore as temperatures decline in the fall. They move generally offshore and southward. The Continental Shelf from Chesapeake Bay to Cape Lookout, North Carolina, appears to be the major wintering ground. Winter trawl data indicate that most weakfish were caught between Ocracoke Inlet and Bodie Island, NC, at depths of 18 –- 55 meters (59 – 180 feet). Some weakfish may remain in inshore waters from North Carolina southward.

Ecological relationships

Weakfish feed primarily on penaeid and mysid shrimps, anchovies, and clupeid fishes (menhaden, river herring, shad). Juvenile weakfish feed mostly on mysid shrimp and anchovies. Older fish feed on cluepeids, anchovies and other fishes including butterfish, herrings, sand lance silversides, juvenile weakfish, Atlantic croaker, spot, scup and killifishes. Invertebrates in the diet in addition to shrimps include squids, crabs, annelid worms and clams. Weakfish are important top carnivores in Chesapeake Bay where they consume high percentages of blue crabs and spot while along the edges of eelgrass habitats as well as other ‘edge habitats’ such as along channel edges, rock and oyster reefs. Weakfish are also found in estuaries without eelgrass, such as in the bays and estuaries of South Carolina.

Abundance and status of stocks

A weakfish stock assessment of data through 1998 was conducted in 1999 and reviewed by the Stock Assessment Review Committee for peer review at the 30th Northeast Regional Stock Assessment Workshop (NMFS 2000). This report indicated that weakfish were “at a high level of abundance and subject to low fishing mortality rates.” This assessment was updated in 2002 with data through 2000.

The 2002 update (Kahn 2002) also indicated that weakfish were at a high level of abundance and fishing mortality was low, suggesting that the management measures put in place in Amendment 3 had resulted in positive trends for the weakfish population. However, it was also noted that the absolute magnitude of impact should be viewed with caution given the uncertainty of the fishing mortality and spawning stock biomass estimates for the most recent year of the assessment (which is often the case with final year estimates).

While these traditional single species assessments were generating high stock size estimates, the recreational and commercial landings of weakfish along the Atlantic coast plummeted to all-time lows between 1999 and 2003 (Figure 4.2-2). This dichotomy of assessment results and fishery performance lead the Weakfish Technical Committee to consider less traditional assessment techniques in their most recent stock assessment covering the period of 1982-2003, which was conducted in 2004-2006 (ASMFC 2006).

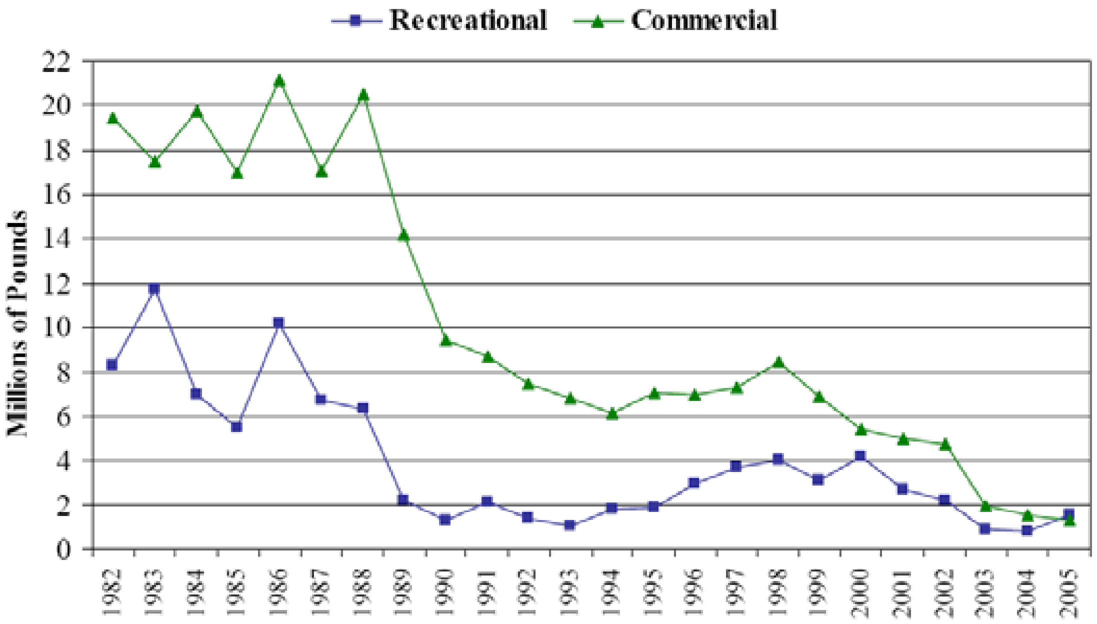


Figure 4.2-2. Annual coastwide weakfish landings (1982-2005). Commercial landings for 2005 are considered preliminary; Massachusetts landings are not included; Georgia landings are confidential but no more than 100 lbs; this maximum value was used in the calculation.

Results from the alternative approaches revealed that a large rise in natural mortality that started in the mid-1990s largely caused weakfish biomass and size structure to decline greatly by 2003 (Figure 4.2-3, Figure 4.2-4). These declines could not be attributed to a slight rise in fishing mortality, which had fallen to moderate levels by 1994 due to conservative management measures. The rapid decline in biomass starting in the late 1990s is reminiscent of rapid transitions between extended periods of high or low commercial landings dating back to the late 1920s. In theory, these rapid changes could reflect an underlying environmental driver whose effect has been accelerated by high fishing or predation rates.

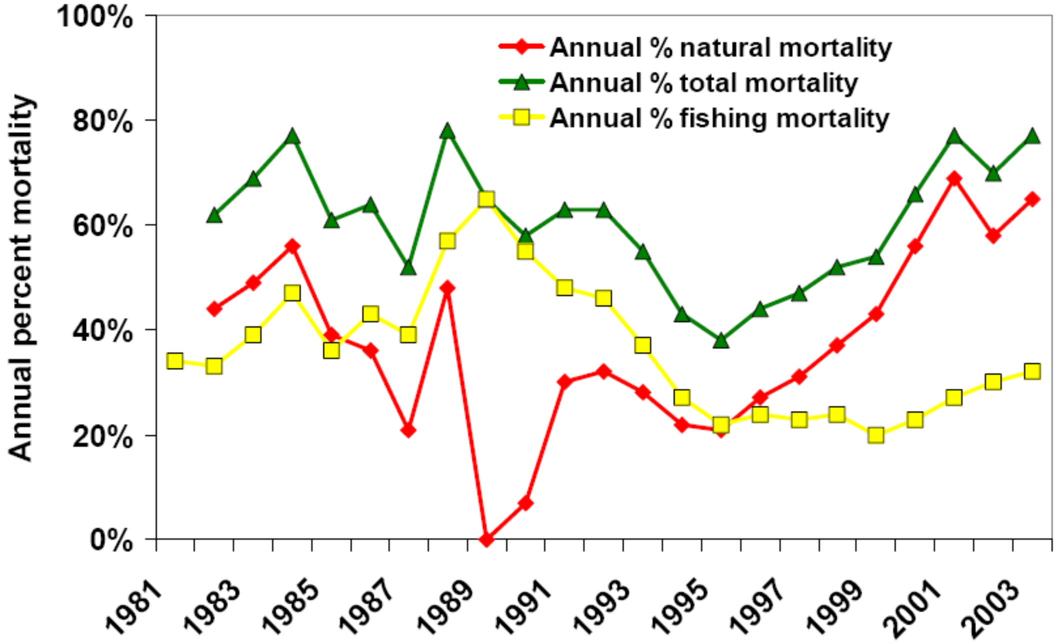


Figure 4.2-3. Coastwide weakfish annual total, natural, and fishing mortality percentages Rates were translated into annual percentages, thus fishing and natural mortality are not additive (Weakfish Technical Committee, 2006).

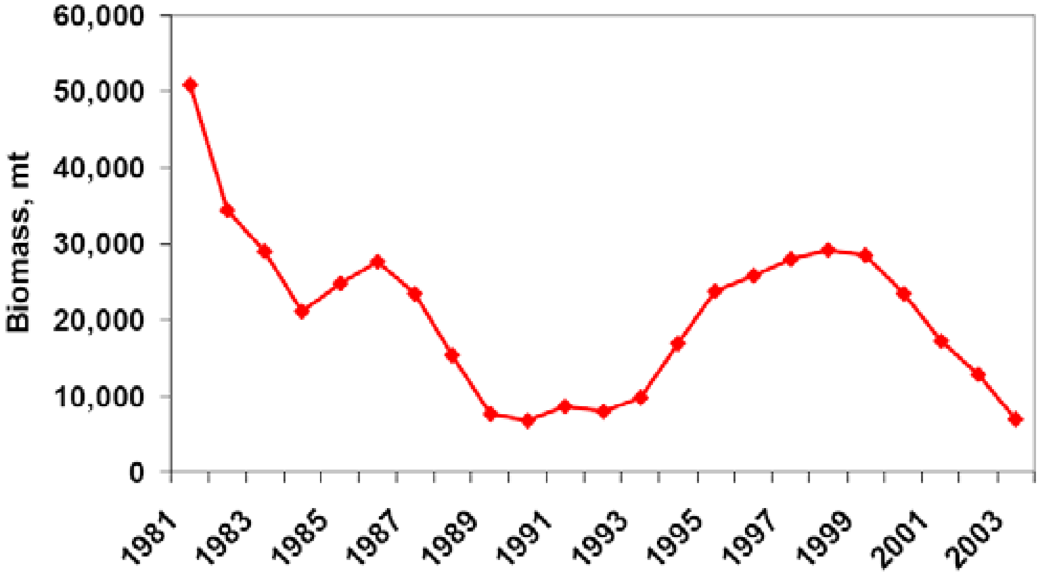


Figure 4.2-4. Estimated coastwide weakfish biomass (Weakfish Technical Committee, 2006).

For the recent stock assessment, the Technical Committee developed and tested specific hypotheses to evaluate candidate predator/competitors (striped bass, summer flounder, bluefish, spiny dogfish and Atlantic croaker), forage species (Atlantic menhaden, bay anchovy, and spot), environmental factors (water temperature and North Atlantic Oscillation index), high bycatch losses, and overfishing. Insufficient forage, especially Atlantic menhaden, and increased predation by striped bass have emerged as leading hypotheses that support rising natural mortality as cause for stock decline (Figure 4.2-5), but contributions by other species or factors may not have been completely detected or tested. While this result does not provide much leverage for recovery by managing the fishery alone, projections did indicate that cuts in fishing mortality are needed for timely recovery if natural mortality declines.

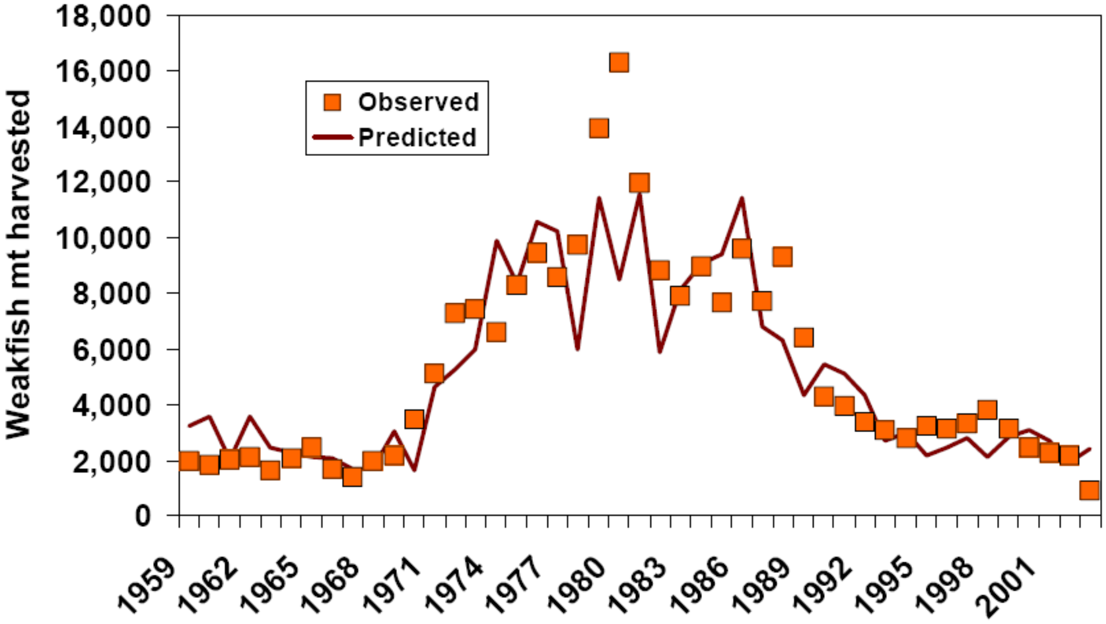


Figure 4.2-5. Food web hypothesis. Weakfish commercial landings are predicted by indices for large bass and menhaden juveniles (multiple regression; both terms significant; menhaden partial r2 = +0.73; bass partial r2 = -0.03) (Weakfish Technical Committee, 2006).

While this assessment was not upheld by an external peer review panel, the Board has accepted for management use five conclusions from the report: 1) the stock is declining; 2) total mortality is increasing; 3) there is not much evidence of overfishing; 4) something other than fishing mortality is causing the decline in the stock; and 5) there is a strong chance that regulating the fishery will not, in itself, reverse stock decline. Due to the difficulty with this last stock assessment and pending management measures, the Technical Committee has been tasked with developing more qualitative techniques for tracking management progress in 2007.

4.2.11 Atlantic Croaker

Description and Distribution

(From SCDNR factsheet available at http://www.dnr.sc.gov/cwcs/pdf/Croaker.pdf)
The Atlantic croaker, *Micropogonias undulatus*, is the only representative of the genus in the western North Atlantic. This species gets its name from the deep croaking sounds created by muscular action on the air bladder. It is one of 23 members of the family Sciaenidae found along the Atlantic and Gulf of Mexico coasts (Mercer 1987). The species has a typical fusiform shape, although it is somewhat vertically compressed. The fish is silvery overall with a faint pinkish-bronze cast. The back and upper sides are grayish, with brassy or brown spots forming wavy

lines on the side (Manooch 1988). The gill cover has three to five prominent spines and there are three to five small chin barbels. It has a slightly convex caudal fin.

It occurs in coastal waters from Cape Cod, Massachusetts to Campeche Bank Mexico, and possibly from southern Brazil to Argentina (Mercer 1987). The species spawns in offshore waters on the continental shelf during fall. Adults in spawning condition have been found in depths of 7 to 131 m (23 to 430 feet) north of Cape Hatteras, and from 5 to 50 km (3 to 31 miles) offshore of South Carolina in depths of 40 to 91 m (131 to 298 feet) (Bearden 1964).

Reproduction

Atlantic croaker spawn in tidal inlets, estuaries, and on the continental shelf, at depths ranging from 7 to 81 m (26 to 266 ft) and in polyhaline and eurohaline zones (Diaz and Onuf 1985). Exact spawning locations may be related to warm bottom waters (Miller et al. 2002). Spawning is reported to occur at water temperatures of 16-25o C in North Carolina (Street et al. 2005). Atlantic croaker have a long spawning season that generally starts in late summer and continues to early spring, with peak reproductive activity occurring in late fall and winter (Diaz and Onuf 1985). In the Chesapeake Bay and North Carolina, spawning begins as early as August and usually peaks in October, whereas peak spawning occurs in November, in the Gulf of Mexico (USFWS 1996).

Development, growth and movement patterns

Eggs and larvae

Pelagic eggs are found in polyhaline and euryhaline waters. After hatching, larvae drift into estuaries by passive and active transport via floodtides, upstream bottom currents, and other large-scale oceanographic processes. Older and larger larvae actively swim into these areas (Miglarese et al. 1982, Petrik et al. 1999). Arrival time into estuaries varies regionally. Larvae are present in the Chesapeake Bay and on the North Carolina and Virginia coasts as late as September and as early as June on the Louisiana coast (USFWS 1996). Localized processes like currents and tidal regimes influence the dispersal of larvae to nursery areas (Petrik et al. 1999). Upon initial arrival in the estuary, larval croaker are restricted to the surface water. However during ebbing tides, larval croakers move to the brackish, bottom waters where they complete their development into juveniles (Miller 2002). Larvae can tolerate colder water temperatures than adults, but extremely cold temperatures may be a major source of larval mortality.

Juveniles

Juveniles use estuaries and tidal riverine habitats along the U.S. Atlantic coast from Massachusetts to northern Florida, and in the Gulf of Mexico, but are most common in coastal waters from New Jersey southward (Able and Fahey 1998; Robbins and Ray 1986; Diaz and Onuf 1985). Recruitment of juveniles into estuaries may be influenced by tidal fluxes in estuaries. For example, in the Pamlico Sound, North Carolina, a shallow estuary where tidal fluxes are largely controlled by wind, recruitment of juveniles is slower than the Cape Fear estuary, where tidal fluxes dictated by lunar cycles average 1.5 meters (Ross 2003). The Cape Fear estuary is representative of most drowned river valley Atlantic Coast estuaries. Juveniles remain in these habitats until early to mid-summer (USFWS 1996). Juveniles migrate downstream as they develop and by late fall, most juveniles emigrate out of the estuaries for open ocean habitats (Miglarese et al. 1982).

Juveniles are associated with areas of stable salinity and tidal regimes and often avoid areas with large fluctuations in salinity. The upper, less saline parts of the estuaries provide the best environment for high growth and survival rates (Ross 2003, Peterson et al. 2004). Juveniles concentrate in oligohaline and mesohaline waters (0.5 to 18 ppt), although they may tolerate more extreme salinities (Diaz and Onuf 1985, Ross 2003). Ross (2003) showed that, juveniles experience reduced mortality in less saline areas. Lower mortality in the less saline areas may be because of lower physiological stress in those environments (Ross 2003). Growth rates in juveniles may be affected by fluctuating salinities and temperatures (Peterson et al. 2004; Chao and Musick 1977). Large changes in salinity can alter the activity of croakers in a way that reduces local abundance; however, smaller changes do not appear to affect juveniles. Sharp fluctuations in salinity can cause intermediate growth rates and increase the bioenergetic costs for juveniles (Peterson et al. 2004). Able and Fahey (1997) suggested that survival in cold December waters in Delaware Bay are not conducive to survival of young croaker. Juvenile croaker prefer deeper tidal creeks because the salinity changes are usually less than in shallow flats and marsh creeks (Diaz and Onuf 1985). Salinity may affect the size distribution of juveniles within an estuary, which may be a result of changing physiological requirements as the juveniles develop (Miglarese et al. 1982). In Delaware Bay, Nemerson and Able (2004) found that the largest concentrations of newly recruited Atlantic croaker were collected over soft bottom habitat having high abundance of benthic invertebrates. Annelids were an important prey component of their diet.

Substrate plays a large role in determining juvenile croaker distribution. Juveniles are positively correlated with mud bottoms with large amounts of detritus that provides sufficient prey (Cowan and Birdsong 1988). Sand and hard substrates are not suitable. Juvenile are often found in more turbid areas of estuaries with higher organic loads that provide a food source for the croakers, but low turbidity is not a limiting factor in juvenile distribution (Diaz and Onuf 1985). The latter stages of young croaker are found more commonly in grass bed in Chesapeake Bay (Olney and Boehlert 1988).

Juvenile Atlantic croaker live at a variety of depths, depending on the estuary. North Carolina estuaries and the coast of the Gulf of Mexico have small tidal fluctuations. In these areas, juvenile croakers amass in shallow, peripheral areas. In estuaries with greater tidal fluctuations such as the Delaware Bay, Chesapeake Bay, or the Cape Fear River Estuary, juvenile croaker assemble in deep channels (Diaz and Onuf 1985).

Field and laboratory data indicate that juveniles are more tolerant of lower temperatures than adults. Juveniles have been found in waters from 0.4° C to 35.5° C (USFWS 1996) but extreme temperature changes can incapacitate juvenile croakers (Diaz and Onuf 1985). Juveniles may favor conditions that can result in low dissolved oxygen, although juveniles will move out of an area if dissolved oxygen levels decrease beyond preferred tolerances (Diaz and Onuf 1985).

Atlantic croaker was described by Petrik et al. (1999) as a habitat generalist. Field surveys of post-settlement croaker in estuarine nursery areas, found no significant differences in abundances among submerged aquatic vegetation, marsh edge, and sandy bottom (Petrik et al. 1999). In a wetland system, Atlantic croaker along the gulf coast preferred non-vegetated bottom adjacent to wetlands, rather than the marsh itself (Rozas and Zimmerman 2000). In North Carolina, Atlantic croaker have been documented to utilize SAV, wetlands, unvegetated soft bottom, and to a lesser extent, shell bottom (Street et al. 2005). Juvenile croaker utilize these habitats for refuge and foraging and as a corridor through the estuary. In North Carolina, Atlantic croaker is one of the dominant juvenile fish species in North Carolina estuaries (DMF, unpub. data). Because croaker utilizes multiple habitats, the effect of habitat change and condition on fish population is difficult to assess.

Juvenile croaker may be affected by hydrological modifications, water quality degradation, or habitat alterations. Hydrological modifications such as ditching and channelization increase the slope of the shoreline and water velocities in the altered stream. Higher water velocity and reduced natural wetland filtration can result in increased shoreline erosion, increasing sediment and non-point pollutant loading in channelized waterbodies (White 1996; EPA 2001). Several studies have found that the size, number, and species diversity of fish in channelized streams are reduced and the fisheries associated with them are less productive than those associated with unchannelized reaches of streams (Tarplee et al. 1971; Hawkins 1980; Schoof 1980). Pate and Jones (1981) compared nursery areas in North Carolina that were altered and unaltered by channelization and found that Atlantic croaker and other estuarine-dependent species were more abundant in nursery habitats with no man-made drainage. They attributed this to the unstable salinity conditions that occurred in areas adjacent to channelized systems following moderate to heavy rainfall (>1 inch/24 hr).

Pollutants negatively affect growth and physical condition of juvenile Atlantic croaker, with significantly reduced growth rates and condition occurring with increasing pollutant conditions (Burke et al. 1993). Low concentrations of heavy metals can accumulate in fine-grained sediments, particularly organic-rich muddy substrates, to toxic levels, and can be resuspended into the water column (Riggs et al. 1991). Primary nursery areas in North Carolina often consist of such fine-grained sediments and are therefore susceptible to toxic contamination of bottom sediments (Street et al. 2005).

Severe hypoxia of bottom water and sediments, often associated with eutrophication, can adversely affect croaker populations through suffocation, reduced growth rates, loss of preferred benthic prey, changes in distribution, or disease (Street et al. 2005). Mass mortality of benthic infauna associated with anoxia has been documented in the deeper portions of the Neuse River estuary in North Carolina, in association with stratification of the water column in the summer (Lenihan and Peterson 1998; Luettich et al. 1999). During these events, oxygen depletion caused mass mortality of up to 90% of the dominant infauna within the affected area (Buzelli et al. 2002). Utilizing a statistical model and field data, it was estimated that the extensive benthic invertebrate mortality, resulting from intensified hypoxia events, reduced total biomass of demersal predatory fish and crabs during summer months by 17-51% in 1997-1998 (Baird et al. 2004). The decrease in available energy from reduced benthos greatly reduced the ecosystem's ability to transfer energy to higher trophic levels at the time of year most needed by juvenile fish (Baird et al. 2004).

Alteration of natural shorelines has been shown to have a negative impact on juvenile Atlantic croaker populations. In a study along the Gulf coast comparing fish abundance between unaltered and altered shorelines (bulkheads or rubble), croaker was most abundant at the unaltered unvegetated shoreline (Peterson et al. 2000). Other anthropogenic activities that can potentially degrade shallow shoreline habitat conditions include dredging and proliferation of docks and marinas (Street et al. 2005).

Adults

Atlantic croaker is one of the most common bottom dwelling, estuarine species on the Atlantic Coast. Atlantic croaker range from the coastal waters of Cape Cod, Massachusetts to Florida, but croaker are uncommon north of New Jersey. Croakers are also found along the Gulf of Mexico coast with high abundances in Louisiana and Mississippi (Lassuy 1983). Temperature and depth are strong predictors of adult croaker distribution and the interaction between the two variables may also influence distribution (Eby and Crowder 2002). Adult croaker generally spend the spring and summer in estuaries, moving offshore and to southern latitudes along the Atlantic coast in the fall. Adults are found in waters from 5° C to 35.5° C, but most catch occurs in temperatures over 24° C (Miglarese et al. 1982). Generally fish over 1 year old are absent in waters below 10° C (Lassuy 1983). Optimal temperatures for growth and survival are not known (Eby and Crowder 2002).

Adult Atlantic croaker prefer muddy and sandy substrates in waters shallow enough to support submerged aquatic plant growth. Adults have also been collected over oyster, coral, and sponge reefs, as well as man-made structures such as bridges and piers. Adult Atlantic croaker also use *Thalassia* sp. beds for refuge although abundance in the seagrass beds is temperature-dependent and changes seasonally (TSNL 1982).

Adults are found in salinity ranges from 0.2-70 ppt, but are most common in waters with salinities ranging from 6-20 ppt (Lassuy 1983, Eby and Crowder 2002). Catch of adult croakers is negatively correlated with increasing salinities (TSNL 1982), but catch also varies with season. In spring, most catch of adult Atlantic croaker is in salinity ranges from 3-9ppt, but in summer, catch peaks in two ranges: the low salinities ranging from 6-12ppt, and high salinities ranging from 24-27 ppt (Miglarese et al. 1982). Generally, adults avoid the mid-salinity ranges (Miglarese et al. 1982, Peterson et al. 2004). Mean total length positively correlates with bottom salinities (Miglarese et al. 1982). Turbidity, nitrate-nitrogen concentrations, and total phosphate-phosphorous concentrations also correlate positively with croaker abundance and catch (TSNL 1982).

The distribution and extent of hypoxic zones in estuaries may also influence habitat use and distribution (Eby and Crowder 2002). Croaker generally shift from deep, hypoxic water to shallow, oxygenated waters during hypoxic events. Their distribution is further limited when hypoxic conditions occur in shallower waters. The lower threshold of dissolved oxygen for Atlantic croaker is about 2.0 mg/L. Below this limit, Atlantic croaker may not survive or may experience sublethal effects. Studies have shown that Atlantic croaker are virtually absent from waters with dissolved oxygen levels below 2.0 mg/L, suggesting they are very sensitive to the amount of dissolved oxygen present (Eby and Crowder 2002).

The size of a hypoxic zone influences habitat use as well. When hypoxic conditions spread in an estuary, Atlantic croaker are forced to use less suitable habitat. Atlantic croaker could incur increased physiological and ecological costs in these areas. For example, Atlantic croaker may face increased intra- and interspecific competition for available space or food in what are essentially compressed habitat zones. To avoid the increased ecological cost, the croaker may return to waters with lower dissolved oxygen (Eby and Crowder 2002).

In spring and fall in moderate water temperatures, moderate hypoxia may not be a limiting factor to Atlantic croaker distribution. However, in summer when water temperatures are higher Atlantic croaker may avoid moderately hypoxic zones in order to avoid the additional physiological costs of staying in waters with less dissolved oxygen (Eby and Crowder 2002). As hypoxia increases in severity and scope within estuarine waters, croaker typically move to shallower parts of an estuary. Large hypoxic zones may limit adult croaker depth and temperature distribution, suggesting a shift in habitat use driven by the severity of a hypoxic event (Eby and Crowder 2002). Atlantic croaker may actually be limited to areas with higher temperatures than their preferred temperatures during hypoxic events (Eby and Crowder 2002).

Ecological relationships

Abundance and status of stocks

(from the 2006 FMP Review)
The latest stock assessment was completed in 2004 and reviewed by the SEDAR peer review panel. The stock assessment committee used an Age Structured Production Model. This assessment only accounts for the mid-Atlantic region (North Carolina and north). There is currently not enough data to assess the South Atlantic region (South Carolina through Florida).

In this assessment, fishing mortality rates (F) are based on the average population weighted F for ages 1-10+. Fishing mortality rates for Atlantic croaker exhibit a cyclical trend over the time series. From 1977 to 1979, F rose rapidly reaching a maximum of 0.5 in 1979. From 1980 onwards, F rapidly declined reaching its lowest levels in 1992 (Figure 4.2-6). Since 1993, F has gradually increased and stabilized in 2002 at around 0.11 (ASMFC 2005a).

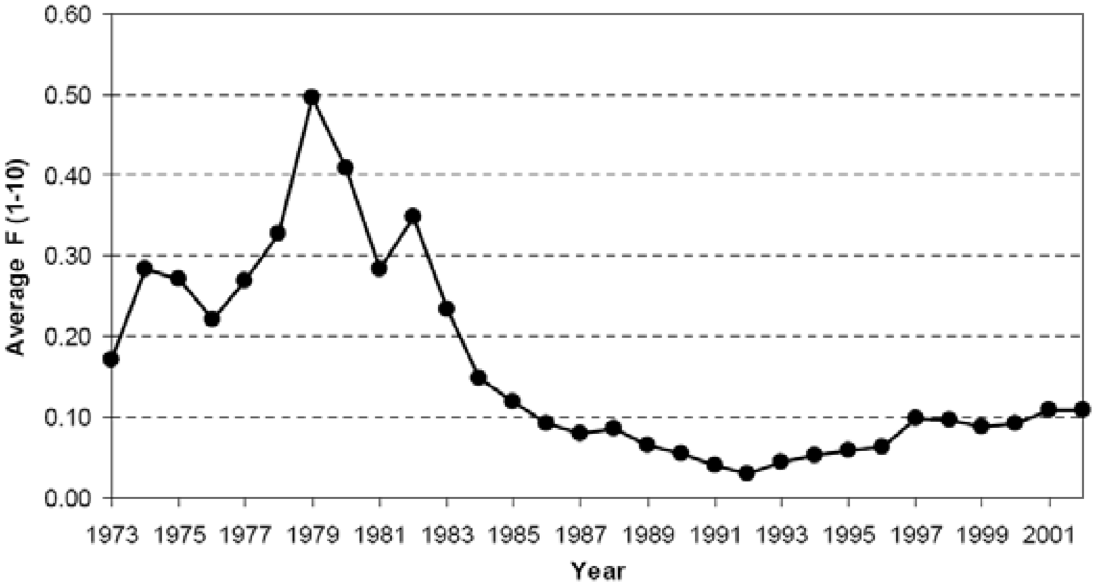


Figure 4.2-6. Average fishing mortality rates (ages 1 –10) for Atlantic croaker in the mid-Atlantic (ASMFC 2005a).

For the base mid-Atlantic run, the trend in population abundance indicates a step-wise increase reaching a peak of 974 million fish in 1999. Population estimates from 1999 to 2002 have ranged from 663 to 974 million fish. Spawning stock biomass (SSB) estimates exhibit a cyclical trend over the time series. From the early 1970's to 1983, SSB declined to its lowest level (11,746 MT). Since 1984, SSB has increased in three distinct phases, with estimates reaching a maximum of 96,686 metric tons in 1996 (Figure 4.2-7). Between 1997 and 2002, SSB estimates range between 80-91,000 metric tons.

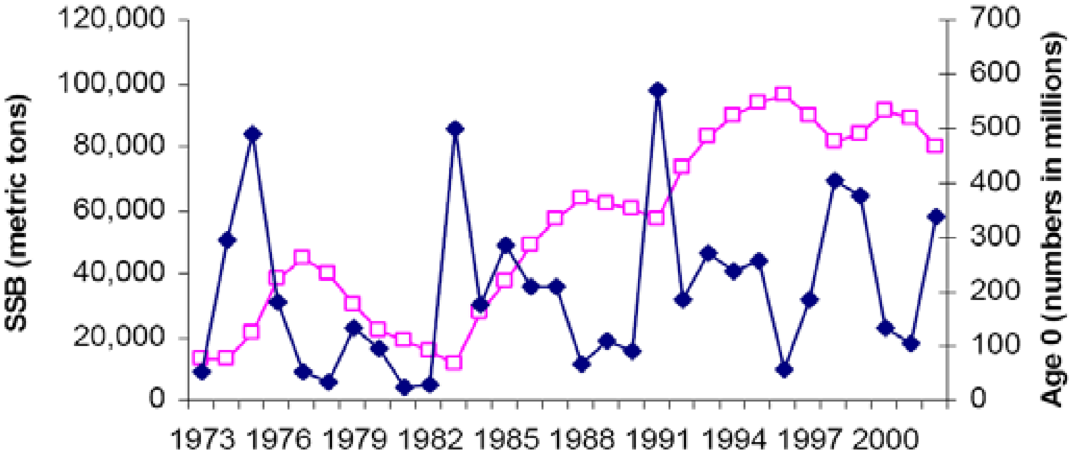


Figure 4.2-7. Spawning stock biomass (metric tons) and age 0 recruits (millions of fish) estimates from the base mid-Atlantic model (ASMFC 2005a).

The mid-Atlantic model, which is the core of the population, indicates fishing mortality rates were high in the mid-1970s, abruptly declined, and has been low and stable since the mid 1990s.

Between 1973 and 2002 the relationship between the different sources of removals has changed. In particular, estimates of scrap/discards reached their peak in 1979 (3,200 MT) and since then declined to their lowest levels in 2002 (425 MT).

Between 1973 and 1995, scrap/discard removals averaged 1,687 MT per year, whereas between 1996-2002 scrap/discards averaged 595 MT per year. It appears that the significant reduction in removals of predominantly age 1 and younger fish may have contributed to relatively stable fishing mortality and spawning stock biomass estimates since the mid 1990's. In relation to the proposed reference points the Atlantic croaker population is not overfished or experiencing overfishing. The commercial and recreational catch-at-age data from recent years also shows an increasing age distribution, with a few fish of 12 years being observed in the commercial landings. Anecdotal evidence from the mid-Atlantic indicates an expansion of the population at the northern part of the range. For example, in Delaware, fishery independent indices indicate a recent increase in abundance of Atlantic croaker in the region (D. Kahn Delaware Div. Fish and Wildlife, personal communication). In addition, both commercial and recreational landings from New Jersey and Delaware have increased recently. The population has benefited from good recruitment in recent years, which may also be tied to the regulatory changes that have affected some of the fisheries that indirectly target Atlantic croaker.

While this analysis does not capture all of the sources of uncertainty, examination of the effects of alternate weightings of the likelihood components and alternate steepness and natural mortality estimates indicate that reference points derived from the base run are relatively robust.

The reference points suggest that there was less than a 10% chance that the population is overfished or undergoing overfishing. Sensitivity analysis evaluating the inclusion/non-inclusion of shrimp bycatch estimates, indicate that SSBmsy estimates are sensitive to the inclusion of Atlantic croaker caught as shrimp bycatch. However, increased SSBmsy estimates are also accompanied by higher SSB estimates. The ratio of SSB_{2002}:SSB_{msy} when shrimp bycatch is included indicates that the stock is unlikely to be below the threshold estimates. Of concern would be management goals that define biomass reference points in absolute terms. There appears to be some justification for revising the reference points for the biomass target and threshold to relative terms until a more comprehensive evaluation of Atlantic croaker from shrimp bycatch can be carried out.

The next stock assessment is scheduled for the fall of 2009, an update assessment through the SEDAR process.

4.2.12 Spot

Description and Distribution

(from SCDNR spot factsheet available at http://www.dnr.sc.gov/cwcs/pdf/Spot.pdf) and the ASMFC Species Profile for Spot)

Spot is a common member of the family Sciaenidae that was first described by Lacepede (1802). Johnson (1978) provides the following description of morphology. The body of the spot is deep and compressed laterally; the back is strongly elevated; the head is obtuse and short with the small mouth positioned ventrally. Spot are bluishgray above and somewhat golden below. They have 12 to 15 oblique dark streaks that may become indistinct in larger specimens. A single large black spot is located above the gill cover.

Spot occur along the U.S. Atlantic coast in estuarine and coastal waters from the Gulf of Maine to Florida, although they are most abundant from Chesapeake Bay south to South Carolina.

Reproduction

To be added

Development, growth and movement patterns

(from scdnr spot factsheet available at http://www.dnr.sc.gov/cwcs/pdf/Spot.pdf)
Following entry to the estuary, spot associate with shallow habitats, particularly tidal creeks. Due to its high productivity, this habitat provides ample prey for spot, which feed mostly on small bottom dwelling worms and crustaceans (Chao and Musick 1977). The habitat is shallow and structurally complex, providing a physical refuge from predators. In addition, spot are well adapted to live in the physiologically stressful low dissolved oxygen, high carbon dioxide environment of small tidal creeks (Cochran 1994). Research in Rose Bay, North Carolina suggests that during their first summer, spot grow and disperse from shallow edges of the bay to all depths (Currin 1984).

While offshore, spot inhabit sandy or muddy bottoms in depths up to 60 meters (197 feet). Following spawning, larvae may take advantage of tidal mechanisms such as tidal bores and internal waves to migrate inshore (Williams 1993). Spot larvae are most dense in midwater and near the bottom during the day, and migrate into surface waters at night. Nearshore, they are most dense on the bottom both day and night, possibly utilizing the salt wedge to enter the estuary.

Spot are strongly associated with the bottom as juveniles and adults and are seasonally dependent on the estuary. Along the east coast of the United States, spawning takes place on the outer continental shelf from October through March. Peak spawning occurs during December and January off the North Carolina coast. As larvae mature, they are passively transported toward shore by currents (Warlen and Chester 1985). Near inlets, the larvae begin to metamorphose into juveniles (Phillips et al. 1989). Young-of-the-year spot typically move first into the upper reaches of the estuary and then disperse to the lower reaches as they mature through their first season. Young-of-the-year may remain in the estuary during their first winter, while older fish migrate offshore to spawn.

Ecological relationships

(from scdnr spot factsheet by Phil Maier http://www.dnr.sc.gov/cwcs/pdf/Spot.pdf)
Spot represent a significant link in the transfer of energy from the estuary to the waters of the adjacent continental shelf. Because of their abundance, they are considered to be ecologically important, influencing the structure and function of estuarine systems (Kjelson and Johnson 1976); as such, spot have the potential to act as an indicator species for estuarine systems. In addition, spot are important to both recreational and commercial anglers in the Mid-Atlantic Region where they comprise the major proportion of the biomass and numbers of fish present (Phillips et al. 1989).

(from the ASMFC Species Profile for Spot)
Spot are opportunistic bottom feeders, eating mainly worms, small crustaceans and mollusks, as well as organic material. The post-larvae prey on plankton, but become bottom feeders as juveniles or adults. Such predators as striped bass, weakfish, summer flounder, bluefish, and sharks eat them in turn.

Abundance and status of stocks

(from ASMFC's 2006 update to the spot FMP)
No coastwide assessment has been performed for spot; however, spot are a target or component of several state surveys using trawl, gillnet, or seine net to sample. Florida assessed the abundance of spot in the Indian River Lagoon in 1997, finding stable juvenile abundance between 1990 and 1996, except for a very high 1993 index, and stable adult abundance during the same time series (McRae et al. 1997). An analysis of spot catches in Maryland's juvenile seine survey showed a trend of increasing abundance from 1957 to l976, and then, a protracted decline, that has been punctuated by occasional high years. The 2005 abundance index increased drastically, reaching its highest value since 1988, but fell back to low levels in 2006 (Durrell 2006). Spot young-of-year abundance in the VIMS Virginia Chesapeake Bay Trawl Survey was relatively high from 1981 through 1991, but remained low from 1992 to 2005, except for fair to moderate-sized yearclasses in 1997 and 2005 (Montane & Fabrizio 2006). The abundance of juvenile spot in the North Carolina Pamlico Sound Survey has fluctuated without trend since 1979. The area of greatest abundance on the Atlantic Coast extends from Chesapeake Bay to South Carolina (ASMFC 1987).

4.2.13 Summer Flounder

From the NEFSC EFH source document for Summer Flounder (1999).

Description and Distribution

The geographical range of the summer flounder or fluke, *Paralichthys dentatus* (Figure 4.2-8), encompasses the shallow estuarine waters and outer continental shelf from Nova Scotia to Florida (Ginsburg 1952; Bigelow and Schroeder 1953; Anderson and Gehringer 1965; Leim and Scott 1966; Gutherz 1967; Gilbert 1986; Grimes et al. 1989), although Briggs (1958) gives their southern range as extending into the northern Gulf of Mexico. The center of its abundance lies within the Middle Atlantic Bight from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina (Hildebrand and Schroeder 1928). North of Cape Cod and south of Cape Fear, North Carolina, summer flounder numbers begin to diminish rapidly (Grosslein and Azarovitz 1982). South of Virginia, two closely related species, the southern flounder (*Paralichthys lethostigma*) and the gulf flounder (*Paralichthys albigutta*) occur and sometimes are not distinguished from summer flounder (Hildebrand and Cable 1930; Byrne and Azarovitz 1982).

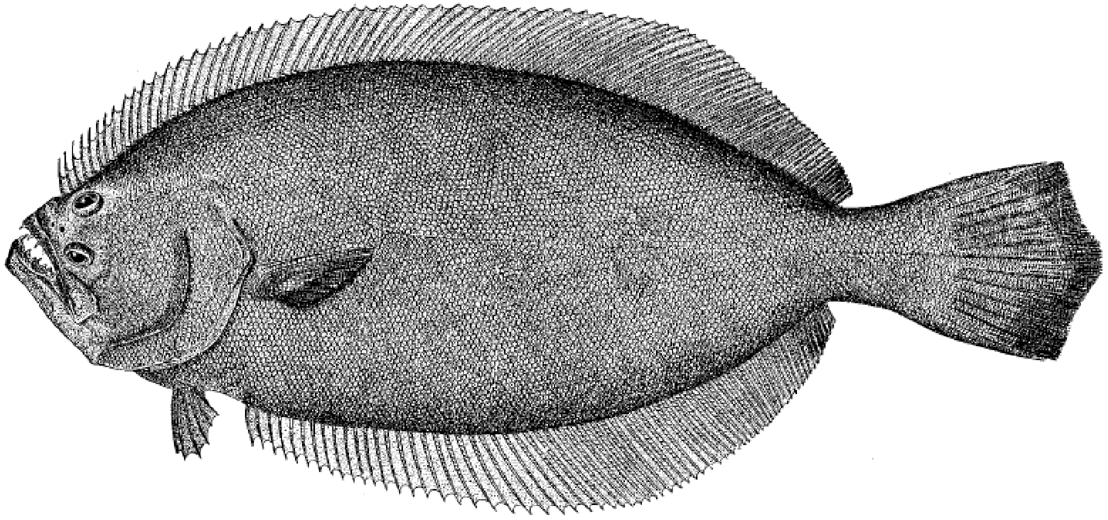


Figure 4.2-8. The summer flounder, *Paralichthys dentatus* (from Goode 1884).

Summer flounder exhibit strong seasonal inshoreoffshore movements, although their movements are often not as extensive as compared to other highly migratory species.

Adult and juvenile summer flounder normally inhabit shallow coastal and estuarine waters during the warmer months of the year and remain offshore during the fall and winter. See Development, Growth and Movement Patterns below for a detailed description of movement patterns.

Reproduction

Powell (1974) noted that the minimum size at maturity of summer flounder from Pamlico Sound, North Carolina was 35.0 cm TL. In the South Atlantic Bight, Wenner et al. (1990a) estimated the L50 to be 28.9 cm TL for males and 30.7 cm TL for females, corresponding to fish approaching age 2. Based on the study by O'Brien et al. (1993) on the L50 of summer flounder sampled from 1985-1989 from Nova Scotia to Cape Hatteras, this report will use the female size of 28 cm (age 2.5) as the divide between all juvenile and adult individuals. The median length at maturity for males in the O'Brien et al. (1993) study was 24.9 cm (age 2). However, as O'Brien et al. (1993) notes, a revision to aging convention (Smith et al. 1981; Almeida et al. 1992) has resulted in median lengths being attained a year earlier than those reported above; thus, for example, the ages of O'Brien et al. (1993) are also off by a year (i.e., the age 2.5 female fish are now age 1.5). These conclusions have been supported by more recent growth studies (Able et al. 1990; Szedlmayer et al. 1992).

Fecundity and length exhibit a curvilinear relationship, but with logarithmic transformations, Morse (1981) expressed the relationship as:

$$\log_{10} \text{Fecundity} = \log_{10} a + b (\log_{10} \text{length})$$

where the intercept (a) = -3.098 and the slope (b) = 3.402.

The relationship between fecundity and weight and ovary weight were expressed by Morse (1981) as:

$$\text{Fecundity} = a + bX$$

where the intercept (aweight) = -101,865.5 and the slope (bweight) = 908.864, and the intercept (aovary weight) = 52,515.161 and the slope (bovary weight) = 10,998.048.

Powell (1974) estimated that females ranging from 50.6-68.2 cm TL have 1.67-1.70 million ova per fish, while Morse (1981) reported fish between 36.6 and 68.0 cm TL have 0.46-4.19 million ova. The relative fecundity, number of eggs produced per gram of total weight of spawning female, ranged from 1,077-1,265 in Morse's (1981) study.

The increase in variability in fecundity estimates as weight increases tends to obscure the true relationship. The high egg production to body weight is maintained by serial spawning. In fact, the weight of annual egg production, assuming an average egg diameter of 0.98 mm and 1.0 specific gravity, equals approximately 40-50% of the biomass of spawning females (Morse 1981).

Morse (1981) calculated the percent of ovary weight to total fish weight as an index for maturity. The mean maturity index increased rapidly from August to September, peaked in October-November, then gradually decreased to a low in July. The wide range in the maturity indices during the spawning season indicates nonsynchronous maturation of females and a relatively extended spawning season. The length and peak spawning time as indicated by the maturity index agree with results determined by egg and larval occurrence (Herman 1963; Smith 1973).

Spawning occurs over the open ocean areas of the shelf. Summer flounder spawn during the fall and winter while the fish are moving offshore or onto their wintering grounds; the offshore migration is presumably keyed to declining water temperature and decreasing photoperiod during the autumn. The spawning migration begins near the peak of the summer flounder`s gonadal development cycle, with the oldest and largest fish migrating first each year (Smith 1973).

The seasonal migratory/spawning pattern varies with latitude (Smith 1973); i.e., gonadal development, spawning and offshore movements occur earlier in the northern part of their range (Rogers and Van Den Avyle 1983). For example, in Delaware Bay, gonads of summer flounder appear to ripen from mid-August through November (Smith and Daiber 1977), while peak gonadal development occurs during December and January for fish around Cape Hatteras (Powell 1974). Spawning begins in September in the inshore waters of southern New England and the Mid-Atlantic. As the season progresses, spawning moves onto Georges Bank as well as southward and eastward into deeper waters across the entire breadth of the shelf (Berrien and Sibunka 1999).

Spawning continues through December in the northern sections of the Middle Atlantic Bight, and through February/March in the southern sections (Smith 1973; Morse 1981; Almeida et al. 1992). Spawning peaks in October north of Chesapeake Bay and November south of the Bay (Smith 1973; Able et al. 1990; note that the latter statement on spawning south of the Bay in

November appears to contradict the published information above concerning peak gonadal development occurring December-January near Cape Hatteras). The half year spawning season reduces larval crowding and decreases the impact of predators and adverse environmental conditions on egg and larval survival (Morse 1981). In the South Atlantic Bight, maturity observations by Wenner et al. (1990a) suggest that spawning begins as early as October, and may continue through February and possibly early March.

Development, growth and movement patterns

Eggs of summer flounder are pelagic and buoyant. They are spherical with a transparent, rigid shell; yolk occupies about 95% of the egg volume. Mean diameter of mature unfertilized eggs is 0.98 mm. Eggs are most abundant between Cape Cod/Long Island and Cape Hatteras; the heaviest concentrations have been reported within 45 km of shore off New Jersey and New York during 1965-1966 (Smith 1973), and from New York to Massachusetts during 1980-1986 (Able et al. 1990). Able et al. (1990) discovered that the highest frequency of occurrence and greatest abundances of eggs in the northwest Atlantic occurs in October and November, although, due to limited sampling in December south of New England, December could be under represented. Festa (1974) also notes an October-November spawning period off New Jersey. Keller et al. (1999) found eggs (maximum density 19.5/100 m^3) from February to June in Narragansett Bay during a December 1989 to November 1990 sampling period. In southern areas, eggs have been collected as late as January-May (Smith 1973; Able et al. 1990). The eggs have been collected mostly at depths of 30-70 m in the fall, as far down as 110 m in the winter and from 10-30 m in the spring.

Planktonic larvae (2-13 mm) are often most abundant 19-83 km from shore at depths of around 10-70 m, and are found in the northern part of the Middle Atlantic Bight from September to February, and in the southern part from November to May, with peak abundances occurring in November (Smith 1973; Able et al. 1990). The smallest larvae (< 6 mm) were most abundant in the Mid-Atlantic Bight from October-December, while the largest larvae (≥11 mm) were abundant November-May with peaks in November-December and March-May (Able et al. 1990). Off eastern Long Island and Georges Bank, the earliest spawning and subsequent larval development occurs as early as September (Able and Kaiser 1994). By October, the larvae are primarily found on the inner continental shelf between Chesapeake Bay and Georges Bank. During November and December they are evenly distributed over both the inner and outer portions of the shelf. By January and February the remaining larvae are primarily found on the middle and outer portions of the shelf. By April, the remaining larvae are concentrated off North Carolina (Able and Kaiser 1994).

From October to May larvae and postlarvae migrate inshore, entering coastal and estuarine nursery areas to complete transformation (Merriman and Sclar 1952; Olney 1983; Olney and Boehlert 1988; Able et al. 1990; Szedlmayer et al. 1992). Larval to juvenile metamorphosis, which involves the migration of the right eye across the top of the head, occurs over the approximate range of 8-18 mm SL (Burke et al. 1991; Keefe and Able 1993; Able and Kaiser 1994). They then leave the water column and settle to the bottom where they begin to bury in the sediment and complete development to the juvenile stage, although they may not exhibit complete burial behavior until mid-late metamorphosis when eye migration is complete, often at sizes as large as 27 mm SL (Keefe and Able 1993, 1994). However, burying behavior of metamorphic summer flounder is also significantly affected by substrate type, water temperature, time of day, tide, salinity, and presence and types of predators and prey (Keefe and Able 1994).

In North Carolina, the highest densities of larvae are found in Oregon Inlet in April, while farther south in Ocracoke Inlet, the highest densities occur in February (Hettler and Barker 1993). J.P. Monaghan, Jr. (North Carolina Dept. of Nat. Res. and Commer. Dev., Morehead City, NC, personal communication) mentions that for the years 1986-1988, peak immigration periods of larvae through Beaufort Inlet and into North Carolina estuaries were from late February through March. In the Cape Fear River Estuary, North Carolina, it has been reported that postlarvae first enter the marshes in March and April and are 9-16 mm SL during peak recruitment (Weinstein 1979; Weinstein et al. 1980b).

Schwartz et al. (1979a, b) also notes that age 0 flounder appear in the Cape Fear River between March and May, depending on the year. Warlen and Burke (1990) found larvae (mean 13.1 mm SL) in the Newport River estuary just inside Beaufort Inlet from February-April, 1986, with peak abundance in early March.

Powell and Robbins (1998) reported larval summer flounder adjacent to live-bottom habitats (rock outcroppings containing rich invertebrate communities and many species of tropical and subtropical fishes) in Onslow Bay (near Cape Lookout) in November (at stations of 17-22 m depth), February (28-30 m depth), and May (14-16 m and 17-22 m depth). Burke et al. (1998) conducted night-time sampling for transforming larvae and juveniles in Onslow Bay, Beaufort Inlet, and the Newport River estuary in February- March 1995. Although flounders were captured both in Onslow Bay and in the surf zone during the immigration period, densities were low and all were transforming larvae (7-15 mm SL). After the immigration period, flounders were absent, as juveniles were not caught. Within the Newport River estuary, flounders were locally very abundant as compared to within Onslow Bay and initial settlement was concentrated in the intertidal zone. During February most were transforming larvae, in March some were completely settled juveniles (11-21 mm SL).

In South Carolina, Burns (1974) captured summer flounder larvae (14.9-17.5 mm) in New Bridge Creek, North Inlet estuary in February-March, while Bearden and Farmer (1972) recorded larvae and postlarvae in Port Royal Sound estuary from January-March. During 1986-1988, Wenner et al. (1990a) found that ingress of recently transformed larval and juvenile summer flounder (10-20 mm TL) into Charleston Harbor, South Carolina estuarine marsh creeks began in January and continued through April. Larvae and postlarvae were also found during this period in the Chainey Creek area (Wenner et al. 1986).

As stated above, juveniles are distributed inshore and in many estuaries throughout the range of the species during spring, summer, and fall (Deubler 1958; Pearcy and Richards 1962; Poole 1966; Miller and Jorgenson 1969; Powell and Schwartz 1977; Fogarty 1981; Rountree and Able 1992a, b, 1997; Able and Kaiser 1994; Walsh et al. 1999). During the colder months in the north there is some movement to deeper waters offshore with the adults, although many juvenile summer flounder will remain inshore through the winter months while some juveniles in southern waters may generally overwinter in bays and sounds (Smith and Daiber 1977; Wilk et al. 1977; Able and Kaiser 1994). In estuaries north of Chesapeake Bay, some juveniles remain in their estuarine habitat for about 10 to 12 months before migrating offshore their second fall and winter; in North Carolina sounds, they often remain for 18 to 20 months (Powell and Schwartz 1977). The offshore juveniles return to the coast and bays in the spring and generally stay the entire summer. Fogarty (1981) examined the distribution patterns of prerecruit (≤ 30.5 cm) summer flounder caught during the 1968-1979 spring surveys and found a striking absence of small fish in northern areas. Both spring and autumn bottom trawl survey data indicated that the concentration of young-of-year summer flounder was south of 39^{o} latitude. The importance of the Chesapeake Bight to this species is demonstrated by the fact that almost all of the young-of-year caught during those spring surveys were from this area.

In Mid-Atlantic estuaries, first year summer flounder can grow rapidly and attain lengths of up to at least 30.0 cm (Poole 1961; Almeida et al. 1992; Szedlmayer et al. 1992). Young-of-the-year summer flounder in New Jersey marsh creeks have average growth rates of 1.3-1.9 mm/d, and increase from about 16.0 cm TL at first appearance in late July to around 26.0 cm by September (Rountree and Able 1992b; Szedlmayer et al. 1992). First year fish from Pamlico Sound, North Carolina obtained mean lengths of 16.7 cm for males and 17.1 cm for females (Powell 1982).

In Charleston Harbor and other South Carolina estuaries from 1986-1988, Wenner et al. (1990a) found transforming larvae were recruited into the estuarine creeks when 1-2 cm TL. Growth accelerated in May and June when they reached modal sizes of 8 and 14 cm TL, respectively. By September, modal size was 16 cm TL and reached from 23-25 cm TL through October and November. Modal lengths of yearlings ranged from 23-25 cm in January through June and generally reached 28 cm by October. In Georgia, lab studies by Reichert and van der Veer (1991) found that juveniles from Duplin River of 28-46 mm SL had a maximum growth rate of about 1.3-1.4 mm/d at laboratory temperatures of 23.7-24.8°C.

Juvenile summer flounder make use of several different estuarine habitats. Estuarine marsh creeks are important as nursery habitat, as has been shown in New Jersey (Rountree and Able 1992b, 1997; Szedlmayer et al. 1992; Szedlmayer and Able 1993), Delaware (Malloy and Targett 1991), Virginia (Wyanski 1990), North Carolina (Burke et al. 1991) and South Carolina (Bozeman and Dean 1980; McGovern and Wenner 1990; Wenner et al. 1990a, b). Other portions of the estuary that are used include seagrass beds, mud flats and open bay areas (Lascara 1981; Wyanski 1990; Szedlmayer et al. 1992; Walsh et al. 1999). Patterns of estuarine use by the juveniles can vary with latitude.

Tagged summer flounder have been recaptured from inshore areas to the northeast of their release sites in subsequent summers, leading to the hypothesis that their major nursery areas are the inshore waters of Virginia and North Carolina, and as they grow older and larger, they would return inshore to areas farther north and east of these nursery grounds (Poole 1966; Murawski 1970; Lux and Nichy 1981). However, tagging studies by Desfosse (1995) indicate that it is not the older and larger fish, but rather the smaller fish (length at tagging) which return to inshore areas north of Virginia. Summer flounder that were recaptured north of their release site in subsequent years were smaller (length at tagging) than those recaptured at their release sites, or to the south, in later years. Desfosse (1995) suggests that while Virginia waters do indeed form part of the nursery grounds for fish which move north in subsequent years, they are primarily a nursery area for fish which will return to these same waters as they grow older and larger.

The estuarine waters of North Carolina, particularly those west and northwest of Cape Hatteras (Monaghan 1996) and in high salinity bays and tidal creeks of Core Sound (Noble and Monroe 1991), provide substantial habitat and serve as significant nursery areas for juvenile Mid-Atlantic Bight summer flounder. Powell and Schwartz (1977) found that juvenile summer flounder were most abundant in the relatively high salinities of the eastern and central parts of Pamlico Sound, all of Croatan Sound, and around inlets. Young-of-the-year disappeared from the catch during late summer, suggesting that the fish are leaving the estuaries at that time (Powell and Schwartz 1977). Upon leaving the estuaries, the juveniles enter the north-south, inshore-offshore migration of Mid-Atlantic Bight summer flounder (Monaghan 1996). Although North Carolina also provides habitat for summer flounder from the South Atlantic Bight, these fish do not exhibit the same inshore-offshore and north-south migration patterns as do Mid-Atlantic Bight fish (Monaghan 1996). Summer flounder > 30 cm are rarely found in the estuaries of North Carolina, although larger fish are found around inlets and along coastal beaches. Powell and Schwartz (1977) also noted that juvenile summer flounder were most abundant in areas with a predominantly sandy or sand/shell substrate, or where there was a transition from fine sand to silt and clay.

Surveys by Hoffman (1991) in marsh creeks in Charleston Harbor, South Carolina showed that recently settled summer flounder were abundant over a wide variety of substrates including mud, sand, shell hash, and oyster bars.

Ecological relationships

Food Habits

The timing of peak spawning in October/November coincides with the breakdown of thermal stratification on the continental shelf and the maximum production of autumn plankton which is characteristic of temperate ocean waters of the northern hemisphere, thus assuring a high probability of adequate larval food supply (Morse 1981).

Previous studies have inferred that larval and postlarval summer flounder initially feed on zooplankton and small crustaceans (Peters and Angelovic 1971; Powell 1974; Morse 1981; Timmons 1995). Grover (1998) studied the food habits of oceanic larval flounder collected north and east of Hudson Canyon. The diets of all stages of larvae were dominated by immature copepodites. The size of other prey was directly related to larval size. Preflexion larvae (1.9-6.9 mm SL) fed on, in order of importance: immature copepodites, copepod nauplii, and tintinnids, as well as bivalve larvae and copepod eggs. Flexion larvae (3.7-7.2 mm SL) fed on immature copepodites (mostly calanoids) and adult calanoid copepods. Premetamorphic (4.8-7.6 mm SL) and metamorphic (5.8-9.0 mm SL) larvae also fed on immature copepodites, but adult calanoid copepods (mostly *Centropages typicus*) and appendicularians were also prey items.

Studies on the food habits of late larval and juvenile estuarine summer flounder reveal that while they are opportunistic feeders and differences in diet are often related to the availability of prey, there also appears to be ontogenetic changes in diet. Smaller flounder (usually < 100 mm) seem to focus on crustaceans and polychaetes while fish become a little more important in the diets of the larger juveniles.

Burke (1991, 1995) in his North Carolina field surveys in the Newport and North Rivers discovered that late larval and early juvenile summer flounder are active infaunal predators. Prey of summer flounder during the immigration period (11-22 mm SL) consisted of common estuarine crustaceans including harpactacoid copepods, polychaetes, and parts of infaunal animals such as polychaete tentacles (primarily from the dominant spionid *Streblospio benedicti*) gills and clam siphons. The appendages of temperature and food availability (i.e., delay of initial feeding) and their effects on survival and growth of summer flounder larvae hatched from Narragansett Bay and Long Island Sound broodstock. Their laboratory observations occurred from the time of hatching throughout the period of feeding on rotifers. The larvae withstood starvation for benthic animals appear to be the most important prey item for postlarval flounders. The increasing importance of polychaetes and clam siphons was suggested with development, while feeding on harpactacoid copepods and amphipods was independent of stage. For juveniles 20-60 mm SL, polychaetes, primarily spionids (*S. benedicti*), were the most important part of the diet.

Burke (1991, 1995) suggests that the distribution of these dominant polychaetes may influence the distribution of summer flounder in this estuary and could explain the movement of juvenile summer flounder into marsh habitat. Other prey items for this size class of summer flounder included invertebrate parts, primarily clam siphons; shrimp, consisting of the mysids *Neomysis americana* and palmonid shrimp; calanoid copepods, primarily *Paracalanus*; amphipods of the genus *Gammarus*; crabs, primarily *Callinectes sapidus*; and fish.

Powell and Schwartz (1979) reported that larger juvenile (100-200 mm TL) summer flounder feed mainly on mysids (mostly *Neomysis americana*) and fishes throughout the year in Pamlico Sound, North Carolina. Mysids were found in relatively greater quantities in the smaller flounder, but as their size increased, the diet consisted of shrimps and fishes in similar quantities.

In South Carolina, Wenner et al. (1990a) reported that juveniles between 50-125 mm TL consumed only mysids and caridean shrimps (*Palaemonetes* sp., *P. pugio*, *P. vulgaris*). The importance of fish (mostly bay anchovy, *Anchoa mitchilli*, and mummichogs) in the diet increased as summer flounder size increased.

In Georgia, Reichert and van der Veer (1991) found that juveniles from the Duplin River of around < 40 mm SL fed principally on harpacticoid copepods; they also report that *Paralichthys* species > 25 mm fed on increasing numbers of other crustaceans including mysids, crabs, *Palaemonetes*, as well as polychaetes. Summer flounder > 100 mm also fed on fish.

Adult summer flounder are opportunistic feeders with fish and crustaceans making up a significant portion of their diet. Differences in diet between habitats or locations may be due to prey availability. The flounder are most active during daylight hours and may be found well up in the water column as well as on the bottom (Olla et al. 1972). Included in their diet are: windowpane (Carlson 1991), winter flounder, northern pipefish, Atlantic menhaden, bay anchovy, red hake, silver hake, scup, Atlantic silverside, American sand lance, bluefish, weakfish, mummichog, rock crabs, squids, shrimps, small bivalve and gastropod mollusks, small crustaceans, marine worms and sand dollars (Hildebrand and Schroeder 1928; Ginsburg 1952; Bigelow and Schroeder 1953; Poole 1964; Smith and Daiber 1977; Allen et al., 1978; Langton and Bowman 1981; Curran and Able 1998).

In South Carolina, Wenner et al. (1990a) showed that flounder 50-313 mm TL consumed mostly decapod crustaceans, especially caridean shrimps (*Palaemonetes* sp., *P. pugio*, *P. vulgaris*). The importance of fish (mostly bay anchovy, Anchoa mitchilli, and mummichogs) in the diet increased as summer flounder size increased.

Co-occurring Species and Predation

Larval and juvenile summer flounder undoubtedly are preyed upon until they grow large enough to fend for themselves. Results of food habit studies by the Northeast Fisheries Science Center (NEFSC) from 1969-1972 showed that Pleuronectiformes occurred in the stomachs of the following piscivores: spiny dogfish, goosefish, cod, silver hake, red hake, spotted hake, sea raven, longhorn sculpin, and fourspot flounder (Bowman et al. 1976). These data do not indicate the proportion of summer flounder among the flatfish prey taken, but it is likely that they are represented.

Lab studies in Georgia by Reichert and van der Veer (1991) on juveniles from the Duplin River found potential predators to be blue crabs (*Callinectes* spp.) and sea robins (*Prionotus* spp.).

Spatial co-occurrence and dietary overlap among summer flounder, scup, and black sea bass have been previously documented (Musick and Mercer 1977; Gabriel 1989; Shepherd and Terceiro 1994). For example, the composition and distribution of fish assemblages in the Middle Atlantic Bight was described by Colvocoresses and Musick (1979) by subjecting NEFSC bottom trawl survey data to the statistical technique of cluster analysis. Summer flounder, scup, northern sea robin, and black sea bass, all warm temperate species, were regularly classified in the same group during spring and fall. In the spring this group was distributed in the warmer waters on the southern shelf and along the shelf break at depths of approximately 152 m. During the fall this group was distributed primarily on the inner shelf at depths of less than 61 m where they were often joined by smooth dogfish.

All of the natural predators of adult summer flounder are not fully documented, but larger predators such as large sharks, rays, and goosefish probably include summer flounder in their diets. Laboratory studies by Lascara (1981) on flounder from lower Chesapeake Bay suggest that in patchy seagrass/sand habitats, the flounder may avoid predation by staying in the sand near the seagrass beds, rather than in the grass beds themselves.

Abundance and status of stocks

The Northeast Fisheries Science Center's Southern Demersal Working Group met in June 2006 to conduct an annual evaluation of summer flounder stock status. The assessment update indicates that the stock is not overfished but overfishing is occurring relative to the biological reference points detailed in Amendment 12. The fishing mortality rate estimated for 2005 is 0.53, which is a significant decline from the 1.32 estimated for 1994 but above the threshold F of 0.276. In addition, total stock biomass has increased substantially since 1989 to 105 million lb

(47.8 million kg) in 2005, slightly above the current biomass threshold of 102 million lb (46.3 million kg). Spawning stock biomass has increased since 1993 to 67.5 million lb (30.6 million kg) in 2005.

Recruitment declined from 1983 to 1988, with the 1988 year class being the weakest at only 13 million fish. Recruitment since 1988 has generally improved, although the 2005 year class is estimated to be well below the median at 14.5 million fish.

An update and peer review of the summer flounder assessment and reference points was conducted by the National Marine Fisheries Service (NMFS) Office of Science and Technology (S&T) during September 14-15, 2006. The 2006 S&T Peer Review Panel recommendations required revision to the summer flounder VPA, biological reference point, and projection calculations. The revised analytical results supersede those presented in the Terceiro (2006) assessment.

The summer flounder stock is not overfished but overfishing is occurring relative to the 2006 S&T Peer Review Panel updated biological reference points. Fishing mortality calculated from the average of the currently fully recruited ages (3-5) was very high during 1982-1997, varying between 0.9 and 2.2. The fishing mortality rate has declined since 1997 and was estimated to be about 0.4 during 2003-2005. The estimate of F for 2005 (0.407) is 45% above the updated FMSY proxy = Fmax = 0.280; therefore overfishing is occurring. The estimate of F for 2005 may understate the actual fishing mortality, as retrospective analysis shows that the current assessment method tends to underestimate recent fishing mortality rates, continuing the pattern observed in recent assessments (NEFSC 2000, MAFMC 2001, NEFSC 2002, Terceiro 2003, SDWG 2004, NEFSC 2005, Terceiro 2006). Over the last 5 years, the annual retrospective increase in fishing mortality has averaged 34%.

Stock biomass (Jan 1; age 1+) increased substantially during the 1990s and through 2005 but decreased slightly in 2006 to 51.317 mt. Spawning stock biomass (SSB; Age 0+) declined 69% from 1983 to 1989 (22,582 mt to 7,025 mt), but with improved recruitment and decreased fishing mortality had increased to 47,498 mt by 2005. The estimate of SSB for 2005 (47,498) is 53% of the updated BMSY proxy = SSBmax = 89,411 mt; therefore the stock is not overfished. Retrospective analysis shows a tendency to overestimate the SSB in the most recent years, continuing the pattern observed in recent assessments (NEFSC 2000, MAFMC 2001, NEFSC 2002, Terceiro 2003, SDWG 2004, NEFSC 2005, Terceiro 2006). Over the last 5 years, the annual retrospective decrease in SSB has averaged 12%.

The 1982 and 1983 year classes were the largest of the VPA series, at 74 and 80 million fish, respectively. The 1988 year class was the smallest of the series, at only 13 million fish. The arithmetic average recruitment from 1982 to 2005 is 37 million fish at age 0, with a median of 33 million fish. The 2005 year class is estimated to be the smallest since 1988, at about 15 million fish.

Retrospective analysis shows a variable pattern in the estimation of recruitment; over the last 5 years, the annual retrospective increase in recruitment has averaged 4%.

The precision and bias of the 2005 fishing mortality rates, 2006 stock sizes, and 2005 SSB estimates are presented in Appendix A of the ASMFC 2006 Plan Review document (ASMFC, 2006). Bias was generally less than 10% for estimated parameters estimated. The bootstrap estimate of the 2005 SSB was relatively precise, with a corrected CV of 11%. There is an 80% chance that SSB in 2005 was between 39,900 and 57,200 mt. The bootstrap estimate of the 2005 F had a corrected CV of 43%. There is an 80% chance that F in 2005 was between about 0.33 and 0.57.

4.2.14 Bluefish

From the NEFSC EFH source document for Bluefish (2006).

Description and Distribution

The bluefish, *Pomatomus saltatrix*, ranges in the western North Atlantic from Nova Scotia and Bermuda to Argentina, but it is rare between southern Florida and northern South America (Robins et al. 1986). They travel in schools of like-sized individuals and undertake seasonal migrations, moving into the Middle Atlantic Bight (MAB) during spring and south or farther offshore during fall. Within the MAB they occur in large bays and estuaries as well as across the entire continental shelf. Juvenile stages have been recorded from all estuaries surveyed within the MAB, but eggs and larvae occur in oceanic waters (Able and Fahay 1998). Bluefish growth rates are fast and they may reach a length of 1.1 m (3.5 ft) and a weight of 12.3 kg (27 lbs) (Bigelow and Schroeder 1953). They live to ages 12 and greater (Salerno et al. 2001).

Juveniles occur in estuaries, bays, and the coastal ocean of the MAB and South Atlantic Bight (SAB), where they are less common. They occur in many habitats, but do not use the marsh surface. Juveniles begin to depart MAB estuaries in October and migrate south to spend the winter months south of Cape Hatteras.

The spring and fall distributions of juvenile bluefish (< 30 cm) relative to bottom water temperature, depth, and salinity are based on 1963-2003 Northeast Fisheries Science Center (NEFSC) bottom trawl surveys from the Gulf of Maine to Cape Hatteras. In the spring, they were found over a temperature range of 8-23°C, with most spread between about 10-19°C. They were found at shallow depths ranging from 1-40 m, with the majority at 1-30 m. Their salinity range was between 33-36 ppt, with a peak in occurrence and catch at 33 ppt. In the fall, the juveniles were spread over a temperature range of 10-28°C, with most between about 17-25°C. They were also found at shallow depths of 1-50 m, with > 60% found at 11-20 m. Their salinity range was between 29-35 ppt, with the majority at 31-32 ppt.

Adult bluefish are blue-green above, silvery below, moderately stout-bodied, and armed with stout teeth along both jaws (Figure 4.2-9). The snout is pointed and the mouth is large and oblique. The caudal fin is large and forked. The fin ray formulae are first dorsal: 7-9 spines; second dorsal: 1 spine and 23-26 rays; anal: 2-3 spines and 25- 28 rays. Vertebrae number 26. The maximum length is about 115 cm and maximum weights are 4.5-6.8 kg, although an occasional heavier fish has been taken. The maximum age is 12 years. The sex ratio is 1:1 for all age groups (Boreman 1982), although Lassiter (1962) reported a ratio of two females per male in North Carolina and Hamer (1959) found a ratio of three females to two males in New Jersey.

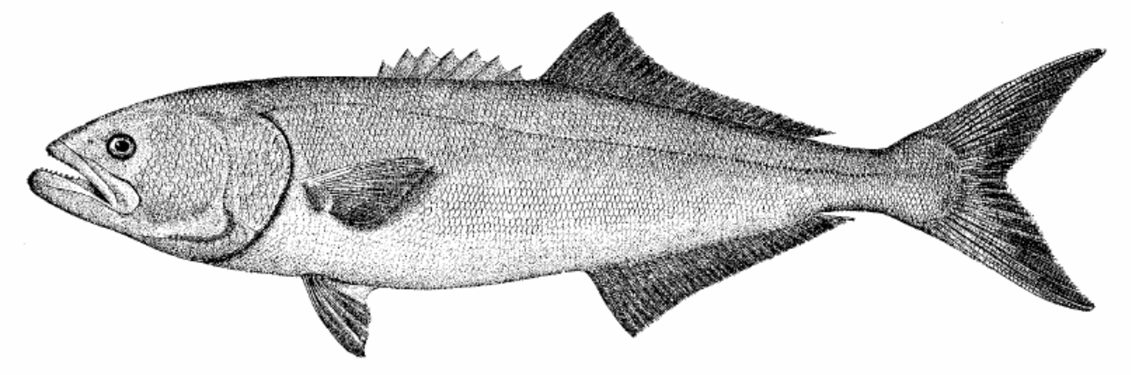


Figure 4.2-9. The adult bluefish, *Pomatomus saltatrix* (from Goode 1884).

Adult bluefish occur in the open ocean, large embayments, and most estuarine systems within their range. Although they occur in a wide range of hydrographic conditions, they prefer warmer temperatures and are not found in the MAB when temperatures decline below 14-16°C.

Reproduction

A seminal study, based largely on the distribution of eggs and larvae, concluded that there were two discrete spawning events in western Atlantic bluefish. The first occurs during March-May near the edge of the continental shelf of the SAB. The second occurs between June and August in the MAB (Kendall and Walford 1979). Recent studies have re-examined this conclusion and refined our knowledge of a complex reproductive pattern, and support the concept of a single, migratory spawning stock (Hare and Cowen 1993; Smith et al. 1994). Sexual maturity and gonad ripening occur in early spring off Florida, early summer off North Carolina, and late summer off New York (Hare and Cowen 1993). In the New York Bight, gonadosomatic studies indicate that both sexes are ripe or ripening between June and September with a strong peak in July (Chiarella and Conover 1990). Larvae re-occur in the SAB in the fall (Collins and Stender 1987) and there are also indications that gonads reach a second peak in ripeness in fish off Florida in September. Most bluefish are mature by age 2 (Deuel 1964). A recent study using histological methods indicates that bluefish are likely group-synchronous batch spawners (Reiss et al. 2002). In South Africa, individuals may spawn repeatedly over a period of 5-6 months (Van der Elst 1976), but there is no comparable information for the U.S. population.

Development, growth and movement patterns

Eggs from the MAB are pelagic and spherical with a diameter of 0.95-1.00 mm. They have a smooth, transparent shell and a homogeneous yolk. The single oil globule is 0.26-0.29 mm in diameter and the perivitelline space is narrow (Fahay 1983). Incubation times depend on temperature. At 18.0-22.2°C, hatching occurs after 46-48 h (Deuel et al. 1966). Eggs from the SAB have not been described.

Larvae are 2.0-2.4 mm long when they hatch; the eyes are unpigmented and the mouth parts are undeveloped. Characteristic pigment includes parallel lines of melanophores along the dorsal fin base, body midline, and anal fin base. Teeth are well developed at 4.3 mm and fin rays are complete at a size of about 13- 14 mm (Fahay 1983). Larvae rarely occur deeper in the water column than 15 m; most are concentrated at a depth of about 4 m during the day, but they are about equally distributed between that depth and the surface at night (Kendall and Naplin 1981). The bluefish transforms from a larva to a “pelagic-juvenile” stage that is specially adapted for an oceanic, near-surface existence after completion of fin ray development. This specialized stage is characterized by a silvery, laterally compressed body, with dark blue counter-coloration on the dorsum. This transition occurs at an age of 18-25 d and at a size of 10-12 mm SL (Hare and Cowen 1994). Scales begin to form at about 12 mm on the posterior part of the lateral line region, then proceed forward, until the head is completely scaled at about 37 mm (Silverman 1975).

Swimming ability in many fish species dramatically improves during this transformation (e.g. Hunter 1981; Stobutzki and Bellwood 1994; Leis et al. 1996) and this improvement presumably applies to bluefish as well. It is during this stage that bluefish arrive at nursery areas in the central part of the MAB, after advection via the Gulf Stream from spawning areas in the SAB and after crossing the Slope Sea (Hare and Cowen 1996; Hare et al. 2001) and the continental shelf (Cowen et al. 1993).

Active larval migration across the shelf is believed to be aided by oceanographic features such as warm-core ring streamers and Gulf-Stream filaments (Hare et al. 2001), or Eckman transport (Munch and Conover 2000). This transport (active or passive) is crucial to the recruitment of these progeny to vital estuarine nursery areas, and therefore this life history stage might be considered a critical bottleneck.

Juveniles have a usual fish shape without unusual features. The caudal fin is forked and the body is somewhat laterally compressed, with a silvery, unpatterned color. The mouth is large and oblique and all fin spines are strong. Two distinct dorsal fins touch at their bases; the second dorsal fin is about the same length as the anal fin base (Able and Fahay 1998). The spring-spawned cohort is 60-76 d old with a mean size of 60 mm when they recruit to estuarine habitats in the MAB in late May to mid-June (McBride and Conover 1991; Cowen et al. 1993). The summer-spawned cohort either remains in coastal nursery areas (Kendall and Walford 1979; Able and Fahay 1998; Secor et al. 2002; Able et al. 2003) or enters estuarine nurseries in mid- to late August when they are 33-47 d old with a mean length of 46 mm (McBride and Conover 1991).

Juveniles of both cohorts depart MAB estuaries and coastal areas in October and migrate to waters south of Cape Hatteras, North Carolina. At this time, members of both cohorts range from 4-24 cm long (Able and Fahay 1998, Able et al. 2003). During most years, the spring-spawned cohort dominates in the emigrating young-of-the-year, although during the past decade, the summer-spawned cohort was dominant (Conover et al. 2003).

Ecological relationships

Food Habits

During their oceanic larval stage, bluefish primarily consume copepods. Fish begin to be included in their diet at sizes of 30 mm, and by 40 mm, fish are the major diet item. Soon after this shift in diet, juveniles migrate inshore to occupy estuarine habitats (Marks and Conover 1993). The results of several studies suggest that bluefish juveniles and adults eat whatever taxa are locally abundant (Table 4.2-6). The components of young-of-theyear bluefish diet in Sandy

Hook Bay, New Jersey and the effects of those components on condition were studied over a three-year period (Friedland et al. 1988). Fish dominated the diet during 1981, while crustaceans and polychaetes were more important during 1983 and 1984. Weight-length relationships indicated that weight at length was significantly greater in 1981 than in the other two years. Thus, not only does the quality of diet differ between estuaries, but the method of foraging may also differ; more benthic foraging was evident in bluefish from Sandy Hook Bay than in bluefish sampled in estuaries in Delaware (Grant 1962) and North Carolina (Lassiter 1962). In the Chesapeake Bay, oyster bar and reef habitats provide an important source of benthic prey, particularly during time periods when preferred small pelagic fish prey are less abundant (Harding and Mann 2001). Depending on age class, diets might change through a season. Spring spawned young-of-the-year prey on invertebrates such as small and shrimp in early summer when the preferred fish prey are less available (Juanes et al. 2001). In Chesapeake Bay, diets of three age classes differed through the summer (Table 4.2-6), but all three concentrated on *Brevoortia tyrannus* in the fall (Hartman and Brandt 1995a, b).

In ocean habitats, young-of-the-year bluefish switch to piscivory with increasing size, similar to estuarine habitats. By 80-100 mm FL bay anchovy become the primary fish prey along ocean beaches in New Jersey (Able et al. 2003). Similar dietary patterns have been observed in juvenile bluefish utilizing ocean habitat in coastal Maryland (Secor et al. 2002) and throughout the MAB (Table 4.2-6). During offshore residence as larger adults, bluefish target larger schooling species of prey such as squids, clupeids and butterfish (Table 4.2-6) (Buckel et al. 1999).

Table 4.2-6. Dietary items of bluefish from several study areas.

Source	**Life History Stage and Study Location**	**Diet Items (in order of importance)**
Texas Instruments Incorporated (1976)	Young-of-the-year, Hudson River (tidal)	*Anchoa mitchilli* (dominated diet through summer), Clupeidae, *Microgadus tomcod*, *Alosa sapidissima*, *Notropis hudsonius*, Cyprinodontidae
Festa (1979)	11-20 cm, Little Egg Harbor estuary, NJ	*Fundulus* spp., Atherinidae, *Anchoa* spp., *Callinectes sapidus*, *Brevoortia tyrannus*, *Crangon septemspinosa*
Friedland et al. (1988)	Juvenile, Sandy Hook, NJ	1981: Teleosts, Crustacea, Polychaeta 1982: Crustacea, Teleostei, Polychaeta 1983: Crustacea, Teleostei, Polychaeta (weight at length significantly greater in 1981)
Hartman and Brandt (1995a, b)	Age 0, Age 1, and Age 2, Chesapeake Bay (Diets of all age classes changed through season)	Age 0: *Anchoa mitchilli*, *Menidia menidia*, *Brevoortia tyrannus* Age 1: *Leiostomus xanthurus*, *A. mitchilli*, *M. menidia*, *B. tyrannus* Age 2: *Micropogonias undulatus*, *A. mitchilli*, *B. tyrannus*

		(*B. tyrannus* becomes important in diets of all age classes in Sep-Oct.)
Buckel and Conover (1997)	Young-of-the-year, Hudson River estuary	Unidentified fish, *Anchoa mitchilli*, *Alosa* spp., *Morone saxatilis*, *Morone americana*
Buckel et al. (1999)	Young-of-the-year, Hudson River estuary	*Morone saxatilis*, *Anchoa mitchilli*, *Menidia menidia*, *Alosa* spp.
Buckel et al. (1999)	Georges Bank and Middle Atlantic Bight continental shelf Young-of-the-year Adult	1994-1995 Bay anchovy, squid, butterfish, striped anchovy, round herring Squid, butterfish, and clupeids.
Juanes et al. (2001)	Young-of-the-year, Great South Bay, NY	Sand shrimp, YOY *Menidia* spp., unidentified fish, menhaden, sand worms
Harding and Mann (2001)	20 – 40 cm Chesapeake Bay	Other fish, polychaete worms, clupeids, unidentified fish, crustacea.
Buckel and McKown (2002)	New York Bight embayments (western Long Island and Staten Island) Young-of-the-year	*Menidia menidia*, *Anchoa mitchilli*, unidentified fish, sand shrimp, mysids, amphipods, polychaete worms, other invertebrates
Able et al. (2003)	Coastal NJ, ocean beaches Young-of-the-year	*Anchoa* spp., unidentified fish, decapods, *Menidia* spp., copepods, amphipods
NEFSC food Habits database [sampling conducted during seasonal surveys on the continental shelf from the Gulf of Maine to Cape Hatteras from 1973 to the present; see	All ages (mean size 35.6 mm FL), continental shelf, Georges Bank and Middle Atlantic Bight Small (< 30 cm FL)	1973-1980: Unidentified fish, *Illex* spp., *Etrumeus teres*, *Loligo* spp., *Peprilus triacanthus*, Cephalopoda 1981-2003: *Anchoa* spp., Unidentified fish, *Peprilus triacanthus*, *Ammodytes dubius*, *Loligo* spp., *Clupea harengus*

Link and Almeida (2000) for methodology]	Medium (>30 cm to < 70 cm FL)	1981-2003: *Clupea harengus*, Unidentified fish, squids, *Peprilus triacanthus*, *Anchoa* spp.,
	Large (> 70 cm FL)	1981-2003: Unidentified fish, squids, *Clupea harengus*, gadids, *Ammodytes* spp., *Anchoa* spp., flatfish, sculpins, butterfish

Predation

Sharks, tunas, and billfishes are the only predators large and fast enough to prey on adult bluefish. They are a major component in the diet of shortfin mako shark, composing 77.5% of the diet by volume (Stillwell and Kohler 1982; Wood 2002). Stillwell and Kohler (1982) estimated that this shark may consume between 4.3 and 14.5% of the bluefish resource between Georges Bank and Cape Hatteras. Bluefish also ranked fourth in number and occurrence and third in volume in swordfish diets, especially off the Carolinas (Stillwell and Kohler 1985). A study of bluefin tuna diet in New England ranked bluefish as one of the top prey items (Chase 2002). Blue sharks and sandbar sharks also prey on bluefish (Kohler 1988; Medved et al. 1985). Young-of-the-year are preyed upon by four oceanic bird species, the Atlantic puffin, Arctic tern, common tern, and roseate tern (Creaser and Perkins 1994; Safina et al. 1990). Cannibalism has only rarely been reported, but occurs in age 1 and older year classes in North Carolina (Lassiter 1962), and bluefish compose a minor component of the diet of larger bluefish collected during NEFSC bottom trawl surveys on the continental shelf from the Gulf of Maine to Cape Hatteras [NEFSC food habits database; see Link and Almeida (2000) for details on methodology].

Migrations

Bluefish are warm water migrants and do not occur in MAB waters at temperatures < 14-16°C (Bigelow and Schroeder 1953). They generally move north in spring-summer to centers of abundance in the New York Bight and southern New England and south in autumn-winter to the waters in the SAB as far as southeastern Florida. There is a trend for larger individuals to occur farther north during the summer (Wilk 1977). Larger adults may limit their southward migration and spend the winter on the outer part of the continental shelf of the MAB, culminating in an aggregation of fish near Cape Hatteras, NC by March.

This winter distribution is suggested by the occurrence of bluefish in commercial catches as reported in vessel logbooks (Shepherd et al., in press). This conclusion is also supported by historical anecdotal evidence. One report witnessed a single fish landed from about 100 m deep off Martha's Vineyard during mid-January 1950 and several hauls of 80-640 kg from the vicinity of Hudson Canyon during early February of the same year (Bigelow and Schroeder 1953). Another study simply reported "boats engaged in the winter trawl fishery for fluke and scup along the outer margin of the continental shelf often bring in a few bluefish" (Hamer 1959). These reports have been perpetuated since (Lund 1961; Miller 1969; Lund and Maltezos 1970; Hardy 1978). Recent winter trawl surveys indicate the presence of bluefish in the MAB during winter near the shelf edge off Cape Hatteras.

Abundance and status of stocks

The Southeast Area Monitoring and Assessment Program (SEAMAP) surveys sampled the coastal region between Cape Hatteras, North Carolina and Cape Canaveral, Florida [see Reid et al. (1999) for details]. After an initial several years when gear and methods were not standardized, methodology became synoptic and standardized between 1990 and 1996 (Beatty and Boylan 1997; Boylan et al. 1998). Bluefish collected during the latter survey period are shown in Figure 4.2-10a. Length frequencies of these collections indicate most were young-of-the-year or age 1 (Figure 4.2-10b). Information on distributions over the offshore portions of the SAB shelf are lacking for any size class. Monthly occurrences of these bluefish are shown in Figure 4.2-10c. Occurrences decreased during spring, were at low levels during summer, and increased during October beginning in the northern part of the bight, which suggests an influx of migrating young-of-theyear from the MAB.

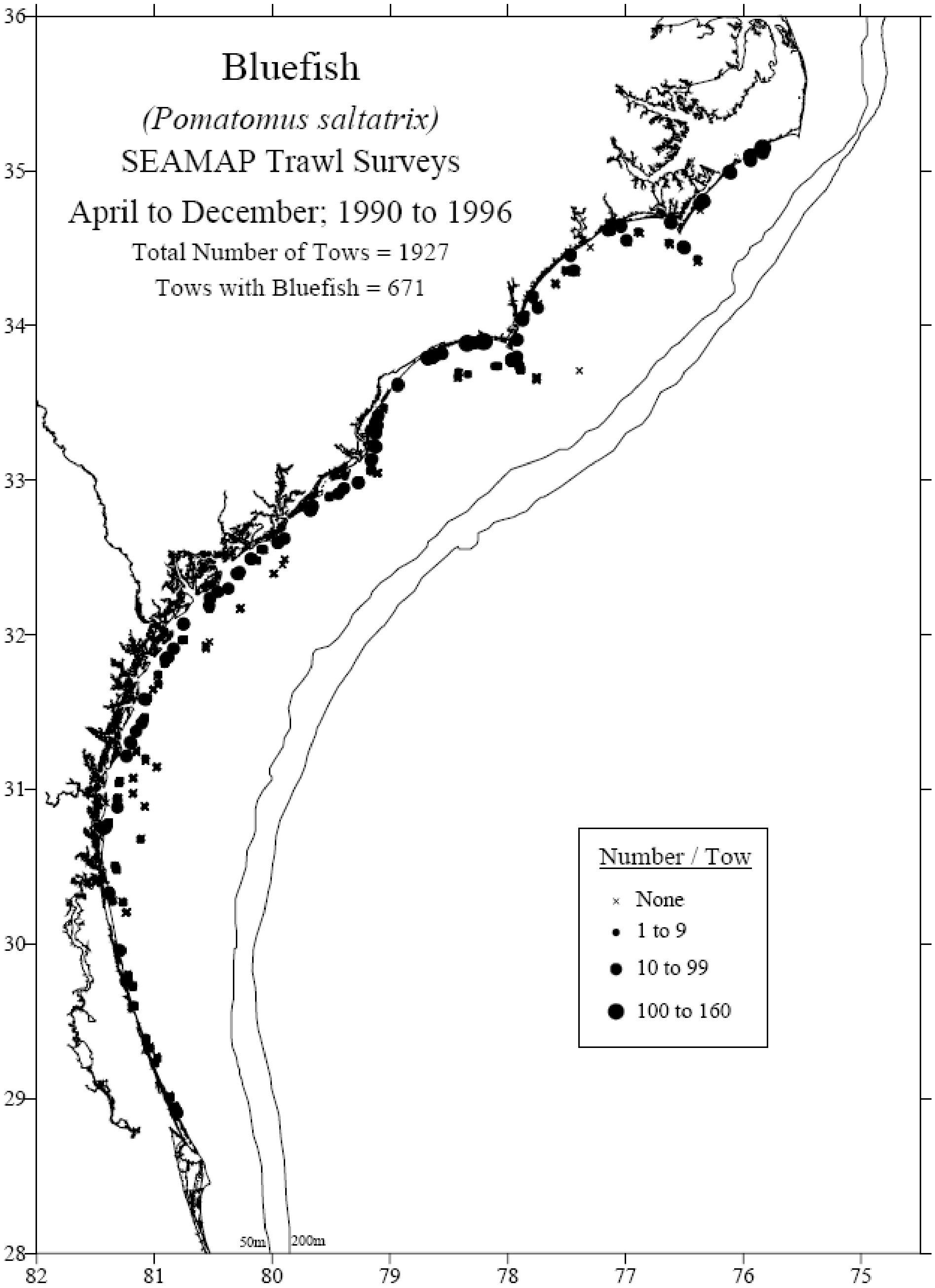


Figure 4.2-10a. Distribution and abundance of bluefish in the South Atlantic Bight collected during SEAMAP bottom trawl surveys [1990-1996, all years combined; see Reid et al. (1999) for details].

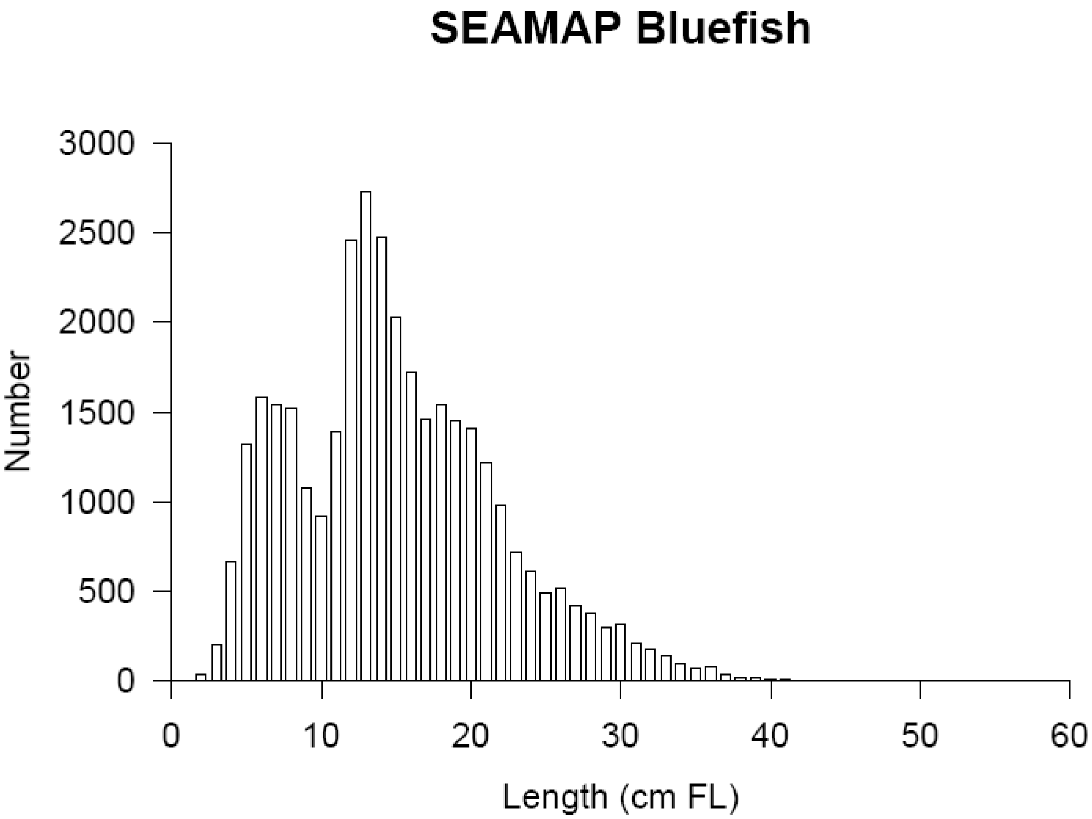


Figure 4.2-10b. Length frequency distribution of bluefish in the South Atlantic Bight collected during SEAMAP bottom trawl surveys (1990-1996, all years combined).

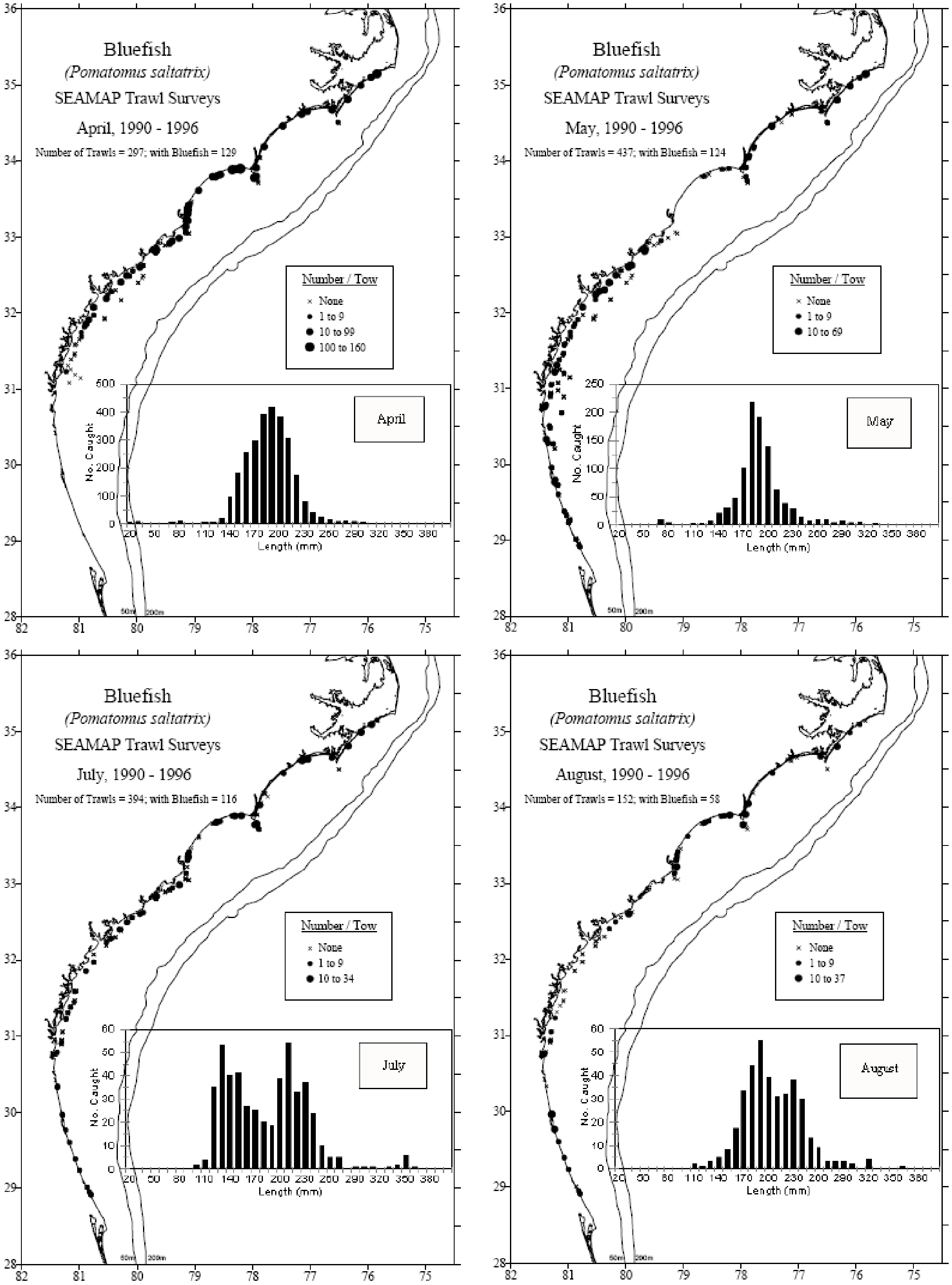


Figure 4.2-10c. Monthly distribution, abundance, and length frequency distribution of bluefish in the South Atlantic Bight collected during SEAMAP bottom trawl surveys (1990-1996, all years combined).

The 2003 update on the status of the stock indicated that fishing mortality rates on bluefish peaked in 1987 at F=0.718 and declined to F=0.184 in 2002. The current stock assessment estimates F=0.19, well below the 2003 and 2004 targets, 0.41 and 0.31, respectively. According to the biological reference points in Amendment 1, the stock is overfished but overfishing is not occurring. However, new biological reference points updated in 2005, but yet to be peer approved, suggest that the stock is not overfished and overfishing is not occurring. The total stock biomass is estimated at 92.3 million pounds for 2004.

4.2.15 Horseshoe Crab

Description and Distribution

(from ASMFC's Species Profile)
Although they are called horseshoe "crabs," they are neither a decapod nor a crustacean but are in their own class that is more closely related to the arachnids (i.e., spiders).
Horseshoe crabs have existed for more than 200 million years; however, some identify the evolutionary existence of horseshoe crabs to be over 400 million years.

Horseshoe crab distribution extends along the Atlantic coast from northern Maine to the Yucatan Peninsula and the Gulf of Mexico. Along the U.S. Atlantic coast, horseshoe crabs are most abundant between Virginia and New Jersey, with the Delaware Bay at the center of the species distribution and the location of the largest population.

Horseshoe crabs are typically associated with estuarine habitats. Adults either remain in the estuary or migrate to the continental shelf during the winter months. Migrations resume in the spring when the horseshoe crabs move to beach areas to spawn.
Juveniles hatch from the beach environment and spend the first two years in nearshore shallow, subtidal flats.

Reproduction

(from ASMC's Species Profile)
Spawning usually coincides with the high tide during the full and new moon. Breeding activity is consistently higher during the full moon than the new moon and is also greater during the night. Adults prefer sandy beach areas within bays and coves that are protected from surf. Eggs are laid in clusters or nest sites along the beach with females laying approximately 88,000 eggs per year in different egg clusters.

(from ASMFC's Horseshoe Crab FMP 1998)
Spawning adults prefer sandy beach areas within bays and coves that are protected from wave energy. Beach habitat also must include porous, well-oxygenated sediments to provide a suitable environment for egg survival and development (Botton, et al., 1988). Optimal spawning areas are limited by the availability of suitable sandy beach habitat. However, spawning may occur along peat banks if there is sand in the upper intertidal regions and along the mouths of salt marsh creeks (Botton, 1995). Shuster (1996) states that spawning may occur along muddy tidal stream banks, but not on peat banks because adults are sensitive to hydrogen sulfide and anaerobic conditions.

Spawning habitat varies throughout the horseshoe crab range. In Massachusetts, New Jersey, and Delaware, beaches are typically coarse-grained and well-drained as opposed to Florida beaches, which are typically fine-grained and poorly drained. These differences affect nest-site selection and nesting synchrony (Penn and Brockmann, 1994).
Thompson (1998) found that preferentially selected spawning sites were located adjacent to large intertidal sand flat areas, which provide protection from wave energy and an abundance of food for juveniles.

Development, growth and movement patterns

Nursery Habitat

The shoalwater and shallow water areas of bays (e.g., Delaware Bay and Chesapeake Bay) are essential nursery areas (Botton, 1995). Juveniles usually spend their first two years on intertidal sand flats (Rudloe, 1981).

Thompson (1998) also found significant use of sand flats by juvenile horseshoe crabs in South Carolina. However, older juveniles and adults are exclusively subtidal, except during spawning.

Adult Habitat

Specific requirements for adult habitat are not known. Although horseshoe crabs have been taken at depths >200 meters, Botton and Ropes (1987a) suggest that adults prefer depths <30 meters. The NMFS Northeast Fishery Center bottom trawl surveys collected 92 percent of their horseshoe crabs at these depths, even though 73 percent of the sampling effort was expended in depths >27 meters. During spawning season adults typically inhabit bay areas adjacent to spawning beaches and feed on bivalves. In the fall, adults may remain in bay areas or migrate into the Atlantic Ocean to overwinter on the continental shelf.

Ecological relationships

(from ASMFC's Species Profile)

Horseshoe crab eggs play an important ecological role in the food web for migrating shorebirds and finfish. The Delaware Bay Estuary is the largest staging area for shorebirds in the Atlantic Flyway and an estimated 425,000 to one million migratory shorebirds converge on the Delaware Bay to feed and rebuild energy reserves prior to completing their northward migration. Horseshoe crabs also provide an important food source for Atlantic loggerhead turtles.

Juvenile and adult horseshoe crabs feed mainly on mollusks, although they also prey on a variety of benthic organisms and vascular plants. The horseshoe crab must molt or shed its chitinous exoskeleton to grow and can increase size by up to 25 percent after each molt. Molting occurs several times during the first two to three years of a horseshoe crab's life. As it grows larger, more time occurs between molts. It usually takes 17 molts to reach sexual maturity (9 – 12 years).

(from 1998 FMP)

Shorebirds

The Delaware Estuary is the largest staging area for shorebirds in the Atlantic Flyway and is the second largest staging site in North America (New Jersey Division of Fish, Game and Wildlife, 1994). An estimated 425,000 to 1,000,000 migratory shorebirds converge on the Delaware Bay to feed and rebuild energy reserves prior to flying an additional 4,000 kilometers to complete their northward migration (Wander and Dunne, 1982; Dunne et al., 1982; Clark et al., 1993). Migratory shorebirds arrive in Delaware Bay and adjacent areas along the Atlantic coast at the peak of horseshoe crab mating in mid-May through early-June, typically spending two weeks in the area. Clark (1996) stated that the number of shorebirds coming to the Delaware Bay on spring migrations is between 900,000 and 1.5 million from six species. At least 11 species of migratory birds use horseshoe crab eggs to replenish their fat supply during their trip from South American wintering areas to Arctic breeding grounds (Myers, 1986). The principal shorebirds observed include ruddy turnstone (*Arenaria interpres*), red knot (*Calidris canutus*), semipalmated sandpiper (*Calidris pusilla*), sanderling (*Calidris alba*), dowitcher (*Limnodromus* spp.), and dunlin (*Calidris alpina*) (Dunne et al., 1982). Other shorebirds frequenting sandy beaches include western sandpiper (*Calidris mauri*), the federally listed (threatened) piping plover (*Charadrius melodus*), black-bellied plover (*Pluvialis squatarola*), semipalmated plover (*Charadrius semipalmatus*), and willet (*Catoptrophorus semipalmatus*) (Burger, et al., 1977). The dominant species of shorebirds that use the Delaware Bay for staging are the red knot, ruddy turnstone, semipalmated sandpiper, and sanderling, representing approximately 88 percent of all shorebirds within the Delaware Bay (Gelvin-Innvaer, 1996).

The Delaware Bay staging area is unique and of particular importance to shorebirds for the following reasons: shorebirds use few major stopovers during the spring migration; shorebirds arrive at stopover sites with little or no fat reserves; and, shorebirds demonstrate fidelity to staging areas (Wander and Dunne, 1982). An estimated 80 percent and 30 percent of the hemispheric population of red knots and sanderlings, respectively, use the Delaware Bay as a staging area (American Bird Conservancy, 1997).

Despite high shorebird abundance within the Delaware Bay, counts of sanderlings and semipalmated sandpipers declined significantly over a 7-year period from 1985 to 1992 (Clark et al., 1993). The decline in shorebirds in the Delaware Bay between 1986 and 1997 is statistically significant ($p<0.05$) (Clark and Niles, unpublished data, 1997).

The Delaware Division of Fish and Wildlife also reports a 45 percent decline in peak counts of shorebirds from 1990-1996 compared to data from 1986-1989. The International Shorebird Survey also indicated a decline in sanderlings between 1975 and 1983. Declines in shorebird numbers may be the result of several threats, including the potential overharvest of horseshoe crabs.

During the 2-3 week staging period, shorebirds undergo weight gains of 40 percent or more (e.g., increasing body weight from 54 to 79 grams over 3 weeks) (Myers, 1986). Much of this weight gain results from feeding on horseshoe crab eggs. In particular, sanderlings are estimated to consume as much as 30.9 grams of eggs per day per bird (approximately 8,300 eggs / day / bird). However, the estimated overall metabolic efficiency is low (i.e., 39 percent) and is among the lowest recorded value of a vertebrate feeding on food of animal origin, based on experiments on captive birds (Castro et al., 1989). Low metabolic efficiency is attributable to the high percentage of eggs that pass through the bird's digestive tract unbroken. Metabolic efficiency of broken horseshoe crabs eggs is much higher (e.g., 69 percent) than the metabolic efficiency of unbroken horseshoe crab eggs (Castro et al., 1989).

Tsipoura and Burger (1998) indicate that under natural conditions, assimilation efficiency of horseshoe crab eggs may be higher than suggested by Castro et al. (1989) because sand in the diet may assist in breaking and grinding down horseshoe crab eggs. Shorebirds require high daily energy inputs due to their high basal metabolic rates. In addition, shorebirds typically have high daily energy expenditures, and are among the longest-distance migrant animals in the world (Kersten and Piersma, 1987; Myers et al., 1985). Castro et al. (1989) concluded that sanderlings (and possibly other shorebirds) compensate for low metabolizable energy of horseshoe crab eggs by consuming large quantities of eggs. This is possibly due to the sheer abundance of eggs, the ease in obtaining them, and the rapidity in which they pass through the digestive tract.
Rather than probing below the surface of the substrate, shorebirds typically forage for horseshoe crab eggs as the eggs are uncovered by successive waves of nesting crabs and erosion from localized storms (Botton et al., 1994).

Horseshoe crab eggs are the most abundant food item on Delaware Bay beaches during the migratory staging of shorebirds. Botton et al. (1994) found few other available macroinvertebrates and concluded that shorebirds are feeding primarily on horseshoe crab eggs, largely because of their abundance. However, it is likely that shorebirds supplement their diet with ingestion of other food items during the stopover period (Botton, 1984b).

Macroinvertebrate densities on the Delaware Bay beaches rarely exceeded 200/m2 during horseshoe crab spawning season and are several orders of magnitude less than horseshoe crab egg densities. As a result, shorebirds showed a preference for beaches with higher number of horseshoe crab eggs (Botton et al., 1994). Access to horseshoe crab eggs by shorebirds may be limited by tidal cycle, human disturbance, and competition among shorebirds and gulls. Burger et al. (1996) concluded that a mosaic of habitat types ranging from mudflats to high marshes is essential to sustain the high population of shorebirds using Delaware Bay during spring migration. In addition, Burger et al. (1996) documented the importance of marshes for foraging in several species of shorebirds. Shorebirds do abandon beaches at night to roost in isolated marshes. This is believed to be related to reducing risk of predation by nocturnal wildlife (Bryant and Pennock, 1991). Clark et al. (1993) estimated that only 15-20 percent of semipalmated sandpipers and up to 30 percent of dunlins were observed in salt marshes (feeding on prey other than horseshoe crab eggs), as opposed to beaches.

Forage data (stomach contents) collected from sanderlings, ruddy turnstones, least sandpipers, semipalmated sandpipers, dunlins, and red knots on Delaware Bay beaches along the New Jersey coast (N=70) indicate that horseshoe crab eggs represent the majority of food items taken by shorebirds (15 to 95 percent) in 1996 and 1997, averaging 57.3 percent (Tsipoura and Burger, 1998). As such, horseshoe crab eggs were not taken to the exclusion of other items, such as polychaete worms and arthropods. Based on fat-free weights, red knot, ruddy turnstone, sanderling, and semipalmated sandpiper increased body mass up to 70 to 80 percent while staging on Delaware Bay (Tsipoura and Burger, 1998). This rate of weight gain is the highest recorded for any stopover site in the world and is considered to be the result of feeding on horseshoe crab eggs. Additionally, Tsipoura and Burger (1998) reported that the mass movement of shorebirds (from the New Jersey side to the Delaware side of the Delaware Bay) is correlated with availability of horseshoe crab eggs. The ruddy turnstone provides one possible exception to the interaction between horseshoe crab egg availability and bird distribution. These birds use their bill to dig into the sand and make holes that are several inches deep, thereby reaching the eggs that are buried deeper in the substrate.

Tsipoura and Burger (1998) found high concentrations of egg membranes in gut samples of ruddy turnstones that were captured on Thompson's Beach, New Jersey and hypothesized that the decline in abundance of surface eggs may not have been a deterrent to the foraging success of this species, as long as there were still sufficient numbers of eggs available in the lower strata.

Despite significant shorebird predation on horseshoe crab eggs, such activity probably has little impact on the horseshoe crab population (Botton et al., 1994). Horseshoe crabs place egg clusters at depths greater than 10 centimeters, which is deeper than most short-billed shorebirds can reach. Horseshoe crab eggs brought to the surface by wave action and burrowing activity by spawning horseshoe crabs that are available for shorebird predation would probably not survive to hatching due to heat stress or desiccation (Botton et al., 1994). Additionally, horseshoe crabs continue to spawn at least one month after the departure of most of the shorebirds. Horseshoe crab larval densities have been observed regularly exceeding 100,000/m2 in July and August (Botton et al., 1992). For these reasons, it is unlikely that shorebird predation has a substantial adverse impact on the reproductive success of horseshoe crabs in Delaware Bay.

The food supply provided by horseshoe crab eggs in Delaware has been estimated at 320 tons (Delaware Department of Natural Resources and Environmental Control, 1987). Castro and Myers (1993) estimated the total energy requirement of shorebirds and calculated that 539 metric tons of horseshoe crab eggs would be needed to sustain the spring migration of shorebirds through the Delaware Bay (assuming the shorebirds ate only horseshoe crab eggs). Based on this estimate, Castro and Myers (1993) estimated that the total number of females needed to lay the eggs consumed by shorebirds is approximately 1,820,000. Assuming a sex ratio of 1:1, approximately 3,640,000 horseshoe crabs are required to sustain the shorebird migration stopover in Delaware Bay. However, these calculations assume that shorebirds feed exclusively on horseshoe crab eggs. Tsipoura and Burger (1998) indicated that horseshoe crab eggs are a significant part of shorebirds diet, but that diet is supplemented by other food resources. Botton et al. (1994) estimated that an average of 44,000 eggs/m^2 would be needed to sustain the entire shorebird population in the Delaware Bay. Their data indicate these densities currently occur within most Delaware Bay beaches. A significant decrease in the number of horseshoe crabs could leave a large portion of migrating shorebirds without either the necessary food resources to complete their trip to the Arctic breeding grounds or the necessary fat reserves upon arrival to initiate egg laying and incubation.

Finfish

Horseshoe crab eggs and larvae are a seasonal food item of invertebrates and finfish. In the Delaware River from May through August, striped bass (*Morone saxatilis*) and white perch (*Morone americana*) eat horseshoe crab eggs. American eel (*Anguilla rostrata*), killifish (*Fundulus* spp.), silver perch (*Bairdiella chrysoura*), weakfish (*Cynoscion regalis*), kingfish (*Menticirrhus saxatilis*), silversides (*Menidia menidia*), summer flounder (*Paralichthys dentatus*), and winter flounder (*Pleuronectes americanus*) also eat eggs and larvae (Shuster, 1982). All crab species and several gastropods, including whelks, feed on horseshoe crab eggs and larvae. Shuster (1982) reported a large leopard shark (*Triakis semifasciatum*) preying on adult horseshoe crabs in southern Florida.

<u>Sea Turtles</u>
Lutcavage and Musick (1985) examined the stomach contents or excreta from 527 loggerhead turtles from Chesapeake Bay and nearby coastal waters and found that the most common prey was horseshoe crab. Musick et al. (1983) examined 27 loggerhead turtles and found horseshoe crabs commonly in stomach contents. Similarly, Lutcavage (1981) found that horseshoe crabs represented up to 42 percent of the diet of loggerhead turtles from Chesapeake Bay (N=6), averaging 22 percent. Data collected by the NMFS Sea Turtle Stranding and Salvage Network along the Atlantic Coast identified horseshoe crabs in 75 percent of loggerhead stomach contents in 1996 (N=8) and 55 percent in 1997 (N=11) (Evans, pers. comm., 1998). Morreale and Standora (1993) found no evidence of horseshoe crabs in loggerhead turtle diets in New York's Long Island Sound; however, diet largely depends on the relative abundance of prey species. Maintaining abundant stocks of adult horseshoe crabs may be an important component of ensuring the long-term survival of loggerhead sea turtles in the Chesapeake Bay area.

Abundance and status of stocks

(from the 2007 ASMFC FMP review)
The initial horseshoe crab stock assessment and peer review was conducted in 1998 (ASMF**C**1999; ASMFC 1998). The Stock Assessment Subcommittee (SAS) and the Peer Review Panel (PRP) concluded that there was inadequate information for a coastwide stock assessment.

Information was not available to establish biological reference points, fishing mortality rates, or recruitment estimates. The Technical Committee and PRP, based on their assessment of the available data, recommended a conservative, risk-averse management approach. This recommendation was based on localized population declines, increased catch and effort, slow maturation, susceptibility of spawning crabs to harvest, population resiliency, and the need for a superabundance of horseshoe crab eggs in the Delaware Bay.

Under the five-year trigger, a horseshoe crab stock assessment update was conducted in 2003 (ASMFC 2004), which employed trend, power and meta-analyses. The addition of several new datasets and the longer time series allowed for improved trend detection. Once again, the assessment methodology was not, in itself, considered a complete stock assessment as it did not provide estimates of biological reference points or stock status. Such estimates are not expected until sufficient data are obtained and incorporated into a model proposed by the Horseshoe Crab Stock Assessment Subcommittee (HSC SAS 2000).

Results from the most recent assessment indicated that horseshoe crab abundance trends varied regionally/sub-regionally. There was no evidence of a decline in the Southeast Region between 1995 and 2003. Four of five indices in western Long Island Sound showed significant or marginally significant positive trends. No trend was detected in eastern Long Island sound.

However, indices trended downward since their peak in the early to mid-1990s and are at levels near or below those encountered in the mid-1980s. In the New England region, the Narragansett

Bay data sets indicated population decline from the mid-1970s to present; however, the trends around Cape Cod were less clear. There was evidence that horseshoe crab abundance in Cape Cod was stable or declining.

Abundance measures in the Delaware Bay declined significantly during the 1990s. Declines from the late 1980s to early 1990s appear to be steeper than declines in recent years. However, the slopes of these declines were not statistically significant. The redesigned Delaware Bay spawning survey showed that bay-wide spawning activity has been stable from 1999 to 2006.

The SAS reviewed the results of three models/studies that focused on horseshoe crab population dynamics and abundance in the Delaware Bay region. It looked at a surplus production model, mark-recapture study, and age-structured model. The general picture that emerges from a synthesis of the assessments indicates that

1) relative abundance has declined through the 1990s to present,
2) relative fishing mortality rate has exceeded F_{MSY} since the mid-1990s with the F/F_{MSY} ratio peaking around 1998 and, on average, declining since then, and
3) current harvest rate is below 10%, but appears to be in excess of F_{MSY}.

4.2.16 Highly Migratory Pelagics

(all text in this section excerpted from the 2006 Consoidated Highly Migratory Species FMP)

Tunas

Life History and Biology

Atlantic Bluefin Tuna

Atlantic bluefin tuna are distributed from the Gulf of Mexico to Newfoundland in the West Atlantic, from roughly the Canary Islands to south of Iceland in the East Atlantic, and throughout the Mediterranean Sea. Historically, catches of bluefin were made from a broad geographic range in the Atlantic and Mediterranean.

Atlantic bluefin tuna can grow to over 300 cm and reach more than 650 kg. The oldest age considered reliable is 20 years, based on an estimated age at tagging of two years and about 18 years at liberty, although it is believed that bluefin tuna may live to older ages. Bluefin tuna are, thus, characterized by a late age at maturity (thus, a large number of juvenile classes) and a long life span. These factors contribute to make bluefin tuna well adapted to variations in recruitment success, but more vulnerable to fishing pressure than rapid growth species such as tropical tuna species. Bluefin tuna in the West Atlantic generally reach a larger maximum size compared to bluefin caught in the East Atlantic.

Bluefin tuna in the West Atlantic are assumed to first spawn at age eight compared to ages four to five in the east Atlantic. Distribution expands with age; large bluefin are adapted for migration to colder waters. Bluefin tuna are opportunistic feeders, with fish, squid, and crustaceans common in their diet. In the West Atlantic, bluefin tuna are thought to spawn from mid-April into June in the Gulf of Mexico and in the Florida Straits. Juveniles are thought to occur in the summer over the continental shelf, primarily from about 35°N to 41°N and offshore of that area in the winter. In the East Atlantic, bluefin tuna generally spawn from late May to July depending on the spawning area, primarily in the Mediterranean, with highest concentrations of larvae around the Balearic Islands, Tyrrhenian Sea, and central and eastern Mediterranean where the sea-surface temperature of the water is about 24°C. Sexually mature fishes have also been recently observed in May and June in the eastern Mediterranean (between Cyprus and Turkey). Bluefin tuna are known to be highly migratory and the nature and extent of their ability to conduct transoceanic migrations are the subject of significant research (see FEP Volume V).

Atlantic Bigeye Tuna

The geographical distribution of bigeye tuna is very wide and covers almost the entire Atlantic Ocean between 50°N and 45°S. This species is able to dive deeper than other tuna species and exhibits extensive vertical movements. Similar to the results obtained in other oceans, pop-up tagging and sonic tracking studies conducted on adult fish in the Atlantic has revealed that they exhibit clear diurnal patterns being much deeper in the daytime than at night. Spawning takes place in tropical waters when the environment is favorable. From the nursery areas in tropical waters, juvenile fish tend to diffuse into temperate waters as they grow larger. Catch information from the surface gears indicate that the Gulf of Guinea is a major nursery ground for this species.

Dietary habits of bigeye tuna are varied such that prey organisms like fish, mollusks, and crustaceans are found in stomach contents. A growth study based on otolith and tagging data resulted in the adoption by the the International Convention for the Conservation of Atlantic Tunas (ICCAT)'s Standing Committee on Research and Statistics (SCRS) of a new growth curve. The curve shows bigeye tuna exhibit relatively fast growth: about 105 cm in fork length at age three, 140 cm at age five and 163 cm at age seven. Bigeye tuna become mature at about age three and a half. Young fish form schools mostly mixed with other tunas such as yellowfin and skipjack. These schools are often associated with drifting objects, whale sharks and sea mounts. This association appears to weaken as bigeye tuna grow larger.

An estimate of natural mortality (M) for juvenile fish was provided based on the results of a tagging program. According to this study, mortality for juvenile fish only is at a similar level of M as that currently used for the entire Atlantic stock as well as the level of M used for all other oceans. Various evidence including; a genetic study, the time-area distribution of fish, and movements of tagged fish, suggest an Atlantic-wide single stock for this species, which is currently accepted by the SCRS. However, the possibility of other scenarios, such as north and south stocks, should not be disregarded.

Atlantic Yellowfin Tuna

Yellowfin tuna is a cosmopolitan species distributed mainly in the tropical and subtropical oceanic waters of the three oceans, where they form large schools. The sizes exploited range from 30 cm to 170 cm fork length (FL). Smaller fish (juveniles) form mixed schools with skipjack and juvenile bigeye, and are mainly limited to surface waters, while larger fish are found in surface and sub-surface waters. The majority of the long-term recoveries of tagged fish have been tagged in the western Atlantic and recovered in the eastern Atlantic, where several recaptures are recorded each year.

Sexual maturity occurs at about 100 cm FL. Reproductive output among females has been shown to be highly variable, although the extent of this is unknown. The main spawning ground is the equatorial zone of the Gulf of Guinea, with spawning occurring from January to April. Juveniles are generally found in coastal waters off Africa. In addition, spawning occurs in the Gulf of Mexico, in the southeastern Caribbean Sea, and off Cape Verde, although the relative importance of these spawning grounds is unknown.

Although such separate spawning areas might imply separate stocks or substantial heterogeneity in the distribution of yellowfin tuna, a single stock for the entire Atlantic is assumed as a working hypothesis (Atlantic Yellowfin Working Group, Tenerife, 1993), taking into account the transatlantic migration (from west to east) indicated by tagging, a 40-year time series of longline catch data that indicates yellowfin are distributed continuously throughout the entire tropical Atlantic Ocean, and other information (e.g., time-area size frequency distributions and locations of fishing grounds).

Growth patterns are variable with size, being relatively slow initially, and increasing by the time the fish leave the nursery grounds. Males are predominant in the catches of larger sized fish. Natural mortality is assumed to be higher for juveniles than for adults. Tagging studies for Pacific yellowfin supports this assumption. New data on biology and catches obtained from the Brazilian longline fishery were presented in 2004.

Atlantic Albacore Tuna

Albacore is a temperate tuna widely distributed throughout the Atlantic Ocean and Mediterranean Sea. For assessment purposes, the existence of three stocks is assumed based on available biological information: northern and southern Atlantic stocks (separated at 5°N), and a Mediterranean stock. Albacore spawning areas in the Atlantic are found in subtropical western areas of both hemispheres and throughout the Mediterranean Sea. Spawning takes place during austral and boreal spring-summer.

Sexual maturity is considered to occur at about 90 cm FL (age five) in the Atlantic, and at smaller size (62 cm, age two) in the Mediterranean. Until this age they are mainly found in surface waters, where they are targeted by surface gears. Some adult albacore are also caught using surface gears but, as a result of their deeper distribution, they are mainly caught using longlines. Young albacore tuna are also caught by longline in temperate waters.

Atlantic Skipjack Tuna

Skipjack tuna is a gregarious species forming schools in the tropical and subtropical waters of the three oceans. Skipjack spawn opportunistically throughout the year in vast areas of the Atlantic Ocean. The size at first maturity is about 45 cm for males and about 42 cm for females in the East Atlantic, while in the West Atlantic sexual maturity is reached at around 51 cm for females and 52 cm for males. Skipjack growth is seasonal, with substantial differences according to the latitude. There remains considerable uncertainty about the variability of the growth parameters between areas. It is, therefore, a priority to gain more knowledge on the growth schemes of this species.

Skipjack is a species that is often associated with floating objects, both natural objects or fish aggregating devices (FADs) that have been used extensively since the early 1990s by purse seiners and baitboats (during the 1991 to 2003 period, about 55 percent of skipjack were caught with FADs). The concept of viscosity (low interchange between areas) could be appropriate for the skipjack stocks. A stock qualified as "viscous" can have the following characteristics:

- It may be possible to observe a decline in abundance for a local segment of the stock;
- Overfishing of that component may have little, if any, repercussion on the abundance of the stock in other areas; and,
- Only a minor proportion of fish may make large-scale migrations.

The increasing use of FADs could have changed the behavior of the schools and the migrations of this species. It is noted that, in effect, the free schools of mixed species were much more common prior to the introduction of FADs than now. These possible behavioral changes ("ecological trap" concept) may lead to changes in the biological parameters of this species as a result of the changes in the availability of food, predation and fishing mortality. Skipjack caught with FADs are usually found associated with other species. The typical catch with floating objects is comprised of about 63 percent skipjack, 20 percent small yellowfin, and 17 percent juvenile bigeye and other small tunas. A comparison of size distributions of skipjack between periods prior to and after the introduction of FADs show that, in the eastern Atlantic, there has been an increase in the proportion of small fish in the catches, as well as a decline in the total catch in recent years in some areas.

The SCRS reviewed the current stock structure hypothesis that consists of two separate management units, one in the east Atlantic and another in the West Atlantic, separated at 30^{o}W. The boundary of 30^{o} West was established when the fisheries were coastal, whereas in recent years the East Atlantic fisheries have extended towards the west, surpassing this longitude, and showing the presence of juvenile skipjack tuna along the Equator, west of 30°W, following the drift of the FADs. This implies the potential existence of a certain degree of mixing. Nevertheless, taking into account the large distances between the east and west areas of the ocean, various environmental constraints, the existence of a spawning area in the east Atlantic as well as in the northern zone of the Brazilian fishery, and the lack of additional evidence (e.g. transatlantic migrations in the tagging data), the hypothesis of separate east and west Atlantic stock is maintained as the most plausible alternative. On the other hand, in taking into account the biological characteristics of the species and the different fishing areas, smaller management units could be considered.

Abundance and status of stocks

(text in this section excerpted from Chapter 3 of the Consolidated HMS FMP)

Atlantic Bluefin Tuna

The last full stock assessments for western Atlantic Bluefin tuna were conducted in 2002 with the next scheduled for 2006. Although the next stock assessment will not be conducted until mid-2006, the 2005 SCRS reported a significant number of new research reports and studies (see FEP Volume V). The assessment results are similar to those from previous assessments (see Table 4.2-7 and Figure 4.2-11). They indicate that the spawning stock biomass (SSB) declined steadily from 1970 (the first year in the assessment time series) through the late 1980s, before leveling off at about 20 percent of the level in 1975 (which has been a reference year used in previous assessments). A steady decline in SSB since 1997 is estimated and leaves SSB in 2001 at 13 percent of the 1975 level. The assessment also indicates that the fishing mortality rate during 2001 on the SSB is the highest level in the series.

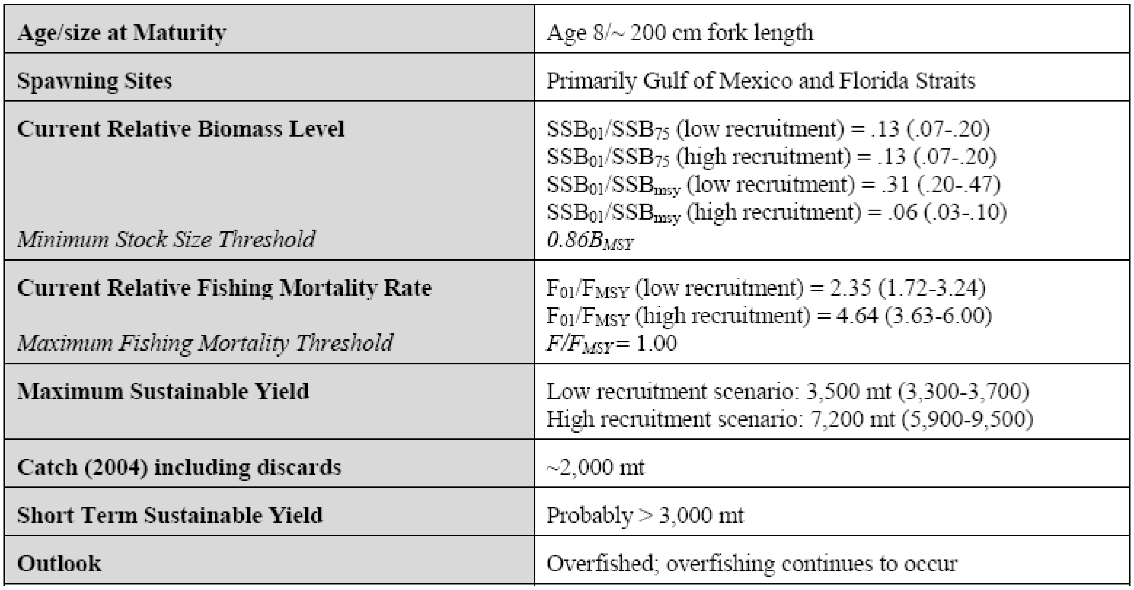
A noteworthy pattern of change in the fisheries since 1998 has been the trend of increase followed by a trend of decrease in catches to below TAC level. The reported total catches of western Atlantic bluefin tuna increased from about 2600 mt in 1998 to about 3,200 mt in 2002 and have subsequently fallen below 2,000 mt in 2004. The 2002 catches were the highest since 1981; however the 2004 catches were the lowest since 1982, when ICCAT catch restrictions were first established.

The Japanese longline fishery catch in the West Atlantic in 2003 was a substantial decrease from its 2002 catch level, but increased in 2004 to a level somewhat below its average catch from 1993 – 2002. This variation resulted from the adjustments made by Japan for previous quota overages. The Canadian reported landings remained at relatively stable levels over the past decade. Recent declines in U.S. landings have been attributed to a general lack of availability of large fish in the fisheries off the northeastern U.S. coast for the past several years.

Estimates of recruitment of age one fish have been generally lower since 1976. However, recruitment of age one fish in 1995 and 1998 is estimated to be comparable in size to some of the year classes produced in the first half of the 1970s. While the large decline in SSB since the early 1970s is clear from the assessment, the potential for rebuilding is less clear. Key issues are the reasons for relatively poor recruitment since 1976, and the outlook for recruitment in the future. One school of thought is that recruitment has been poor because the SSB has been low.

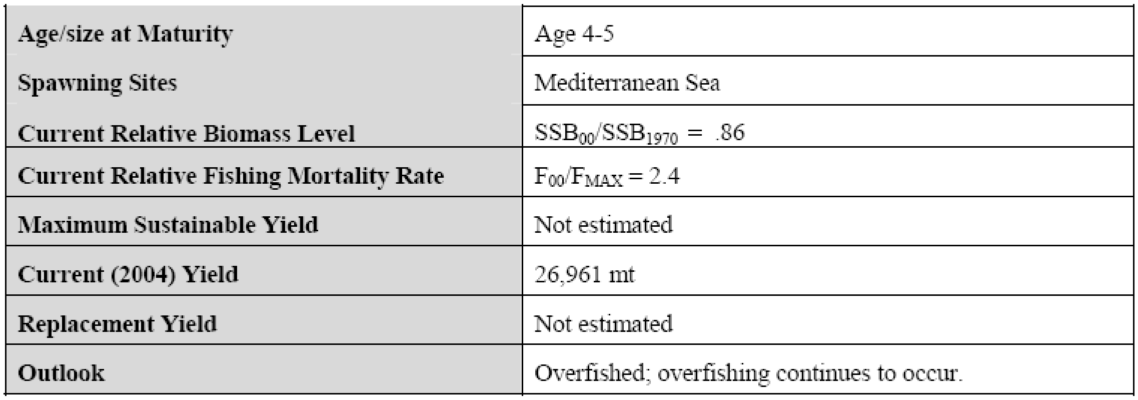
If so, recruitment should improve to historical levels if SSB is rebuilt. Another school of thought is that the ecosystem changed such that it is less favorable for recruitment and thus recruitment may not improve even if SSB increases. To address both schools of thought, the SCRS considered two recruitment scenarios as described below and summarized in Table 4.2-7 (East Atlantic Bluefin tuna summary data are also provided for comparison purposes). For both scenarios, the assessment indicates that the fishing mortality on the western Atlantic bluefin resource exceeds FMSY and the SSB is below BMSY (thus overfished according to ICCAT's objective of maintaining stocks at the MSY-biomass level and as indicated in NMFS, Report to Congress, Status of Fisheries, 2005).

Table 4.2-7. Summary Table for the Status of West Atlantic Bluefin Tuna. Source: ICCAT, 2005.



Age/size at Maturity	Age 8/~ 200 cm fork length
Spawning Sites	Primarily Gulf of Mexico and Florida Straits
Current Relative Biomass Level *Minimum Stock Size Threshold*	SSB_{01}/SSB_{75} (low recruitment) = .13 (.07-.20) SSB_{01}/SSB_{75} (high recruitment) = .13 (.07-.20) SSB_{01}/SSB_{msy} (low recruitment) = .31 (.20-.47) SSB_{01}/SSB_{msy} (high recruitment) = .06 (.03-.10) $0.86B_{MSY}$
Current Relative Fishing Mortality Rate *Maximum Fishing Mortality Threshold*	F_{01}/F_{MSY} (low recruitment) = 2.35 (1.72-3.24) F_{01}/F_{MSY} (high recruitment) = 4.64 (3.63-6.00) F/F_{MSY} = 1.00
Maximum Sustainable Yield	Low recruitment scenario: 3,500 mt (3,300-3,700) High recruitment scenario: 7,200 mt (5,900-9,500)
Catch (2004) including discards	~2,000 mt
Short Term Sustainable Yield	Probably > 3,000 mt
Outlook	Overfished; overfishing continues to occur

Summary Table for the Status of East Atlantic Bluefin Tuna. Source: ICCAT, 2005.



Age/size at Maturity	Age 4-5
Spawning Sites	Mediterranean Sea
Current Relative Biomass Level	SSB_{00}/SSB_{1970} = .86
Current Relative Fishing Mortality Rate	F_{00}/F_{MAX} = 2.4
Maximum Sustainable Yield	Not estimated
Current (2004) Yield	26,961 mt
Replacement Yield	Not estimated
Outlook	Overfished; overfishing continues to occur.

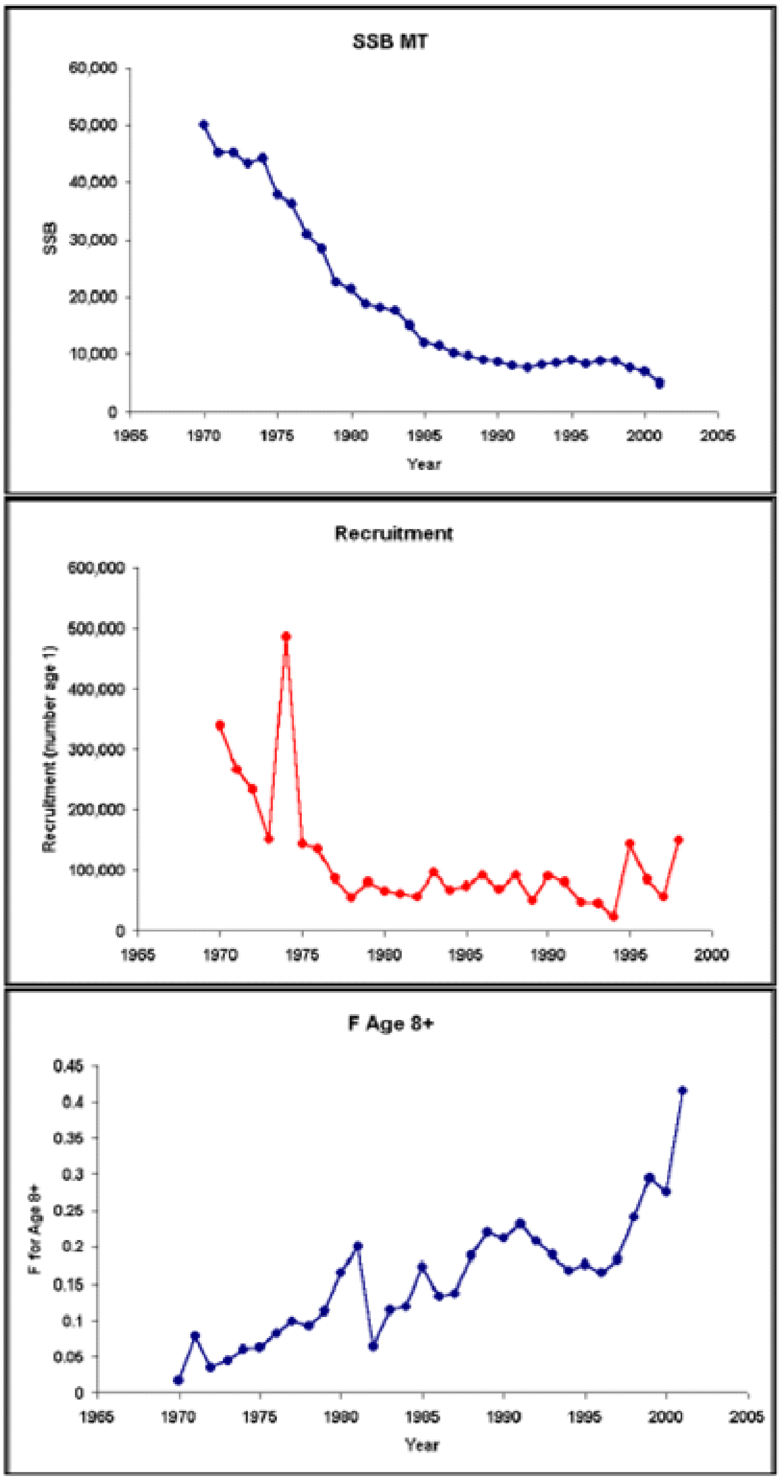


Figure 4.2-11. Western Atlantic bluefin tuna spawning biomass (t), recruitment (numbers) and fishing mortality rates for fish of age 8+, estimated by the Base Case VPA run. Source: ICCAT, 2004.

In general, the outlook for bluefin tuna in the West Atlantic is similar to the outlook reported based on the 2000 western Atlantic bluefin tuna assessment session.

The assessment and projection results for the present assessment are somewhat less optimistic than in 2000 but the confidence in the strength of the 1994 year class has increased. Therefore, the increases associated with different levels of future catch projected for the short-term are smaller but are estimated more confidently. It should be noted that the 1995 year class was estimated to be strong in 2000, but it is now estimated to be only of average strength.

Western Atlantic bluefin tuna catches have not varied very much since 1983 (the range over this period is 2,106 to 3,011 mt), and the estimated spawning stock size (Spawning Stock Biomass (SSB) measured as the biomass of fish age 8+) has been relatively stable, notwithstanding the indication of a decline in the most recent years. Thus, over an extended period of time, catches around recent levels have maintained stock size at about the same level, in spite of several past assessments that predicted the stock would either decline or grow if the current catch was maintained. This observation highlights the challenge of predicting the outlook for this stock.

In order to provide advice relative to rebuilding the western Atlantic bluefin resource, the SCRS conducted projections for two scenarios about future recruitment. One scenario assumed that future average recruitment will approximate the average estimated recruitment (at age one) since 1976, unless spawning stock size declines to low levels (such as the current level estimated in the assessment, but generally lower than estimates during most of the assessment history). The second scenario allowed average recruitment to increase with spawning stock size up to a maximum level no greater than the average estimated recruitment for 1970 to 1974. These scenarios are referred to as the low recruitment and high recruitment scenarios, respectively. The low and high recruitment scenarios implied that the BMSY (expressed in SSB) is 42 percent and 183 percent of the biomass in 1975, respectively. With the current information the SCRS could not determine which recruitment scenario is more likely, but both are plausible, and recommended that management strategies should be chosen to be reasonably robust to this uncertainty.

Table 4.2-8 below summarizes the results of projections of both scenarios at different catch levels. The projections for the low recruitment scenario estimated that a constant catch of 3,000 mt per year has an 83 percent probability of allowing rebuilding to the associated SSBMSY by 2018. A constant catch of 2,500 mt per year has a 35 percent probability of allowing rebuilding to the 1975 SSB by 2018.

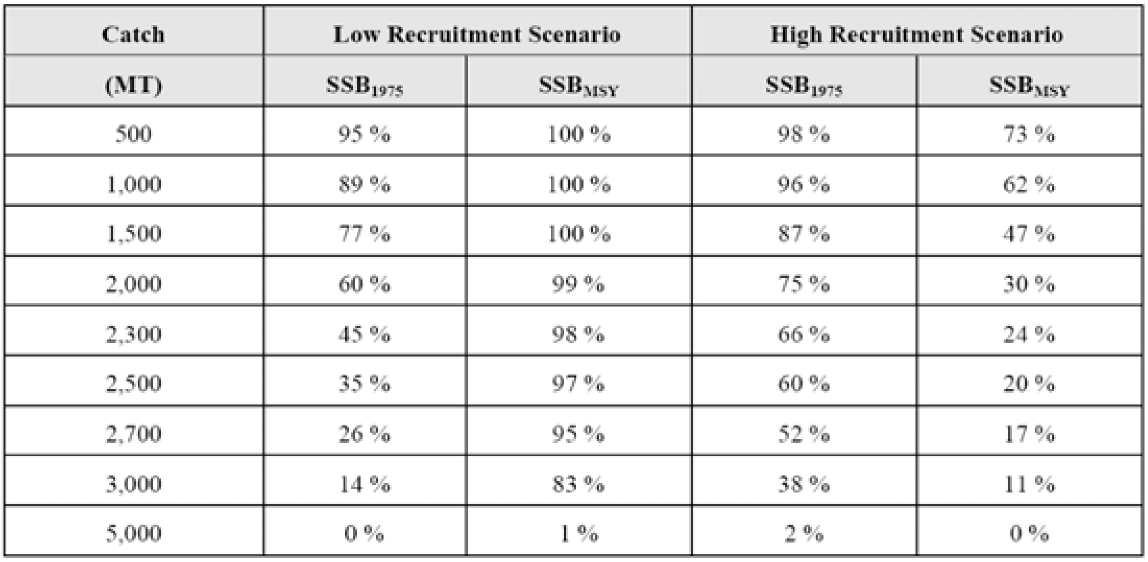
The results of projections based on the high recruitment scenario estimated that a constant catch of 2,500 mt per year has a 60 percent probability of allowing rebuilding to the 1975 level of SSB, and there is a 20 percent chance of rebuilding SSB to SSBMSY by 2018. If the low recruitment scenario is valid, the TAC could be increased to at least 3,000 mt without violating ICCAT’s rebuilding plan. If the high recruitment scenario is valid, the TAC should be decreased to less than 1,500 mt to comply with the plan.

The estimate of SSBMSY for the high recruitment scenario is critical to inferences regarding the probability of achieving rebuilding under different future levels of catch, and also less well determined by the data than SSBMSY for the low recruitment scenario.

In particular, the estimates of SSBMSY based on the high recruitment scenario are substantially larger than the largest spawning stock size included in the assessment. This extrapolation considerably increases the uncertainty associated with these estimates of SSBMSY. Previous meetings have used SSB1975 as a rebuilding target in the context of interpreting projections. Arguably SSB1975 is appropriate as a target level for interpreting the implications of projections based on the high recruitment scenario. Under such a target level for the high recruitment scenario, a TAC of 2,700 mt has an estimated probability of reaching the rebuilding level of about 50 percent.

The SCRS cautioned that these conclusions do not capture the full degree of uncertainty in the assessments and projections. An important factor contributing to uncertainty is mixing between fish of eastern and western origin. Furthermore, the projected increases in stock size are strongly dependent on estimates of recent recruitment, which are a particularly uncertain part of the assessment. A sensitivity test in which the estimates of the below average 1996 and the strong 1997 year classes were excluded from the analysis gave somewhat less optimistic results in terms of the estimated probabilities of recovery by 2018. However, these projections still predicted increases in spawning biomass for both recruitment scenarios, except for extreme increases in catch.

Table 4.2-8. Probability of western Atlantic bluefin tuna achieving rebuilding target by 2018. Source: ICCAT, 2004.



Catch	Low Recruitment Scenario		High Recruitment Scenario	
(MT)	SSB_{1975}	SSB_{MSY}	SSB_{1975}	SSB_{MSY}
500	95 %	100 %	98 %	73 %
1,000	89 %	100 %	96 %	62 %
1,500	77 %	100 %	87 %	47 %
2,000	60 %	99 %	75 %	30 %
2,300	45 %	98 %	66 %	24 %
2,500	35 %	97 %	60 %	20 %
2,700	26 %	95 %	52 %	17 %
3,000	14 %	83 %	38 %	11 %
5,000	0 %	1 %	2 %	0 %

Atlantic Bigeye Tuna

ICCAT's SCRS conducted a new stock assessment for bigeye tuna in July 2004 using various types of models. However, there were considerable sources of uncertainty arising from the lack of information regarding (a) reliable indices of abundance for small bigeye from surface fisheries, (b) the species composition of Ghanaian fisheries that target tropical tunas, and (c) details on the historical catch and fishing activities of Illegal, Unregulated, Unreported (IUU) fleets (e.g., size, location and total catch).

Three indices of relative abundance were available to assess the status of the stock (Figure 4.2-12). All were from longline fisheries conducted by Japan, Chinese Taipei and United States. While the Japanese indices have the longest duration since 1961 and represent roughly 20 - 40 percent of the total catch, the other two indices are shorter and generally account for a smaller fraction of the catch than the Japanese fishery. These three indices primarily relate to medium and large-size fish.

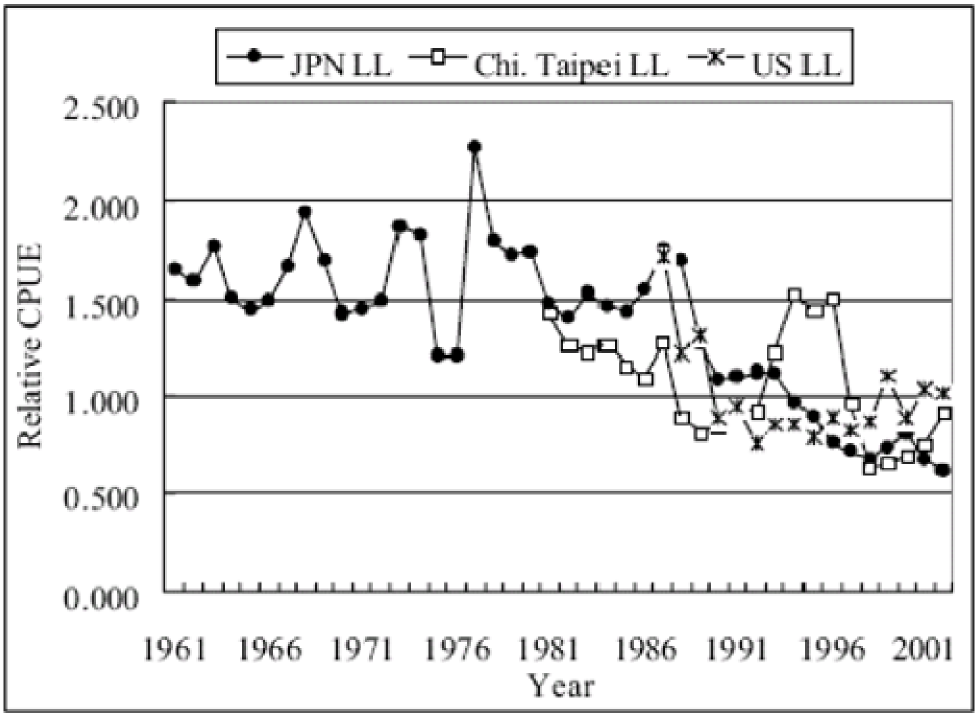


Figure 4.2-12. Abundance indices in numbers of Bigeye Tuna. All ages are aggregated. Source: ICCAT, 2004.

Various types of production models were applied to the available data and the SCRS notes that the current year's model fits to the data were better than in past assessments, although they required similar assumptions regarding stock productivity.

The point estimates of MSY obtained from different production models ranged from 93,000 mt to 113,000 mt. The lower limit of this range is higher than the one estimated in the 2002 assessment, probably due to the revised indices and the addition of a new index. An estimate obtained from another age-aggregated model was 114,000 mt. The inclusion of estimation uncertainty would broaden this range considerably.

These analyses estimate that the total catch was larger than the upper limit of MSY estimates for most years between 1993 and 1999, causing the stock to decline considerably, and leveling off thereafter as total catches decreased. These results also indicate that the current biomass is slightly below or above (85 – 107 percent) the biomass at MSY (Figure 4.2-13), and that current fishing mortality is also in the range of 73 percent to 101 percent of the level that would allow production of MSY (Table 4.2-9).

However, indications from the most targeted and wideranging fishery are of a more pessimistic status than implied by these model results. Several types of age-structured analyses were conducted using the above-mentioned longline indices from the central fishing grounds and catch-at-age data converted from the available catch-at-size data. In general, the trajectories of biomass and fishing mortality rates are in accordance with the production model analyses. Model fits appeared improved over those of past assessments, apparently as a result of using a new growth curve for the calculation of catch at age.

The most noteworthy trend in fisheries observed is the general declining trend in catches for all gears after a high peak (121,000 mt) in 1999. After that, the total annual catch has steadily declined to a current low of 72,000 mt for 2004. The decline of longline catch is mostly attributable to the decrease of Japanese and estimated IUU catches while the other country/entity’s catches are generally maintained. Other gears (purse seine and baitboat) also indicated a similar but more variable decline. The decline of the Japanese catch is related to the reduced fishing effort as well as the declined CPUE in the major fishing grounds in tropical waters.

Among the fisheries catching bigeye, two changes are noted. One is an increase in catch from the northern Islands (Azores and Madeira) area due to baitboat fisheries after four years of low catch for 2000 – 2003. Another change is also observed for the fishing area of Japanese longline fishery. Since around 2001, some of the fleet had operated in central north Atlantic between 25°N – 35°N and 40°W – 75°W. In addition to the above changes in fisheries, several countries increased their individual catch levels in 2004, although the overall catch total did not significantly increase. Such increases are reported for Philippines (1,850 mt), Venezuela (1,060 mt) and Korea (630 mt). The current reported catch of Chinese Taipei for 2003 is considered under-estimated. Chinese Taipei will re-estimate the bigeye catch for 2003 in near future. The new estimate is expected to be higher than the current reported catch.

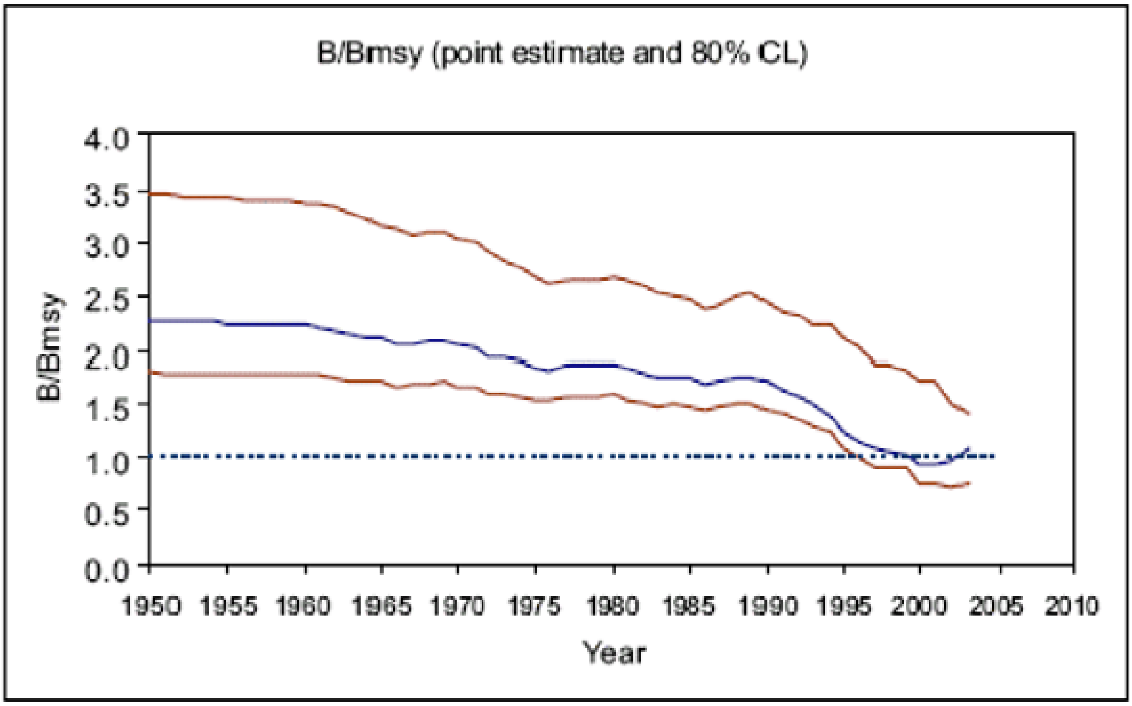


Figure 4.2-13. Trajectory of the Bigeye Tuna biomass modeled in production model analysis (middle line) bounded by upper and lower lines denoting 80 percent confidence intervals. Source: ICCAT, 2004.

Table 4.2-9. Summary Table for the Status of Atlantic Bigeye Tuna. Source: ICCAT, 2005.

Age/size at Maturity	Age 3/~100 cm curved fork length
Spawning Sites	Tropical waters
Current Relative Biomass Level *Minimum Stock Size Threshold*	B_{03}/B_{MSY} = 0.85 - 1.07 $0.6B_{MSY}$ (age 2+)
Current Relative Fishing Mortality Rate *Maximum Fishing Mortality Threshold*	F_{02}/F_{MSY} = 0.73-1.01 F_{year}/F_{MSY} = 1.00
Maximum Sustainable Yield	93,000 - 114,000 mt
Current (2003) Yield	85,000 mt
Current (2003) Replacement Yield	89,000 - 103,000 mt
Outlook	Overfished; overfishing is occurring

This assessment indicated that the stock has declined due to the large catches made since the mid-1990s to around or below the level that produces the MSY, and that fishing mortality exceeded FMSY for several years during that time period. Projections indicate that catches of more than 100,000 mt will result in continued stock decline. ICCAT should be aware that if major countries were to take the entire catch limit set under the ICCAT Recommendations and other countries were to maintain recent catch levels, then the total catch could exceed 100,000 mt. The SCRS highly recommended that catch levels of around 90,000 mt or lower be maintained at least for the near future for ICCAT to rebuild the stock.

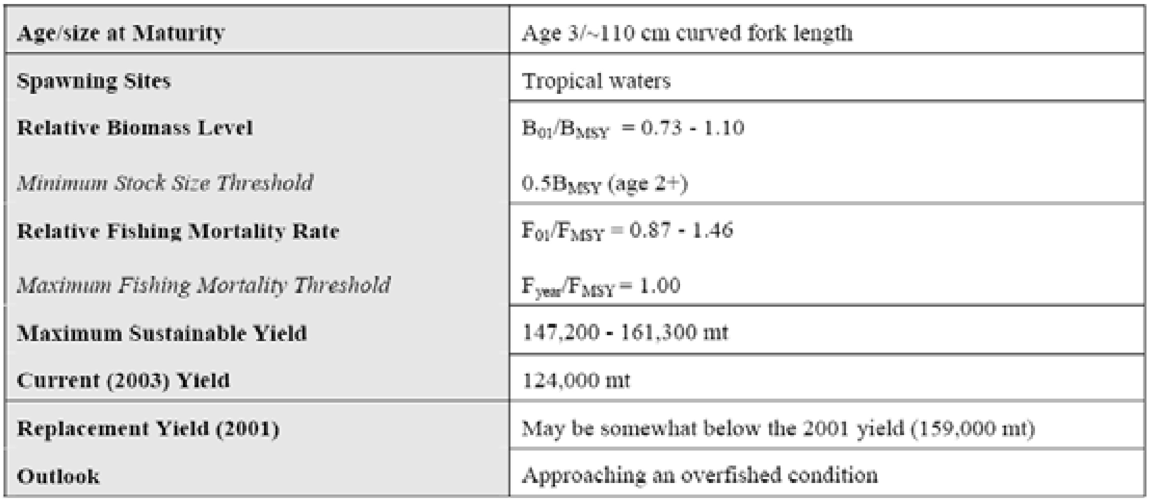
Atlantic Yellowfin Tuna

A full assessment was conducted for yellowfin tuna in 2003 applying various age-structured and production models to the available catch data through 2001. Unfortunately, at the time of the assessment meeting, only 19 percent of the 2002 catch had been reported (calculated relative to the catch reports available at the time of the SCRS Plenary). The results from all models were considered in the formulation of the SCRS's advice.

The variability in overall catch-at-age is primarily due to variability in catches of ages zero and one (note that the catches in numbers of ages zero and especially one were particularly high during the period 1998 - 2001). Both equilibrium and non-equilibrium production models were examined in 2003 and the results are summarized in Table 4.2-10. The estimate of MSY based upon the equilibrium models ranged from 151,300 to 161,300 mt; the estimates of F2001/FMSY ranged from 0.87 to 1.29. The point estimate of MSY based upon the non-equilibrium models ranged from 147,200 - 148,300 mt. The point estimates for F2001/FMSY ranged from 1.02 to 1.46. The main differences in the results were related to the assumptions of each model. The SCRS was unable to estimate the level of uncertainty associated with these point estimates. An age-structured virtual population analysis (VPA) was made using eight indices of abundance. The results from this model were more comparable to production model results than in previous assessments, owing in part to a greater consistency between several of the indices used. The VPA results compare well to the trends in biomass (Figure 4.2-14) and fishing mortality (Figure 4.2-15) estimated from production models. The VPA estimates that the spawning biomass (Table 4.2-10) and the levels of fishing mortality (Table 4.2-10) in recent years have been very close to MSY levels. The estimate of MSY derived from these analyses was 148,200 mt.

In summary, the age-structured and production model analyses implied that although the 2001 catches of 159,000 mt were slightly higher than MSY levels, effective effort may have been either slightly below or above (up to 46 percent) the MSY level, depending on the assumptions. Consistent with these model results, yield-per-recruit analyses also indicated that 2001 fishing mortality rates could have been either above or about the level which could produce MSY. Yield-per-recruit analyses further indicated that an increase in effort is likely to decrease the yield-per-recruit, while reductions in fishing mortality on fish less than 3.2 kg could result in substantial gains in yield-per-recruit and modest gains in spawning biomass-per-recruit.

Table 4.2-10. Summary Table for the Status of Atlantic Yellowfin Tuna. Source: ICCAT, 2004.



Age/size at Maturity	Age 3/~110 cm curved fork length
Spawning Sites	Tropical waters
Relative Biomass Level	B_{01}/B_{MSY} = 0.73 - 1.10
Minimum Stock Size Threshold	$0.5B_{MSY}$ (age 2+)
Relative Fishing Mortality Rate	F_{01}/F_{MSY} = 0.87 - 1.46
Maximum Fishing Mortality Threshold	F_{year}/F_{MSY} = 1.00
Maximum Sustainable Yield	147,200 - 161,300 mt
Current (2003) Yield	124,000 mt
Replacement Yield (2001)	May be somewhat below the 2001 yield (159,000 mt)
Outlook	Approaching an overfished condition

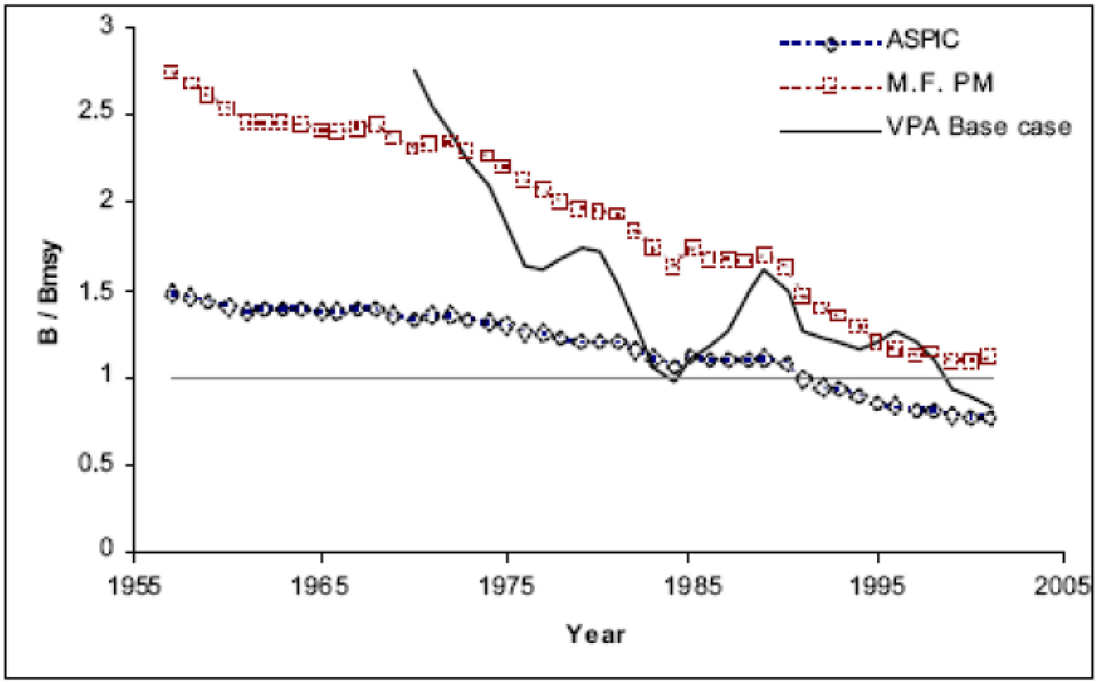


Figure 4.2-14. Comparison of relative biomass trends calculated using VPA and non-equilibrium production models. Source: ICCAT, 2004.

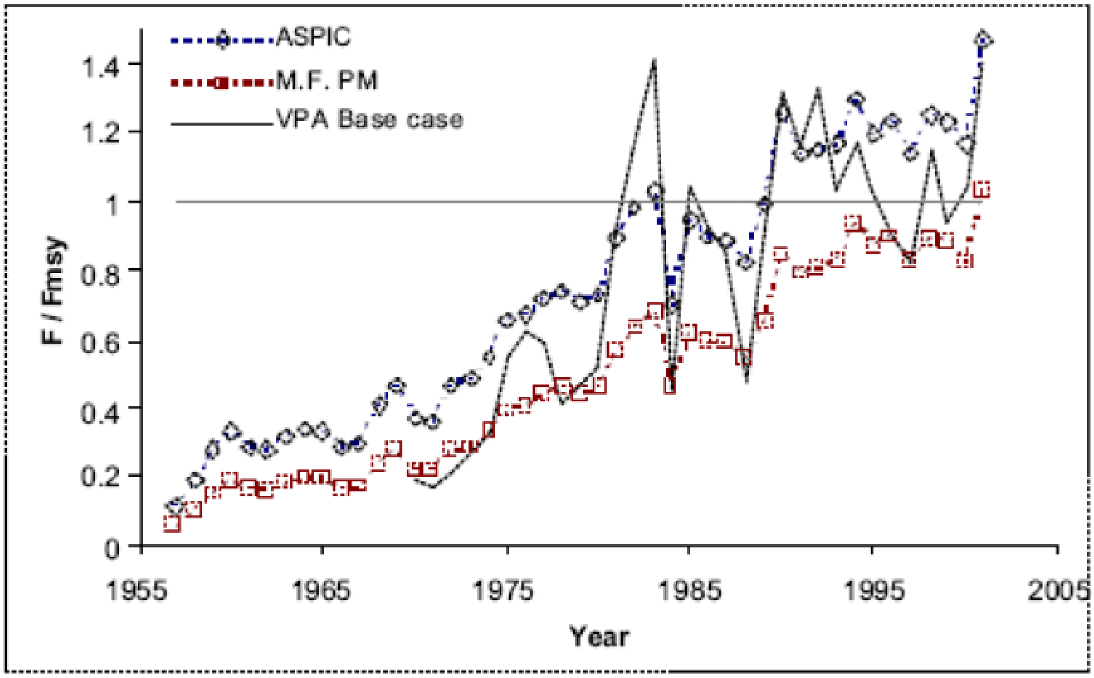


Figure 4.2-15. Comparison of relative fishing mortality trends calculated using VPA and non-equilibrium production models. Source: ICCAT, 2004.

In contrast to the increasing catches of yellowfin tuna in other oceans worldwide, there has been a steady decline in overall Atlantic catches since 2001. Atlantic surface fishery catches have shown a declining trend from 2001 to 2004, whereas longline catches have increased. In the eastern Atlantic, purse seine catches declined from 89,569 mt in 2001 to 58,632 mt in 2004, a 35 percent reduction. Baitboat catches declined by 23 percent, from 19,886 mt to 15,277 mt. This decrease is almost entirely due to reduced catches by Ghana baitboats, which resulted from a combination of reduced days fishing, a lower number of operational vessels, and the observance of the moratorium on fishing using floating objects. Catches by other baitboat fleets were generally increasing. In the western Atlantic, with the majority of the landings reported by the United States, Mexico, Venezuela, Brazil and St. Vincent and Grenadines, purse seine catches declined from 13,072 mt to 3,217 mt, a 75 percent reduction. In addition, baitboat catches also declined by eight percent from 7,027 mt to 6,735 mt. However, for the same time period, longline catches were increasing. In the eastern Atlantic, longline catches increased from 5,311 mt to 10,851 mt, a 104 percent increase. In the western Atlantic, longline catches increased from 12,740 mt to 15,008 mt, an 18 percent increase. At the same time, the nominal effort in the purse seine fishery was declining. As an indicator, the number of purse seiners from the European and associated fleet operating in the Atlantic declined from 46 vessels in 2001 to 34 vessels in 2004. On the other hand, the European and associated baitboat fleet increased from 16 to 22 vessels during the same period.

Of the relevant scientific documents presented to the 2005 SCRS, most were descriptive of the catches by country fleets. Three papers discussed observer programs in Ghana, Uruguay, and Spain, and three papers analyzed catches in the context of the moratorium. No new standardized catch rate information has been presented since the last assessment. However, examination of nominal catch rate trends from purse seine data suggest that catch-per-unit effort was stable or possibly declining since 2001 in the East Atlantic, and was clearly declining in the West Atlantic.

Since effort efficiency was estimated to have continued to increase, adjustments for such efficiency change would be expected to result in a steeper decline. Also, the average weights in European purse seine catches have been declining since 1994, which is at least in part due to changes in selectivity associated with fishing on floating objects.

Recent signals in the fishery data could result in a substantially different evaluation of stock status than that which is summarized above. It is important that the next assessment take these and other indicators (such as age of vessels and any loss of regional yellowfin fisheries) into account.

Atlantic Albacore Tuna

The last assessment of the northern stock was conducted in 2000, using data from 1975 to 1999, and that of the southern stock in 2003; no assessment of the Mediterranean stock has ever been carried out. To coordinate the timing of the assessments of northern and southern albacore tuna, the stock assessment for northern albacore was postponed at the 2004 ICCAT meeting from 2006 to 2007 (note the management measures for northern albacore expire at the end of 2006). The SCRS noted the considerable uncertainty that continues to remain in the catch-at-size data for the northern and southern stocks, and the profound impact this has had on attempts to complete a satisfactory assessment of northern albacore tuna.

North Atlantic

In 2003, the SCRS concluded that it was inappropriate to proceed with a VPA assessment based on the catch-at-age until the catch-at-size to catch-at-age transformation is reviewed and validated. In 2005, a document was presented on the analyses of catch-at-size and identifying the source of bias in the catch-at-age of the North Atlantic albacore stock. The SCRS recommends holding a data preparatory working group meeting to allow for a thorough revision of the North Atlantic stock prior to the next assessment in 2007. Consequently, the current state of the northern albacore stock is based primarily on the last assessment conducted in 2000 together with observations of CPUE and catch data provided to the SCRS in 2003. The results, obtained in 2000, showed consistency with those from previous assessments (Table 4.2-11a).

The SCRS noted that CPUE trends have varied since the last assessment in 2000, and in particular differed between those representatives of the surface fleets (Spain Troll age two and Spain Troll age three) and those of the longline fleets of Japan, Chinese Taipei, and the United States. The Spanish age two troll series, while displaying an upward trend since the last assessment, nonetheless declined over the last ten years. For the Spanish age three troll series, the trend in the years since the last assessment is down; however, the trend for the remainder of the last decade is generally unchanged. For the longline fleets, the trend in CPUE indices is either upwards (Chinese Taipei and United States) or unchanged (Japan) in the period since the last assessment. However, variability associated with all of these catch rate estimates prevented definitive conclusions about recent trends of albacore catch rates.

Equilibrium yield analyses, carried out in 2000 and made on the basis of an estimated relationship between stock size and recruitment, indicate that spawning stock biomass was about 30 percent below that associated with MSY. However, the SCRS noted considerable uncertainties in these estimates of current biomass relative to the biomass associated with MSY (BMSY), owing to the difficulty of estimating how recruitment might decline below historical levels of stock biomass. Thus, the SCRS concluded that the northern stock is probably below BMSY, but the possibility that it is above it should not be dismissed (Figure 4.2-16). However, equilibrium yield-per-recruit analyses made by the SCRS in 2000 indicate that the northern stock is not being growth overfished (F < Fmax).

In terms of yield per recruit, the assessment carried out in 2000 indicates that the fishing intensity is at, or below, the fully exploited level. Concerning MSY-related quantities, the SCRS recalls that they are highly dependent on the specific choice of stock-recruitment relationship. The SCRS believed that using a particular form of stock-recruitment relationship that allows recruitment to increase with spawning stock size provided a reasonable view of reality. This hypothesis together with the results of the assessment conducted in 2000 indicate that the spawning stock biomass (B1999) for the northern stock (29,000 mt) was about 30 percent below the biomass associated with MSY (42,300 mt) and that current F (2000) was about 10 percent above FMSY. However, an alternative model allowing for more stable recruitment values in the range of observed SSB values would provide a lower estimate of SSB at MSY, below the current value.

South Atlantic

In 2003, an age-structured production model, using the same specifications as in 2000, was used to provide a base case assessment for southern Atlantic albacore. Results were similar to those obtained in 2000, but the confidence intervals were substantially narrower in 2003 than in 2000 (Table 4.2-11b). In part, this may be a consequence of additional data now available, but the underlying causes need to be investigated further. The estimated MSY and replacement yield from the 2003 base case (30,915 mt and 29,256 mt, respectively) were similar to those estimated in 2000 (30,274 mt and 29,165 mt). In both 2003 and 2000, the fishing mortality rate was estimated to be about 60 percent of FMSY. Spawning stock biomass has declined substantially relative to the late 1980s, but the decline appears to have leveled off in recent years and the estimate for 2002 remains well above the spawning stock biomass corresponding to MSY.

Catches of albacore in the South Atlantic in 2001 and 2002 were above replacement yield, and were below estimates of MSY in 2003. Nevertheless, both the 2000 and 2003 albacore assessments estimated that the stock is above BMSY. There is now greater confidence in these estimates of MSY and therefore there is justification to base a TAC recommendation on MSY instead of replacement yield estimates from the model as in 2000. This results from the SCRS's view that current stock status is somewhat above BMSY and catch of this level, on average, would be expected to reduce the stock further towards BMSY. Recent estimates of high recruitment could allow for some temporary increase in adult stock abundance under a 31,000 mt catch, but this result is uncertain.

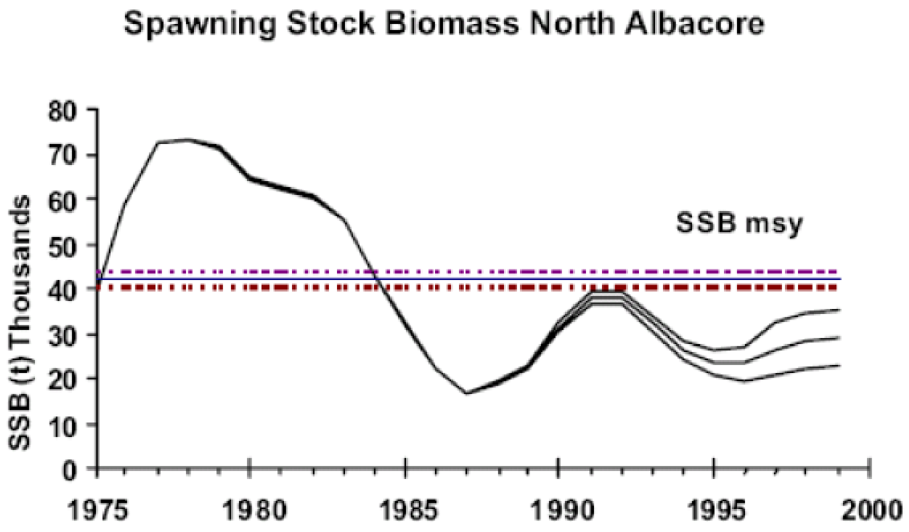
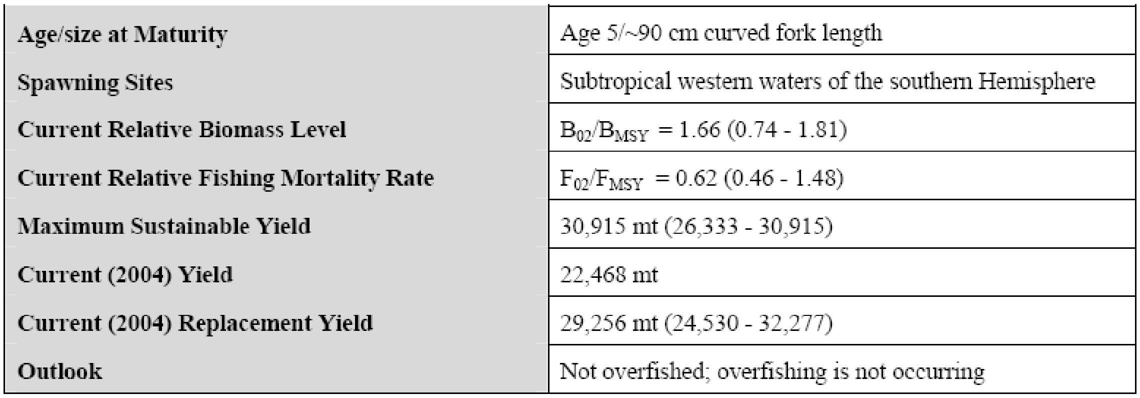


Figure 4.2-16. North Atlantic albacore spawning stock biomass and recruits with 80 percent confidence limits. Source: ICCAT, 2004.

Table 4.2-11a. Summary Table for the Status of North Atlantic Albacore Tuna. Source: ICCAT, 2005.

Age/size at Maturity	Age 5/~90 cm curved fork length
Spawning Sites	Subtropical western waters of the northern Hemisphere
Current Relative Biomass Level *Minimum Stock Size Threshold*	B_{99}/B_{MSY} = 0.68 (0.52 - 0.86) *$0.7B_{MSY}$*
Current Relative Fishing Mortality Rate *Maximum Fishing Mortality Threshold*	F_{99}/F_{MSY} = 1.10 (0.99 - 1.30) *F_{year}/F_{MSY}* = 1.00
Maximum Sustainable Yield	32,600 mt [32,400 - 33,100 mt]
Current (2004) Yield	25,460 mt
Current (2004) Replacement Yield	not estimated
Outlook	Overfished; overfishing is occurring

Table 4.2-11b. Summary Table for the Status of South Atlantic Albacore Tuna. Source: ICCAT, 2005.



Age/size at Maturity	Age 5/~90 cm curved fork length
Spawning Sites	Subtropical western waters of the southern Hemisphere
Current Relative Biomass Level	B_{02}/B_{MSY} = 1.66 (0.74 - 1.81)
Current Relative Fishing Mortality Rate	F_{02}/F_{MSY} = 0.62 (0.46 - 1.48)
Maximum Sustainable Yield	30,915 mt (26,333 - 30,915)
Current (2004) Yield	22,468 mt
Current (2004) Replacement Yield	29,256 mt (24,530 - 32,277)
Outlook	Not overfished; overfishing is not occurring

Atlantic Skipjack Tuna

The last ICCAT/SCRS assessment on Atlantic skipjack tuna was carried out in 1999 (Table 4.2-12). The state of the Atlantic skipjack stock(s), as well as the stocks of this species in other oceans, show a series of characteristics that make it extremely difficult to conduct an assessment using current models. Among these characteristics, the most noteworthy are:

- The continuous recruitment throughout the year, but heterogeneous in time and area, making it impossible to identify and monitor the individual cohorts;
- Apparent variable growth between areas, which makes it difficult to interpret the size distributions and their conversion to ages; and
- Exploitation by many and diverse fishing fleets (baitboat and purse seine), having distinct and changing catchabilities, which makes it difficult to estimate the effective effort exerted on the stock in the east Atlantic.

For these reasons, no standardized assessments have been carried out on the Atlantic skipjack stocks. Notwithstanding, some estimates were made, by means of different indices of the fishery and some exploratory runs were conducted using a new development of the generalized production model.

Eastern stock

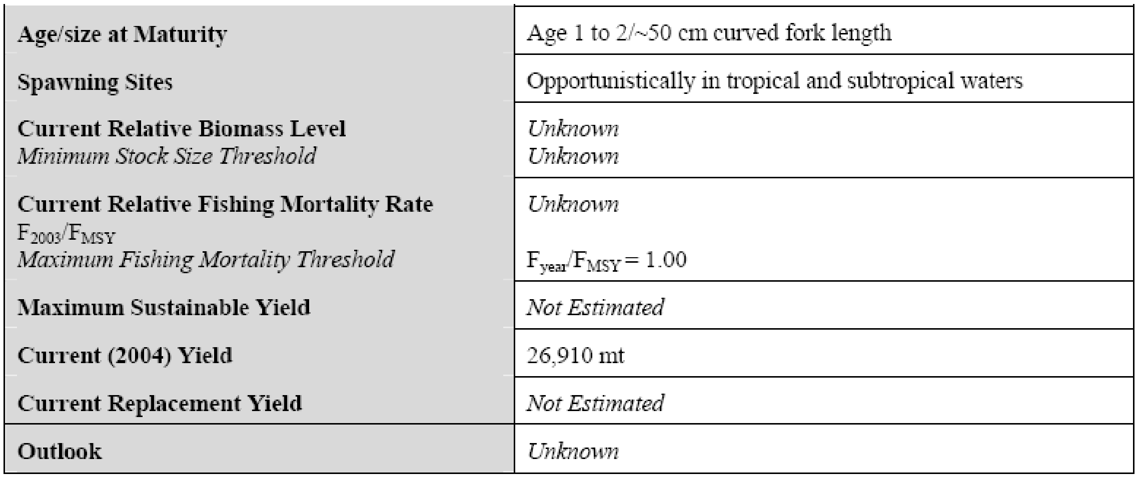
Standardized catch rates are not available. However, an analysis was made, for the 1969 – 2002 period, of the different indices of the purse seine fishery that could provide valuable information on the state of the stock. For the majority of the indices, the trends were divergent, depending on the area, which may indicate the viscosity of the skipjack stock, with limited mixing rates between areas. Because of the difficulties in assigning ages to the skipjack catches, the estimates of the values of natural mortality by age and obtaining indices of abundance (especially for the eastern stock), no catch-by-age matrices were developed and, consequently, no analytical assessment methods were applied.

There is no quantified information available on the effective fishing effort exerted on skipjack tuna in the East Atlantic. It is supposed, however, that the increase in fishing power linked to the introduction to improved technologies on board the vessels as well as to the development of fishing under floating objects have resulted in an increase in the efficiency of the various fleets. An estimate of the increase in the coefficient of total mortality (Z) between the early 1980s and the end of the 1990s was carried out with a model using tagging data (Workshop on the mortality of juveniles in July 2005). For the range of sizes considered (about 40 – 60 cm FL), the increase in Z on the order of a factor 3 would reflect this increase in efficiency. This interpretation is supported by a comparison of skipjack size distributions in the East Atlantic between the periods prior to, and following, the use of FADs as an increase is observed in the proportion of small fish in the catches.

A document on the Spanish observer program on board purse seiners, presented during the 2005 SCRS, shows that for the 2001-2005 period the average rate of discards of skipjack tunas under FADs in the East Atlantic is estimated at 42 kg per ton of skipjack landed. In the West Atlantic, fishing effort of the Brazilian baitboats (which comprises the major skipjack fishery) decreased by half between 1985 and 1996, but seems to be stabilized since, after a slight increase.

Western stock
Standardized abundance indices up to 1998 were available from the Brazilian baitboat fishery and the Venezuelan purse seine fishery, and in both cases the indices seem to show a stable stock status. Uncertainties in the underlying assumptions for the analyses prevent the extracting of definitive conclusions regarding the state of the stock. However, the results suggest that there may be over-exploitation within the FAD fisheries, although it was not clear to what extent this applies to the entire stock. The SCRS could not determine if the effect of the FADs on the resource is only at the local level or if it had a broader impact, affecting the biology and behavior of the species. Under this supposition, maintaining high concentrations of FADs would reduce the productivity of the overall stock. However, since 1997, and due to the implementation of a voluntary Protection Plan for Atlantic tunas, agreed upon by the Spanish and French boat owners in the usual areas of fishing with objects, which later resulted in an ICCAT regulation on the surface fleets that practice this type of fishing, there has been a reduction in the skipjack tuna catches associated with FADs. Maintaining this closure would continue to have a positive effect on the resource. The development of nominal abundance indices of Brazilian baitboat fisheries and Venezuelan purse seiners, obtained up to 2004, seemed to show a stable stock status.

Table 4.2-12. Summary Table for the Status of West Atlantic Skipjack Tuna. Source: ICCAT, 2005.



Age/size at Maturity	Age 1 to 2/~50 cm curved fork length
Spawning Sites	Opportunistically in tropical and subtropical waters
Current Relative Biomass Level *Minimum Stock Size Threshold*	*Unknown* *Unknown*
Current Relative Fishing Mortality Rate F_{2003}/F_{MSY} *Maximum Fishing Mortality Threshold*	*Unknown* $F_{year}/F_{MSY} = 1.00$
Maximum Sustainable Yield	*Not Estimated*
Current (2004) Yield	26,910 mt
Current Replacement Yield	*Not Estimated*
Outlook	*Unknown*

Swordfish

Life History and Biology

Swordfish are members of the family Xiphiidae, in the suborder Scombroidei. Atlantic swordfish (*Xiphias gladius*) are one of the largest and fastest predators in the Atlantic Ocean, reaching a maximum size of 530 kg (1165 lb). Like other highly migratory species, they have developed a number of specialized anatomical, physiological, and behavioral adaptations (Helfman et al., 1997). Swordfish are distinguished by a long bill that grows forward from the upper jaw. This bill differs from that of marlins (family Istiophoridae) in that it is flattened rather than round in cross section, and smooth rather than rough. Swordfish capture prey by slashing this bill back and forth in schools of smaller fish or squid, stunning or injuring their prey in the process. They may also use the bill to spear prey, or as a defense during territorial encounters. Broken swordfish bills have been found embedded in vessel hulls and other objects (Helfman *et al.,* 1997).

Atlantic swordfish are usually found in surface waters but occasionally dive as deep as 650 meters. These large pelagic fishes feed throughout the water column on a wide variety of prey including groundfish, pelagics, deep-water fish, and invertebrates.

Swordfish show extensive diel migrations and are typically caught on pelagic longlines at night when they feed in surface waters (SCRS, 2004). They are capable of migrating long distances to maximize prey availability and, as noted above, can prey upon various trophic levels during their daily vertical migrations (NMFS, 1999). As adults and juveniles, swordfish feed at the highest levels of the trophic food chain, implying that their prey species occur at low densities. The foraging behavior of swordfish reflects the broad distribution and scarcity of appropriate prey; they often aggregate in places where they are likely to encounter high densities of prey, including areas near current boundaries, convergence zones, and upwellings (Helfman et al., 1997).

Swordfish move thousands of kilometers annually and are distributed globally in tropical and subtropical marine waters. Their broad distribution, large spawning area, and prolific nature have contributed to the resilience of the species in spite of the heavy fishing pressure being exerted on it by many nations. During their annual migration, North Atlantic swordfish follow the major currents which circle the North Atlantic Ocean (including the Gulf Stream, Canary and North Equatorial Currents) and the currents of the Caribbean Sea and Gulf of Mexico.

The primary habitat in the western north Atlantic is the Gulf Stream, which flows northeasterly along the U.S. coast, then turns eastward across the Grand Banks. North-south movement along the eastern seaboard of the United States and Canada is significant (NMFS, 2003). They are found in the colder waters during summer months and all year in the subtropical and tropical area (SCRS, 2003). Additional information on life history relating to habitat can be found in the 2006 Consolidated Highly Migratory Species FMP (NMFS 2006).

Like most large pelagic species, swordfish have adapted body contours that enable them to swim at high speeds. Their streamlined bodies are round or slightly compressed in cross section (fusiform), and their stiff, deeply forked tails minimize drag. This streamlined physical form is enhanced by depressions or grooves on the body surface into which the fins can fit during swimming. The extremely small second dorsal and anal fins of the swordfish may function like the finlets of tuna, reducing turbulence and enhancing swimming performance.

Their method of respiration, known as ram gill ventilation, requires continuous swimming with the mouth open to keep water flowing across the gill surfaces, thereby maintaining an oxygen supply. This respiratory process is believed to conserve energy compared to the more common mechanism whereby water is actively pumped across the gills (Helfman et al., 1997). In addition to the benefits of speed and efficiency, their search for prey is aided by coloring that provides camouflage in pelagic waters. This shading is darker along the dorsal side and lighter underneath, enhanced by silvery tones.

Swordfish exhibit other physiological characteristics that enable them to extend their hunting range. For example, swordfish can maintain elevated body temperatures, conserving the heat generated by active swimming muscles. Swordfish have developed a heat exchange system that allows them to swim into colder, deepwater in pursuit of prey. Because warm muscles contract faster than cool ones, heat conservation is believed to enable these predatory fishes to channel more energy into swimming speed. The internal temperatures of these fishes remain fairly stable even as they move from surface waters to deepwaters. Swordfish have also adapted specialized eye muscles for deepwater hunting. Because their eye muscles do not have the ability to contract, they produce heat when stimulated by the nervous system, locally warming both the brain and eye tissues (Helfman et al., 1997). With this modification, swordfish are able to hunt in the frigid temperatures of deep-water ocean environments without experiencing a decrease in brain and visual function that might be expected under such harsh conditions.

Juvenile swordfish are characterized as having exceptionally fast growth during the first year (NMFS, 1999). Swordfish exhibit dimorphic growth, where females show faster growth rates and attain larger sizes than males. Young swordfish grow very rapidly, reaching about 130 cm lower jaw-fork length (LJFL) by age two. Swordfish are difficult to age, but 53 percent of females are considered mature by age 5, at a length of about 130 cm LJFL (SCRS, 2003; SCRS, 2004). Approximately 50 percent of males attain maturity by 112 cm LJFL (Arocha, 1997). All males are mature by 145 to 160 cm LJFL (37 to 50 kg ww), approximately age five, and all females are mature by 195 to 220 cm LJFL (93 to 136 kg ww), approximately age nine. In general, swordfish reach 140 cm LJFL (33 kg ww) by age three and are considered mature by age five. Individual females may spawn numerous times throughout the year (NMFS, 1999).

Swordfish stocks consist of several age classes, a condition that may serve as a buffer against adverse environmental conditions and confer some degree of stability on the stocks.

Swordfish are also at a high trophic level, which may make the species less vulnerable to shortterm fluctuations in environmental conditions (NMFS, 1999).

When ICCAT's SCRS scientists assess the status of Atlantic swordfish, the stock is split between the North Atlantic, South Atlantic, and Mediterranean Sea. The SCRS continues to examine existing information, including spawning data, tagging information, genetic studies, and abundance indices to better define stock structure. For the purposes of domestic management, the swordfish population is considered to consist of two discrete stocks divided at 5° N.

Abundance and status of stocks

The most recent assessment of North and South Atlantic swordfish stocks was conducted in 2002. In that assessment, updated CPUE and catch data through 2001 were examined. Sex and age-specific (North Atlantic) and biomass standardized catch rates (North and South Atlantic) from the various fleets were updated. The updated North Atlantic CPUE data showed similar trends to previous years, and also showed signs of improvement in stock status since 1998. In particular, the recruitment index (1997 – 2001) and the catch-at-age used in the 2002 North Atlantic assessment showed signs of substantially improved recruitment (age one), which has manifested in several age classes and the biomass index of some fisheries, and have allowed for increases in spawning biomass and a more optimistic outlook. The strong recruitments of the late 1990s promoted improvement in spawning stock biomass and should result in further improvement, if these year classes are not heavily harvested. The CPUE patterns in the South Atlantic by fleet showed contradictory patterns. Lack of important CPUE information from some fleets fishing in the South Atlantic prevented the SCRS from reconciling these conflicts (SCRS, 2004).

North Atlantic Swordfish (all weights are given in whole weight)

An updated estimate of maximum sustainable yield from production model analyses is 14,340 mt (range 11,500 to 15,500 mt). Since 1997, North Atlantic swordfish catches have been estimated to have remained below 14,340 mt, but the most recent years are provisional and probably represent underestimates. Details of catches for recent years are presented below. The biomass at the beginning of 2002 was estimated to be 94 percent (range: 75 to 124 percent) of the biomass needed to produce MSY. This estimate is up from an estimate of 65 percent of MSY in the 1998 assessment. The 2001 fishing mortality rate was estimated to be 0.75 times the fishing mortality rate at MSY (range: 0.54 to 1.06). The replacement yield for the year 2003 and beyond was estimated to be about the MSY level. As the TAC for North Atlantic swordfish for 2002 was 10,400 mt, it was considered likely that biomass would increase further under those catch levels. The TAC set for 2003 – 2005 was 14,000 mt (ICCAT Recommendation 02 – 02). Given recent fishing mortality patterns, the spawning biomass likely will increase largely owing to the very large recruitments estimated for 1997 – 2000 (SCRS, 2005). Further, given that recent (2002 – 2003) reported catch has been below estimated replacement yield, the North Atlantic swordfish biomass may have already achieved the BMSY level. However, noting the uncertainties inherent in the assessment, the SCRS warned against large increases over the current TAC (SCRS, 2004). The next assessment is scheduled for 2006.

South Atlantic Swordfish

The SCRS noted that reported total catches have been reduced since 1995, as was recommended by the SCRS. SCRS had previously expressed serious concern about the trends in stock biomass of South Atlantic swordfish based on the pattern of rapid increases in catch before 1995 that could result in rapid stock depletion, and in declining CPUE trends of some bycatch fisheries. For the 2002 stock assessment, standardized CPUE series were available for three fleets, the targeted fishery of European Community (EC) - Spain, and the bycatch fisheries of Chinese Taipei and Japan. There was considerable conflict in trends among the three CPUE series and it is unclear which, if any, of the series tracks total biomass. It was noted that there was little overlap in fishing area among the three fleets, and that the three CPUE trends could track different components (or cohorts) of the population. To address this possibility, an agestructured production model was run as a sensitivity test. For the base case production model, the Committee selected the bycatch CPUE series combined using a simple unweighted mean and the targeted CPUE series. Due to some inconsistencies in the available CPUE trends reliable stock assessment results could not be obtained (SCRS, 2004). As stated above, the next assessment is scheduled for 2006.

Reported catches of Atlantic swordfish, including discards for the period 1950 – 2004 can be found in Figure 4.2-17. Estimated fishing mortality rate relative to the FMSY for the period 1959 – 2001 can be found in Figure 4.2-18a. Annual yield for North Atlantic swordfish relative to the estimated MSY can be found in Figure 4.2-18b. A summary of Atlantic swordfish stock status can be found in Table 4.2-13.

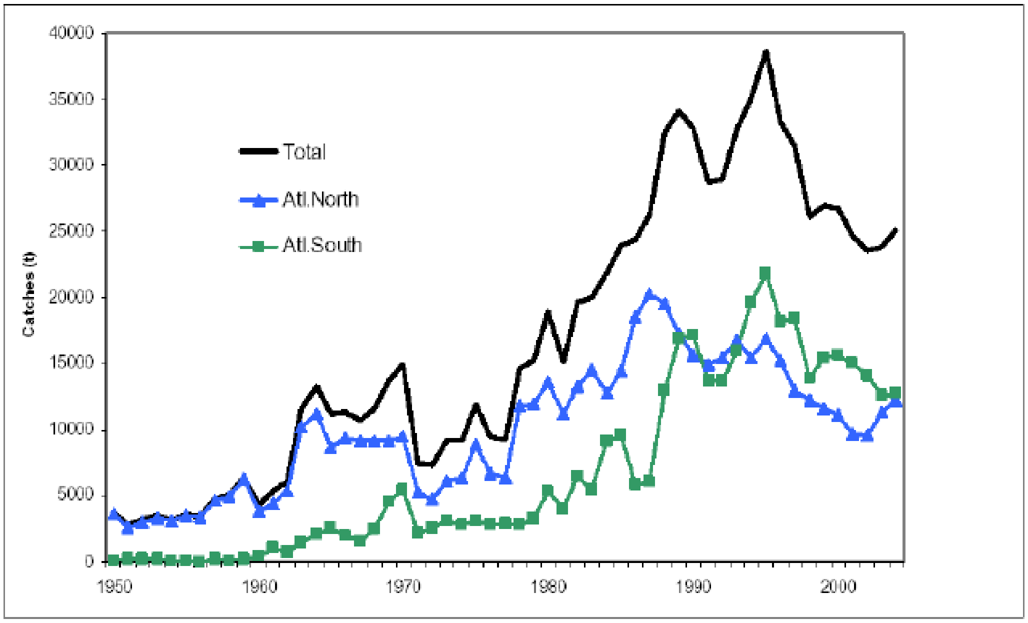


Figure 4.2-17. Reported catches (mt whole weight) of Atlantic Swordfish, including discards for 1950-2004. Source: SCRS, 2005.

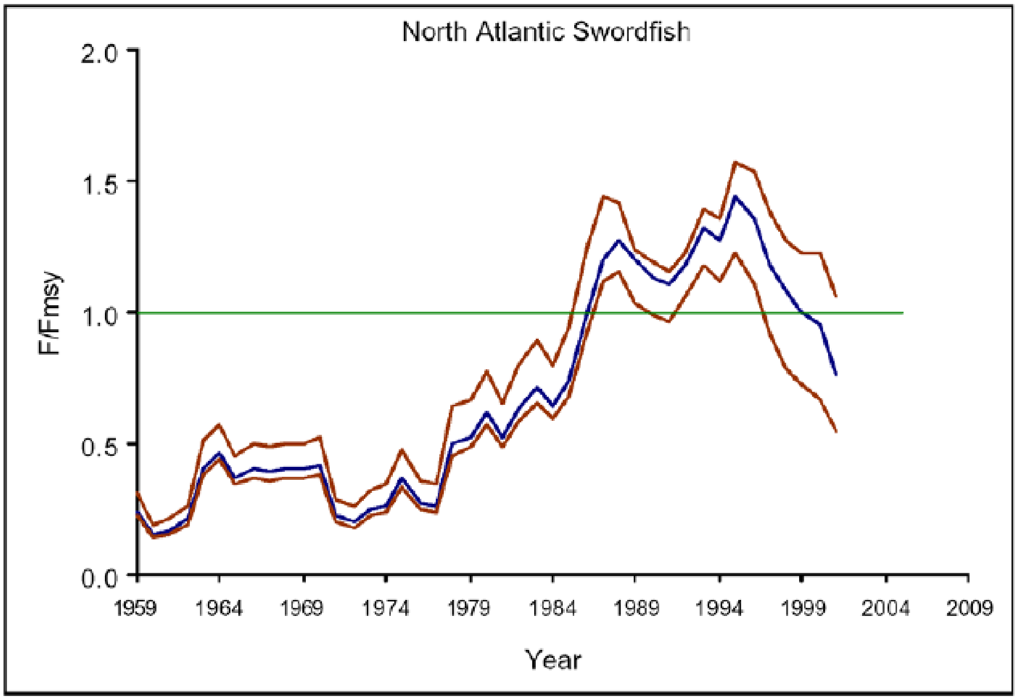


Figure 4.2-18a. Estimated fishing mortality rate relative to FMSY (F/FMSY) for the period 1959-2001 (median with 80 percent confidence bounds based on bootstrapping are shown). Source: SCRS 2004.

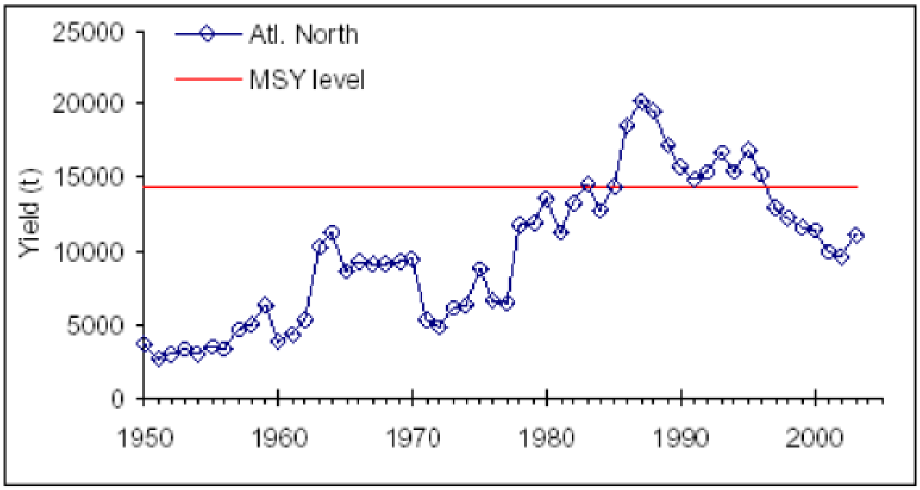
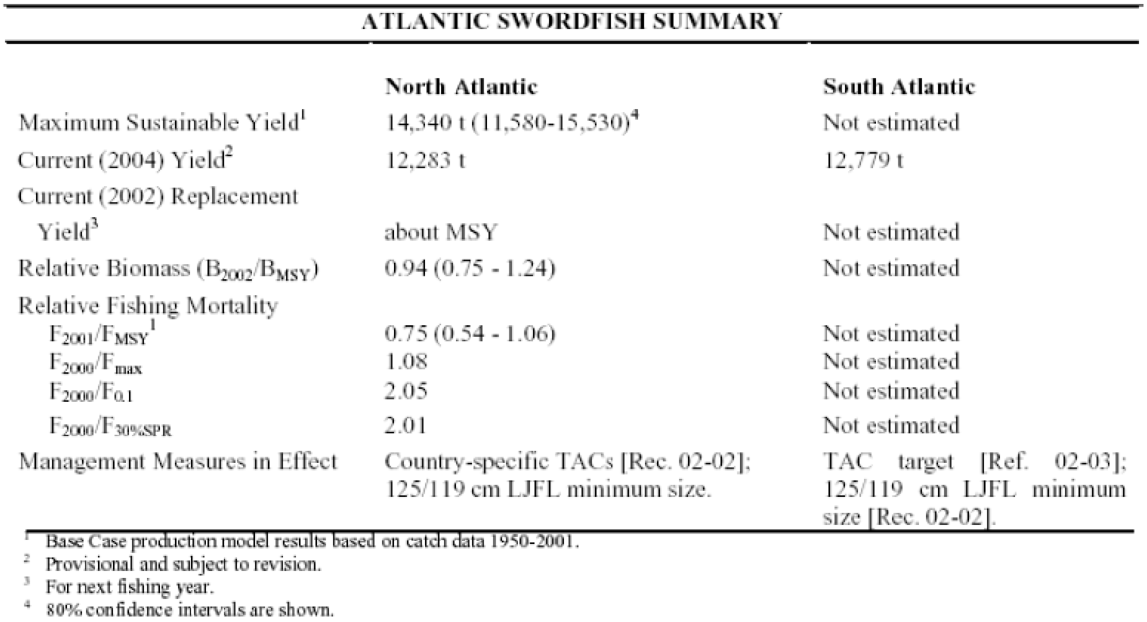


Figure 4.2-18b. Annual yield (mt) (whole weight) for North Atlantic swordfish relative to the estimated MSY level. Source: SCRS 2004.

Table 4.2-13. Atlantic Swordfish Stock Summary (weights given in mt ww). Source: SCRS, 2005.



ATLANTIC SWORDFISH SUMMARY

	North Atlantic	South Atlantic
Maximum Sustainable Yield[1]	14,340 t (11,580-15,530)[4]	Not estimated
Current (2004) Yield[2]	12,283 t	12,779 t
Current (2002) Replacement Yield[3]	about MSY	Not estimated
Relative Biomass (B_{2002}/B_{MSY})	0.94 (0.75 - 1.24)	Not estimated
Relative Fishing Mortality		
F_{2001}/F_{MSY}[1]	0.75 (0.54 - 1.06)	Not estimated
F_{2000}/F_{max}	1.08	Not estimated
$F_{2000}/F_{0.1}$	2.05	Not estimated
$F_{2000}/F_{30\%SPR}$	2.01	Not estimated
Management Measures in Effect	Country-specific TACs [Rec. 02-02]; 125/119 cm LJFL minimum size.	TAC target [Ref. 02-03]; 125/119 cm LJFL minimum size [Rec. 02-02].

[1] Base Case production model results based on catch data 1950-2001.
[2] Provisional and subject to revision.
[3] For next fishing year.
[4] 80% confidence intervals are shown.

Billfish

Life History and Biology

Billfish are classified into the family Istophoridae in the suborder Scombroidei. These fishes are some of the largest and fastest predators in the sea and are distinguished by a long, round, rough bill (swordfish have a flat, smooth bill). Billfish capture prey fish by swimming through schools while slashing the bill back and forth to stun prey. Spearing fish can also be used for defensive purposes or during territorial encounters.

Billfish move thousands of kilometers annually throughout the world's tropical, subtropical, and temperate oceans and adjacent seas. Blue and white marlin are found throughout tropical and temperate waters of the Atlantic ocean and adjacent seas, and range from Canada to Argentina on the west side, and from the Azores to South Africa on the eastern side. Sailfish and spearfish have a pan-tropical distribution.

As adults and juveniles they feed at the top of the food web on a wide variety of fish and squid and are found predominately in the open ocean near the upper reaches of the water column.

Blue Marlin

Blue marlin (*Makaira nigricans*) range from Canada to Argentina in the western Atlantic and from the Azores to South Africa in the eastern Atlantic. Blue marlin are large apex predators with an average weight of 100 – 175 kg (220 – 385 lb). Female blue marlin grow faster and reach a larger maximum size than males. Young blue marlin are one of the fastest growing teleosts, reaching 30 – 45 kg (66 – 99 lb) after the first year. The maximum growth rate of these fish is 1.66 cm/day (0.65 inches/day) which occurs at 39 cm LJFL (15.3 inches) (NMFS, 1999).

Life expectancy for blue marlin is between 20 – 30 years based on age and growth analyses of dorsal spines. Estimates of natural mortality rates for juvenile and adult billfish would be expected to be relatively low, generally in the range of 0.15 to 0.30, based on body size, behavior and physiology (NMFS, 1999). Sagitta otolith weight is suggested to be proportional to age, indicating that both sexes are equally long-lived, based on the maximum otolith weight observed for each sex. Predicting age from length or weight is imprecise due to many age classes in the fishery, and otoliths may provide a more accurate measure of age.

Blue marlin have an extensive geographical range, migratory patterns that include trans-Atlantic as well as trans-equatorial movements, and are generally considered to be a rare and solitary species relative to the schooling Scombrids (tunas). Graves et al. (2002) captured eight blue marlin with recreational fishing gear and then implanted fish with satellite pop-up tags. These fish moved 74 – 248 km (40–134 nautical miles (nm)) over five days, with a mean displacement of 166 km (90 nm). Fish spent the vast majority of their time in waters with temperatures between 22 and 26°C (71–78°F) and at depths less than 10 m. Prince et al. (2005) tagged one blue marlin with a PSAT tag off the coast of Punta Cana, Dominican Republic and found that this fish moved 406.2 km (219.3 nm) during a 40-d deployment (10.15 km/day (5.48 nm/day)). The maximum time at liberty recorded of a tagged individual was 4,024 days (about 11 years) for a blue marlin that was estimated to weigh 29.5 kg (65 lb) at the time of release. Junior et al. (2004) found the depth of capture for blue marlin with pelagic longline gear ranged from 50 – 190 m (164 – 623 feet), with most individuals captured at 90 m (295 feet).

The Cooperative Tagging Center (CTC) program has tagged 24,108 and recaptured over 220 blue marlin and found that these fish moved an average of 903 km (488 nm) (Ortiz et al., 2003). Some individuals have exhibited extended movement patterns, and strong seasonal patterns of movement of individuals between the United States and Venezuela are evident. A blue marlin released off Delaware and recovered off the island of Mauritius in the Indian Ocean represents the only documented inter-ocean movement of a highly migratory species in the history of the CTC. The minimum straight-line distance traveled for a blue marlin was 14,893 km (8,041 nm) and the maximum number of days at large was 4,024 d.

Adults are found primarily in the tropics within the 24°C (75°F) isotherm, and make seasonal movements related to changes in sea surface temperatures. In the northern Gulf of Mexico they are associated with the Loop Current, and are found in blue waters of low productivity rather than in more productive green waters. Off of Puerto Rico, the largest numbers of blue marlin are caught during August, September, and October. Equal numbers of both sexes occur off northwest Puerto Rico in July and August, with larger males found there in May and smaller males in September. Very large individuals, probably females, are found off the southern coast of Jamaica in the summer and off the northern coast in winter, where males are caught in December and January.

There has not been an Atlantic wide survey of spawning activity for blue marlin, however, these fish generally reproduce between the ages of two and four, at 220 – 230 cm (86 – 90 inches) in length, and weigh approximately 120 kg (264 lb). Female blue marlin begin to mature at approximately 47 – 60 kg (104 – 134 lb), while males mature at smaller weights, generally from 35 – 44 kg (77 – 97 lb). There are likely two separate spawning events that occur at different times in the North and South Atlantic. South Atlantic spawning takes place between February and March (NMFS, 1999). Peak spawning activity in the North Atlantic Ocean occurs between

July and October, with females capable of spawning up to four times per reproductive season (de Sylva and Breder, 1997). Prince et al. (2005) conducted 23 neuston tows in the vicinity of Punta Cana, Dominican Republic between 23 April and 17 May and successfully identified four larval blue marlin; the size of the larvae indicated that spawning activity was taking place in the same general area where these samples were conducted. Serafy et al. (2003) identified 90 blue marlin larvae in the vicinity of Exuma Sound, Bahamas in the month of July, indicating that spawning activity had taken place 18 days prior to sampling.

During the spawning season, blue marlin release between one and eleven million small (1 – 2 mm), transparent pelagic planktonic eggs. The number of eggs has been correlated to interspecific sizes among billfish and the size of individuals within the same species. Ovaries from a 147 kg (324 lb) female blue marlin from the northwest Atlantic Ocean were estimated to contain 10.9 million eggs, while ovaries of a 125 kg (275 lb) female were estimated to contain seven million eggs. Males are capable of spawning at any time.

Blue marlin are generalist predators feeding primarily on epipelagic fish and cephalopods in coastal and oceanic waters, however, mesopelagic fish and crustaceans associated with rocky, sandy, and reef bottoms are also important components of the diet. Feeding in mesopelagic areas probably takes place at night (Rosas-Alayola et al., 2002). Diet studies of blue marlin off the northeastern coast of Brazil indicate that oceanic pomfret (*Brama brama*) and squid (*Ornithoteuthis antillarum*) were the main prey items and present in at least 50 percent of stomachs. Other important prey species vary by location and include dolphin fishes, bullet tuna (*Auxis*. spp) around the Bahamas, Puerto Rico, and Jamaica, and dolphin fishes and scombrids in the Gulf of Mexico. Stomach contents have also included deep-sea fishes such as chiasmodontids.

Constant ingestion of small quantities of food is necessary. Blue marlin have relatively small stomachs, reducing the proportion of the body allocated for visceral mass, and allocating more volume to musculature for swimming speed and endurance (Junior et al., 2004). In the Pacific Ocean, changes in the diet observed are related more with abundance and distribution of prey than preferences in food items, with Auxis spp. (bullet and frigate tunas) well represented in all locations. Predators of blue marlin are relatively unknown. Sharks will attack hooked blue marlin, but it is not known if they attack free-swimming, healthy individuals.

White Marlin

White marlin (*Tetrapturus albidus*) are found exclusively in tropical and temperate waters of the Atlantic Ocean and adjacent seas, unlike sailfish and blue marlin, which are also found in the Pacific Ocean. White marlin are found at the higher latitudes of their range only in the warmer months. Junior et al. (2004) captured white marlin with pelagic longline gear off northeastern Brazil in depths ranging from 50 – 230 m (164 – 754 feet), with no obvious depth layer preference. White marlin generally prefer water temperatures above 22°C (71° F) with salinities between 35 – 37 ppt (NMFS, 1999). They may occur in small, same-age schools, however, are generally solitary compared to the Scombrids (tunas). Catches in some areas may include a rare species (*Tetrapturus georgei*) which is superficially similar to white marlin. The so-called "hatchet marlin" may also represent (*T. georgei*), and has been caught occasionally in the Gulf of Mexico and South Atlantic (NMFS, 1999).

White marlin are generally 20 – 30 kg (44 – 66 lb) at harvest. These fish grow quickly, with females attaining a larger maximum size than males, and have a life span of 18 years (SCRS 2004). Adult white marlin grow to over 280 cm (110 inches) TL and 82 kg (184 lb). White marlin exhibit sexually dimorphic growth patterns; females grow larger than males, but the dimorphic growth differences are not as extreme as noted for blue marlin.

This species undergoes extensive movements, although not as extreme as those of the bluefin tuna and albacore. Trans-equatorial movements have not been documented for the species. There have been 31,483 white marlin tagged and released by the CTC program, with 577 reported recaptures (1.83 percent of all releases) (Ortiz et al., 2003). The majority of releases took place in the months of July through September, in the western Atlantic off the east coast of the United States.

Releases of tagged white marlin also occurred off Venezuela, in the Gulf of Mexico, and in the central west Atlantic. The longest distance traveled is 6,517 km (4,049 miles) and the maximum days at large is 5,488 days (approx. 15 years). A substantial number of individuals moved between the Mid-Atlantic coast of the United States and the northeast coast of South America. Overall, 1.1 percent of documented white marlin recaptures have made trans-Atlantic movements. The longest movement was for a white marlin tagged during July 1995 off the east coast near Cape May, NJ and recaptured off Sierra Leone, West Africa, in November, 1996. The fish traveled a distance of at least 6,517 km (3,519 nm) over 476 days (NMFS, 1999). Prince et al. (2005) tagged six white marlin off the coast of Punta Cana, Dominican Republic and found their displacement to be between 58.7 and 495.8 km (31.7 – 267.7 nm), ranging from 2.1 – 13.3 km/day (mean = 6.3 km/day).

White marlin spawn in the spring (March through June) in the northwestern Atlantic Ocean and females are generally 20 kg (44 lb) in mass and 130 cm (51.2 inches) in length at sexual maturity. White marlin spawn in tropical and sub-tropical waters with relatively high surface temperatures and salinities (20 – 29°C (68 – 84°F) and over 35 ppt) and move to higher latitudes during the summer. There has not been an Atlantic-wide study of the spawning behavior of white marlin. Spawning seems to take place in more offshore areas than for sailfish, although larvae are not found as far offshore as blue marlin. Females may spawn up to four times per spawning season (de Sylva and Breder, 1997). It is believed there are at least three spawning areas in the western north Atlantic: northeast of Little Bahama Bank off the Abaco Islands; northwest of Grand Bahama Island; and southwest of Bermuda. Prince et al. (2005) found eight white marlin larvae in neuston tows in April/May off the coast of Punta Cana, Dominican Republic indicating that there had been recent spawning activity in this general area.

Larvae have also been collected from November to April, but these may have been sailfish larvae (*Istiophorus platypterus*), as the two can not readily be distinguished (NMFS, 1999). Spawning concentrations occur off the Bahamas, Cuba, and the Greater Antilles, probably beyond the U.S. EEZ, although the locations are unconfirmed.

Concentrations of white marlin in the northern Gulf of Mexico and from Cape Hatteras, NC to Cape Cod, MA are probably related to feeding rather than spawning (NMFS, 1999).

White marlin are primarily piscivorous. Oceanic pomfret and squid were the most important food items in a study that sampled stomachs collected off the coast of Brazil in the southwestern Atlantic Ocean (Junior et al., 2004). The number of food items per stomach ranged from 1 – 12 individuals. The largest prey observed in white marlin stomachs were snake mackerel (*Gempylus serpens*), that were 40 – 73 cm (15.7 – 28.7 inches) in length (Junior et al., 2004). Squid, dolphin, hardtail jack, flying fish, bonitos, mackerels, barracuda, and puffer fish are the most important prey items in the Gulf of Mexico.

Data from a large sport fishery for white marlin that occurs during the summer between Cape Hatteras, NC and Cape Cod, MA indicates that white marlin inhabit offshore (148 km (80 nm)) submarine canyons, extending from Norfolk Canyon in the Mid-Atlantic to Block Canyon off eastern Long Island. Concentrations of white marlin are associated with rip currents and weed lines (fronts), and with bottom features such as steep drop-offs, submarine canyons, and shoals. Sport fishing for white marlin also occurs in the Straits of Florida, southeast Florida, the Bahamas, and off the north coasts of Puerto Rico and the Virgin Islands. Summer concentrations in the Gulf of Mexico are found off the Mississippi River Delta and at DeSoto Canyon, with a peak off the delta in July, and in the vicinity of DeSoto Canyon in August. In the Gulf of Mexico, adults appear to be associated with blue waters of low productivity, being found with less frequency in more productive green waters. While this is also true of the blue marlin, there appears to be a contrast between the factors controlling blue and white marlin abundance, as higher numbers of blue marlin are generally caught when catches of white marlin are low, and vice versa. It is believed that white marlin prefer slightly cooler temperatures than blue marlin.

Sailfish

Sailfish (*Istiophorus platypterus*) have a pan-tropical distribution and prefer water temperatures between 21 and 28°C (69 – 82°F). Although sailfish are the least oceanic of the Atlantic billfish and have higher concentrations in coastal waters (more than any other Istiophorid), they are also found in offshore waters. They range from 40°N to 40°S in the western Atlantic and 50°N to 32°S in the eastern Atlantic. No trans-Atlantic movements have been recorded, suggesting a lack of mixing between east and west. Although sailfish are generally considered to be rare and solitary species relative to the schooling Scombrids, sailfish are known to occur along tropical coastal waters in small groups consisting of at least a dozen individuals. Junior et al. (2004) captured sailfish in the southwestern Atlantic Ocean with pelagic longline gear at depths between 50 – 210 m (164 – 688 feet), with most individuals captured at 50 m.

Sailfish are the most common representative of the Atlantic Istiophorids in U.S. waters (SCRS, 2005). Female sailfish grow faster, and attain a larger maximum size, than males while both sexes have a life expectancy of 15 years (NMFS,1999).

In the winter, sailfish are found in schools around the Florida Keys and eastern Florida, in the Caribbean, and in offshore waters throughout the Gulf of Mexico. In the summer, they appear to migrate northward along the U.S. coast as far north as the coast of Maine, although there is a population off the east coast of Florida year-round. During the summer, some of these fish move north along the inside edge of the Gulf Stream. In the winter, they regroup off the east coast of Florida. Sailfish appear to spend most of their time above the thermocline, which occurs at depths of 10 – 20 m (32.8 – 65.6 feet) and 200 – 250 m (656 – 820 feet), depending on location. The 28EC (82°F) isotherm appears to be the optimal temperature for this species.

Sailfish are mainly oceanic but migrate into shallow coastal waters. Larvae are associated with the warm waters of the Gulf Stream (NMFS, 1999). A total of 65,868 sailfish have been tagged and released through the efforts of the CTC program, with reported recapture of 1,204 sailfish (1.83 percent of all releases). Most releases occurred off southeast Florida, from north Florida to the Carolinas, the Gulf of Mexico, Venezuela, Mexico, the northern Bahamas and the U.S. Virgin Islands. One tagged and recaptured specimen traveled from Juno, FL to the Mid-Atlantic, a distance of 2,972 km (1,745 miles). The longest movement tracked by tagging was 3,861 km (2,084 miles) and the longest time at large was 6,658 days (18.2 years) (Ortiz et al., 2003). During the winter, sailfish are restricted to the warmer parts of their range and move farther from the tropics during the summer.

The summer distribution of sailfish does not extend as far north as for marlins, especially white marlin. Tag-and-recapture efforts have recovered specimens only as far north as Cape Hatteras, NC. Few trans-Atlantic or trans-equatorial movements have been documented using tagrecapture methods (NMFS, 1999).

Most sailfish examined that have been caught off Florida are under three years of age. Mortality is estimated to be high in this area, as most of the population consists of only two year classes. The longest period a recaptured-tagged animal was found to be at-large was 16.1 years. Unfortunately, the size at release is not available for this fish. Growth rate in older individuals is very slow (0.59 kg/yr (1.3 lb/year). Sailfish are probably the slowest growing of the Atlantic istiophorids. Sexual dimorphic growth is found in sailfish, but it is not as extreme as with blue marlin (NMFS, 1999).

Female sailfish spawn at age three and are generally 13 – 18 kg and 157 cm (28.6 – 39.6 lb and 61.8 inches), whereas males generally mature earlier at 10 kg and 140 cm (22 lb and 55.1 inches). Spawning takes place between April and October (de Sylva and Breder, 1997). Spawning has been reported to occur in shallow waters 9 – 12 m (30 – 40 ft) around Florida, from the Florida Keys to the region off Palm Beach on the east coast. Spawning is also assumed to occur, based on presence of larvae, offshore beyond the 100 m (328 feet) isobath from Cuba to the Carolinas, from April to September. However, these spawning activities have not been observed. Sailfish can spawn multiple times in one year, with spawning activity-moving northward in the western Atlantic as the summer progresses. Larvae are found in Gulf Stream waters in the western Atlantic, and in offshore waters throughout the Gulf of Mexico from March to October (NMFS, 1999). Serafy et al. (2003) found three larval sailfish in Exuma Sound, Bahamas, in the month of July indicating that there had been recent spawning activity in this vicinity. In the Pacific Ocean, sailfish spawn in waters between 27 – 30°C (Hernandez-H and Ramirez-H, 1998).

Sailfish are generally piscivorous, but also consume squid. Larvae eat copepods early in life then switch to fish at 6.0 mm (0.2 inches) in length (NMFS, 1999). The diet of adult sailfish caught around Florida consists mainly of pelagic fishes such as little tunny (*Euthynnus alletteratus*), halfbeaks (*Hemiramphus* spp.), cutlassfish (*Trichiurus lepturus*), rudderfish (*Strongylura* *notatus*), jacks (*Caranx* spp.), pinfish (*Lagodon rhomboides*), and squids (*Argonauta argo* and *Ommastrephes bartrami*). Sailfish are opportunistic feeders and there is evidence that they may feed on demersal species such as sea robin (Triglidae), cephalopods and gastropods found in deepwater. Sailfish collected in the western Gulf of Mexico contained a large proportion of shrimp in their stomachs in addition to little tunny, bullet tuna (*Auxis* spp.), squid, and Atlantic moonfish (*Vomer setapinnis*). Junior et al. (2004) determined that squid were actually the second most important food item in the southwestern Atlantic off the coast of Brazil. Number of food items per stomach ranged from 1-14, and 6 percent of the stomachs were empty upon collection (Junior et al., 2004). Adult sailfish are probably not preyed upon often, but predators include killer whales (*Orcinus orca*), bottlenose dolphin (*Tursiops truncatus*), and sharks.

Participants from many nations target sailfish in both the western and eastern Atlantic Ocean. Sailfish are found predominantly in the upper reaches of the water column and are caught in directed sport fisheries (recreational) and as bycatch in the offshore longline fisheries for swordfish and tunas and as a directed catch in coastal fisheries. In coastal waters, artisanal fisheries use many types of shallow water gear to target sailfish (NMFS, 2003).

Longbill Spearfish

The longbill spearfish (*Tetrapturus pfluegeri*) are the most rare of the Atlantic istiophorids, and were identified as a distinct species in 1963. There is relatively little information available on spearfish life history. A related istiophorid, the Mediterranean spearfish (*Tetrapturus belone*), is the most common representative of this family in the Mediterranean Sea.

Longbill spearfish are known to occur in epipelagic waters above the thermocline, off the eastcoast of Florida, the Bahamas, the Gulf of Mexico, and from Georges Bank to Puerto Rico. Junior et al. (2004) captured spearfish off the coast of Brazil at depths ranging from 50 – 190 m (164 – 623 feet). The geographic range for this species is from 40°N to 35°S.
Spearfish spawn from November to May and females are generally 17 – 19 kg (37.4 – 41.8 lb) and 160 – 170 cm (63 – 66 inches) at first maturity.

These fish are unique among istiophorids in that they are winter spawners. Larval spearfish have been identified from the vicinity of the Mid-Atlantic ridge from December to February, indicating that this species spawns in offshore waters (de Sylva and Breder, 1997).

Common prey items include fish and squid. Specifically, Junior et al. (2004) observed 37 stomachs and found that oceanic pomfret and squid comprised 63 percent of the items identified in stomachs. Most prey items were between 1 and 10 cm (0.39 – 3.9 inches) in length, with a mean length of 6.7 cm (2.63 inches). The maximum number of prey items found in any individual stomach was 33.

Similar to sailfish, spearfish are caught incidentally or as bycatch in offshore longline fisheries by many nations. There are also artisinal fisheries that take place in the Caribbean Sea and in the Gulf of Guinea. Directed recreational fisheries for spearfish are limited due to the fact that the fish are generally located further offshore than other istiophorids. The reported catches of sailfish/spearfish (Task I) for 2003 are 1,310 and 416 mt (2,888,055 and 917,123 lb) for the west and east Atlantic, respectively. The 2001 – 2003 reported catch of unclassified billfish was 12 percent of the reported catch for all billfish and, for some fisheries, this proportion is much greater. This is a problem for species like spearfish for which there is already a paucity of data (SCRS, 2004).

Abundance and status of stocks

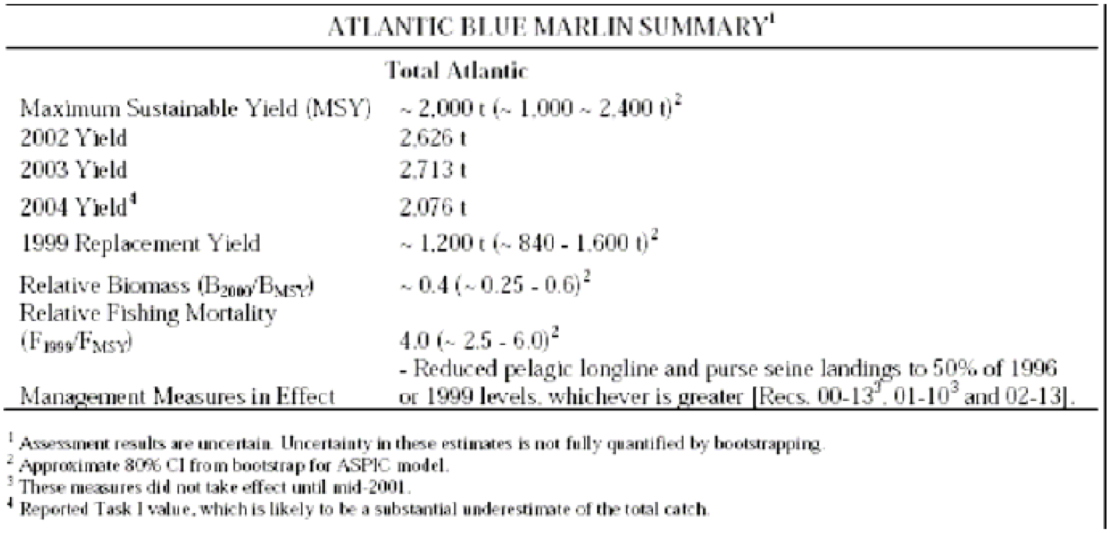
Blue Marlin

Since 1995, blue marlin have been managed under a single stock hypothesis because of tagging data and mitochondrial DNA evidence that are consistent with one Atlantic-wide stock. The last stock assessment for blue marlin was in 2000 using similar methods to the previous assessment (1996), however, data was revised in response to concerns raised since the 1996 assessment. The assessment reflects a retrospective pattern wherein improvement in estimated biomass ratios result in estimated lower productivity. The 2000 assessment was slightly more optimistic than the 1996 assessment. Atlantic blue marlin are at approximately 40 percent of BMSY and overfishing has taken place for the last 10 – 15 years. BMSY is estimated at 2,000 mt (4,409,245 lb) and current fishing mortality is approximately four times higher than FMSY (Table 4.2-14) (SCRS, 2005). There is uncertainty in the assessment because the historical data is not well quantified. The 2000 assessment estimated that overfishing was still occurring and that productivity (MSY and a stock's capacity to replenish) was lower than previously estimated. Therefore, it is expected that landings in excess of estimated replacement yield would result in further stock decline (SCRS, 2005).

No additional assessment information became available in 2005 to modify recommendations currently in force. The current assessment indicates that the stock is unlikely to recover if the landings contemplated by the 1996 ICCAT recommendation continue into the future. While there is additional uncertainty in stock status and replacement yield, estimates are not reflected in bootstrap results, these uncertainties can only be addressed through substantial investment in research into habitat requirements of blue marlin and further verification of historical data. The SCRS recommended that the ICCAT take steps to reduce the catch of blue marlin as much as possible, including: reductions in fleet-wide effort, a better estimation of dead discards, establishment of time area closures, and scientific observer sampling for verification of logbook data. The SCRS noted that future evaluation of management measures relative to the recovery of the blue marlin stock are unlikely to be productive unless new quantitative information on the biology and catch statistics of blue marlin, and additional years of data are available (SCRS, 2004 and 2005).

A summary of Atlantic blue marlin stock assessment data can be found in Table 4.2-14. Estimated catches of Atlantic blue marlin by region for the period 1956 – 2001 can be found in Figure 4.2-19. A composite CPUE series for blue marlin for the period 1955 – 2000 can be found in Figure 4.2-20. The estimated median relative fishing mortality trajectory for Atlantic blue marlin can be found in Figure 4.2-21. Estimated catches (including landings and dead discards in t) of blue marlin in the Atlantic by region (1950-2004) is shown in Figure 4.2-22. A stock assessment for blue marlin is scheduled for 2006.

Table 4.2-14. Summary of Atlantic Blue Marlin Stock Assessment data. Weights are in metric tons, whole weight. Source: SCRS, 2005.



ATLANTIC BLUE MARLIN SUMMARY[1]	
	Total Atlantic
Maximum Sustainable Yield (MSY)	~ 2,000 t (~ 1,000 ~ 2,400 t)[2]
2002 Yield	2,626 t
2003 Yield	2,713 t
2004 Yield[4]	2,076 t
1999 Replacement Yield	~ 1,200 t (~ 840 - 1,600 t)[2]
Relative Biomass (B_{2000}/B_{MSY})	~ 0.4 (~ 0.25 - 0.6)[2]
Relative Fishing Mortality (F_{1999}/F_{MSY})	4.0 (~ 2.5 - 6.0)[2]
Management Measures in Effect	- Reduced pelagic longline and purse seine landings to 50% of 1996 or 1999 levels, whichever is greater [Recs. 00-13[3], 01-10[3] and 02-13].

[1] Assessment results are uncertain. Uncertainty in these estimates is not fully quantified by bootstrapping.

[2] Approximate 80% CI from bootstrap for ASPIC model.

[3] These measures did not take effect until mid-2001.

[4] Reported Task I value, which is likely to be a substantial underestimate of the total catch.

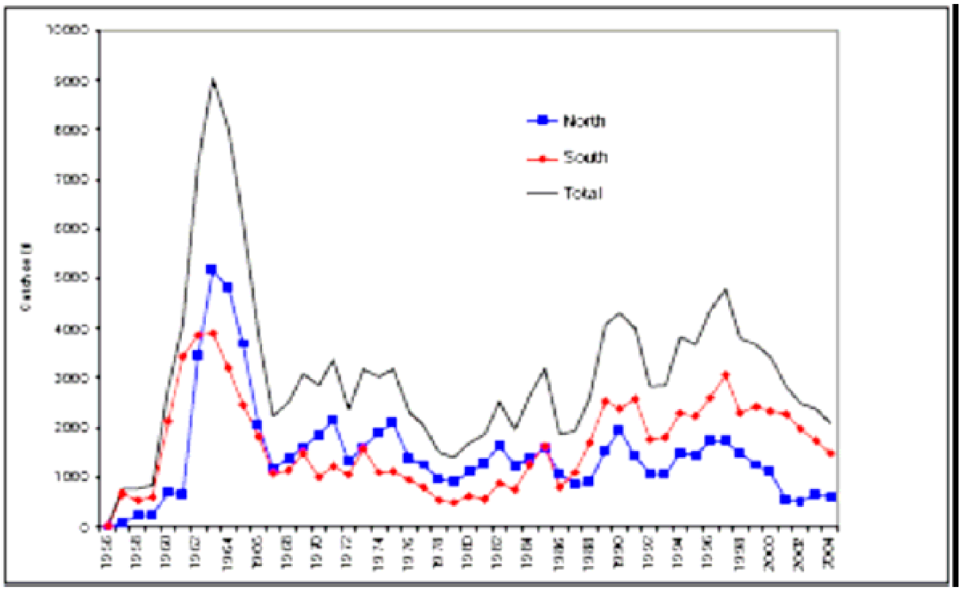


Figure 4.2-19. Estimated catches (including landings and dead discards in mt) of blue marlin in the Atlantic by region. The 2003 catch reported to ICCAT is preliminary and is not included in this figure. Weights are in metric tones, whole weight. Source: SCRS, 2005.

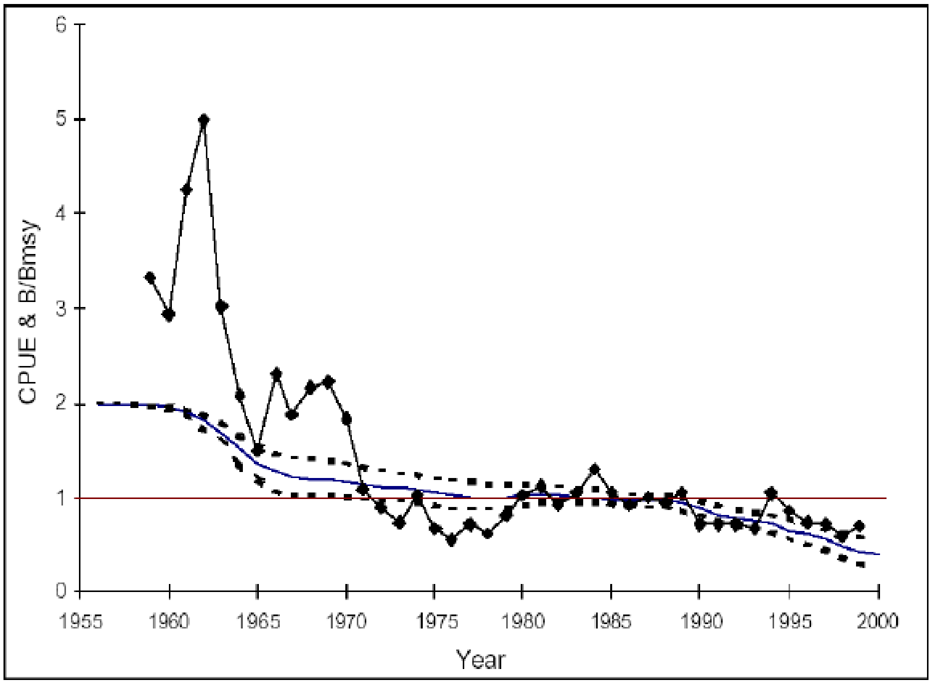


Figure 4.2-20. Composite CPUE series (symbols) used in the blue marlin assessment compared to model estimated median relative biomass (solid lines) from bootstrap results (80 percent confidence bounds shown by dotted lines). Source: SCRS, 2005.

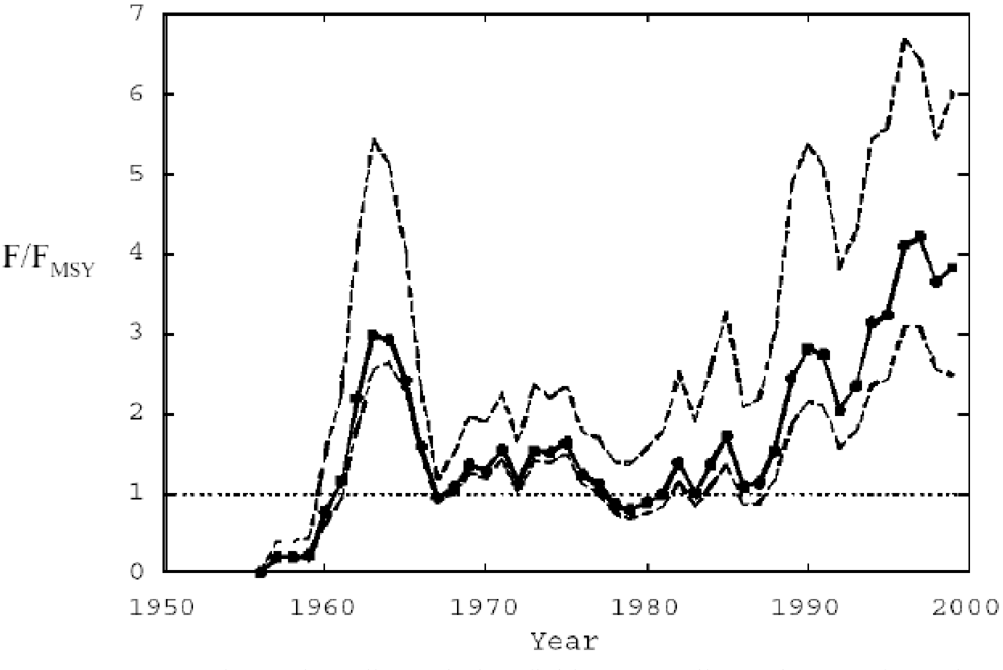


Figure 4.2-21. Estimated median relative fishing mortality trajectory for Atlantic blue marlin (center, dark line) with approximate 80 percent confidence range (light lines) obtained from bootstrapping. Source: SCRS, 2005.

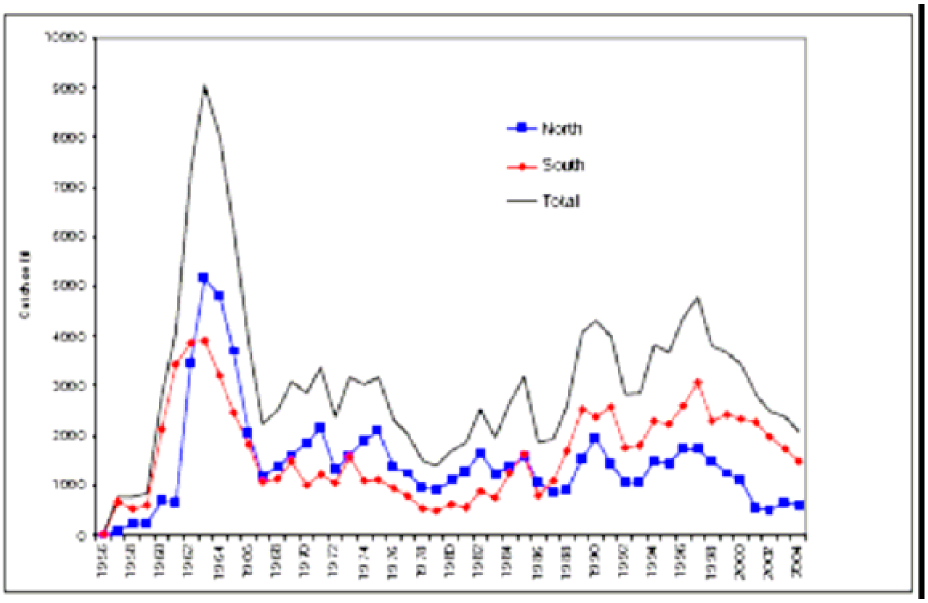


Figure 4.2-22. Estimated catches (including landings and dead discards in t) of blue marlin in the Atlantic by region (1950-2004). Source: SCRS, 2005.

White Marlin

White marlin have been managed under a single stock hypothesis by ICCAT since 2000. The most recent stock assessments for white marlin (1996, 2000, and 2002) all indicated that biomass of white marlin has been below BMSY for more than two decades and the stock is overfished. In 2004, the SCRS indicated that in spite of significant improvements in the relative abundance estimates made available during the last three assessments, they are still not informative enough to provide an accurate estimate of stock status (SCRS, 2004). The 2002 assessment indicated that the relative fishing mortality is 8.28 times that permissible at FMSY (Figure 4.2-23). Given that the stock is severely depressed, the SCRS concluded that ICCAT should take steps to reduce the catch of white marlin as much as possible, first by increasing observer coverage to improve estimates of catch and dead discards of white marlin. Furthermore, SCRS recommended that Contracting Parties conduct research into habitat requirements and post-release survival of white marlin and take steps to verify historical fishery data.

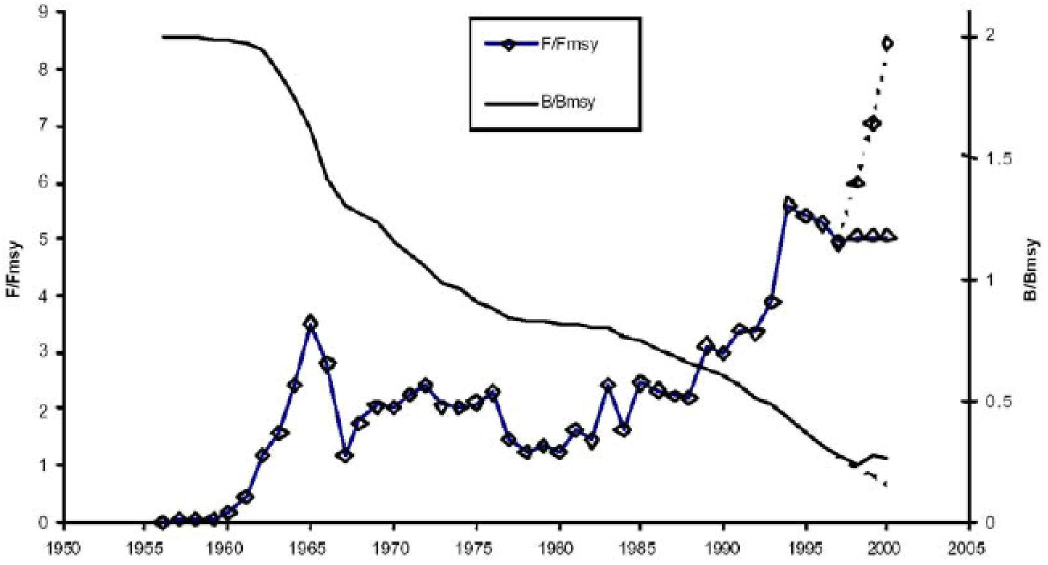


Figure 4.2-23. Estimated biomass ratio B2000/ BMSY (solid line, no symbols) and fishing mortality ratio F2000/FMSY (solid line with symbols) from the production model fitted to the continuity case for white marlin. Ratios of last three years have been adjusted for retrospective pattern. Broken lines show unadjusted ratios. Note that scales are different for each ratio. Source: SCRS, 2004.

The SCRS suggested that ICCAT take steps to make sure that the intended reductions in catch are complied with, and monitored, so that proper evaluation can be carried out in the future.

The SCRS recommended improving observer programs so that better estimates of catch and dead discards of white marlin are obtained. The SCRS further recommended that, in the absence of observing a change in population status resulting from the most recent management measures, the potential for increasing stock size of white marlin may require future catches to be reduced beyond the level apparently intended by its most recent recommendations. However, the SCRS also stated that more definitive advice should be available after several years of data become available. The SCRS also noted that future evaluation of management measures relative to the recovery of the white marlin stock is unlikely to be productive unless new quantitative information on the biology and catch statistics of white marlin, and additional years of data, are available (SCRS, 2004). As such, ICCAT postponed the next white marlin assessment until 2006. A summary of Atlantic white marlin stock assessment data can be found in Table 4.2-15. Reported catch of white marlin in the North and South Atlantic by gear is shown in Figure 4.2-24.

New standardized catch rate information was presented in 2005, updating catch rates from U.S. recreational fisheries in the northwest Atlantic and Gulf of Mexico and the Venezuelan longline and artesinal fisheries. In spite of the progress made, the SCRS can not interpret the historic CPUE trends for white marlin (SCRS, 2005). In 2002, an ESA listing review was completed by NMFS. NMFS determined that listing Atlantic white marlin under the Endangered Species Act was not warranted at that time. NMFS has committed to conducting another ESA listing review in 2007.

Table 4.2-15. Summary of Atlantic White Marlin Stock Assessment data. Weights are in metric tons, whole weight. Source: SCRS, 2005.

ATLANTIC WHITE MARLIN SUMMARY[1]

	Likely value	*Continuity case[2] estimate (80% conf. limit)*	*Retrospective adjusted estimate[3]*	*Range of sensitivity[4] estimates*
Maximum Sustainable Yield	Below 2000 Yield	964 t (849-1070)		323-1,320 t
2002 Yield	822 t	--		--
2003 Yield	615 t	--		--
2004 Yield[5]	532 t			
2001 Replacement Yield	Below 2000 Yield	222 t (101-416)	371 t	102-602 t
Relative Biomass (B_{2001}/B_{MSY})	<1 (Over-fished)	0.12 (0.06-0.25)	0.22	0.12-1.76
Relative Fishing Mortality (F_{2000}/F_{MSY})	>1 (Over-fishing)	8.28 (4.5-15.8)	5.05	0.80-10.30
Management Measures in Effect:	- In 2001 and 2002, PS and LL fisheries limit landings to 33% of max (1996, 1999) level. [Rec. 00-13], [Rec. 01-10] and [Rec. 02-13].			

[1] Assessment results are highly uncertain.

[2] The data used are not sufficiently informative to choose a "best case". For consistency, the continuity case presented here is based on data and assumptions that closely resemble the analyses made in 2000. Confidence limits from bootstrapping are conditional on this model-data set and thus may underestimate the real uncertainty.

[3] These results are for the continuity case except that they were adjusted for retrospective biases.

[4] The sensitivity analyses made were not chosen in a systematic way; the range is presented only for qualitative guidance.

[5] Reported Task I value for 2004, which is likely an underestimate of total catch.

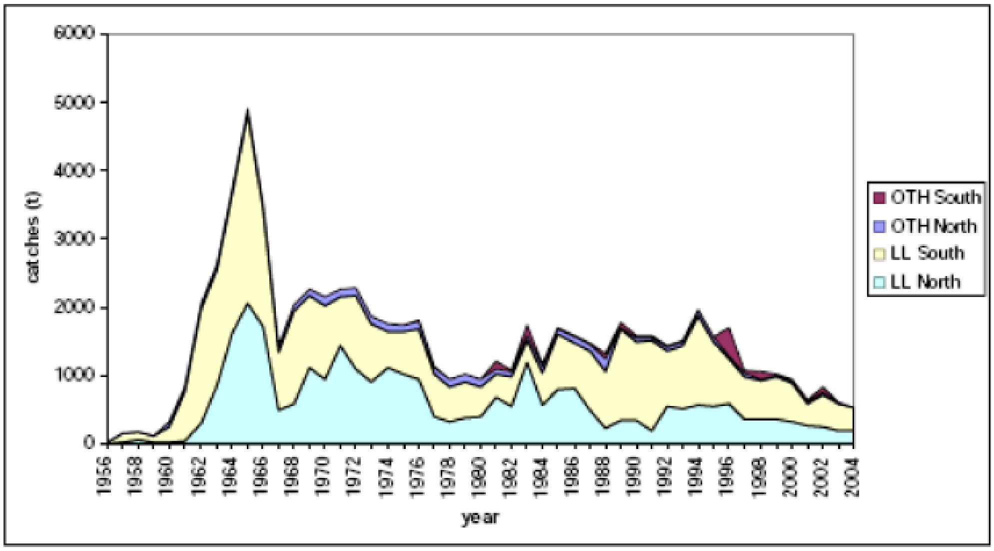


Figure 4.2-24. Reported catch of white marlin (Task I) in the North and South Atlantic for longline (LL) gear and other (OTH) gears. Source: SCRS, 2005.

Sailfish

Sailfish and longbill spearfish landings have historically been reported together in annual ICCAT landing statistics. An assessment was conducted in 2001 for the western Atlantic sailfish stock based on sailfish/spearfish composite catches and sailfish "only" catches. The assessment tried to address shortcomings of previous assessments by improving abundance indices and separating the catch of sailfish from that of spearfish in the offshore longline fleets. The 2001 assessment looked at catches reported between 1956 and 2000 and all the quantitative assessment models used produced unsatisfactory fits, therefore the SCRS recommended applying population models that better accounted for these dynamics in order to provide improved assessment advice. For the western Atlantic stock, annual sailfish catches have averaged about 700 mt (1,543,235 lb) over the past two decades and the abundance indices have remained relatively stable. The 2000 yield was 506 mt (1,115,539 lb) (Table 4.2-16). The reported catches of sailfish/spearfish (Task I) for 2004 were 1,017 and 1,088 mt for the west and east Atlantic, respectively. Recent analyses did not provide any information on the MSY or other stock benchmarks for the 'sailfish only' stock. In the eastern Atlantic, abundance indices based on coastal/inshore fisheries for sailfish have decreased in recent years, while those attained from the Japanese longline fishery indicate constant estimates of abundance since the mid-1970s (SCRS, 2004).

Based on the 2001 assessment, it is unknown if the western or eastern sailfish stocks are undergoing overfishing or if the stocks are currently overfished. Therefore, SCRS recommended that Contracting Parties consider methods to reduce fishing mortality rates, overall, and that western Atlantic catches should not be increased above current levels. Furthermore, the SCRS expressed concern about the incomplete reporting of catches, particularly in recent years.

A summary of Atlantic sailfish stock assessment data is given in Table 4.2-16. The evolution of estimated sailfish/spearfish catches in the Atlantic during the period 1956 – 2002 for both east and west stocks is given in Figure 4.2-25. Available CPUE for western Atlantic sailfish/spearfish for the period 1967 – 2000 is shown in Figure 4.2-25b. Estimated sailfish only catches from 1956 – 2000 are shown in Figure 4.2-25c Evolution of estimated sailfish/spearfish catches in the Atlantic (landings and dead discards, reported and carried over) in the ICCAT Task I database during 1956-2004 for the east and west stocks is shown in Figure 4.2-25d.

Table 4.2-16. Summary of Atlantic Sailfish Stock Assessment data. Weights are in metric tons, whole weight. Source: SCRS, 2004.

ATLANTIC SAILFISH "ONLY" SUMMARY	West Atlantic	East Atlantic
Maximum Sustainable Yield (MSY)	Not estimated	Not estimated
Recent Yield (2000)[1]	506 t[2]	969 t[2]
2000 Replacement Yield	~ 600 t	Not estimated
Management Measures in Effect	None	None

[1] Estimated yield includes that carried over from previous years.
[2] Recent yield (2000) was estimated during the 2001 sailfish assessment. To estimate the 2001, 2002 and 2003 yield, catches of sailfish and spearfish would have to be separated. A separation similar to the one conducted in the 2001 assessment has not yet been conducted.

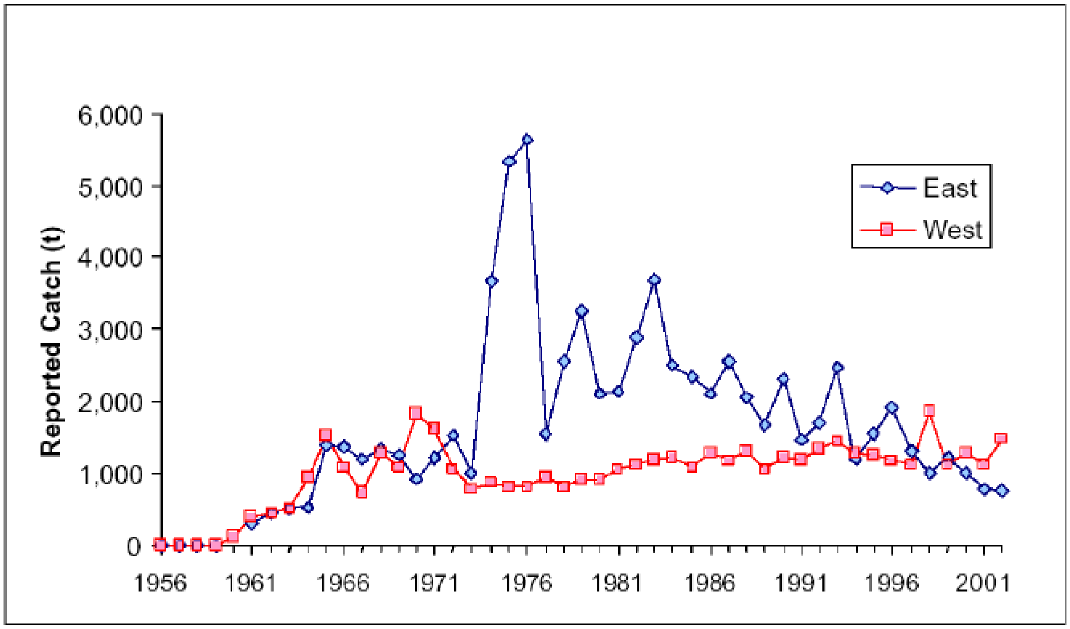


Figure 4.2-25a. Evolution of estimated sailfish/spearfish catches in the Atlantic (landings and dead discards, reported and carried over) in the ICCAT Task I database during 1956-2002 for the east and west stocks. The 2003 catch reported to ICCAT is preliminary and is not included in this figure. Weights are in metric tons, whole weight. Source: SCRS, 2005.

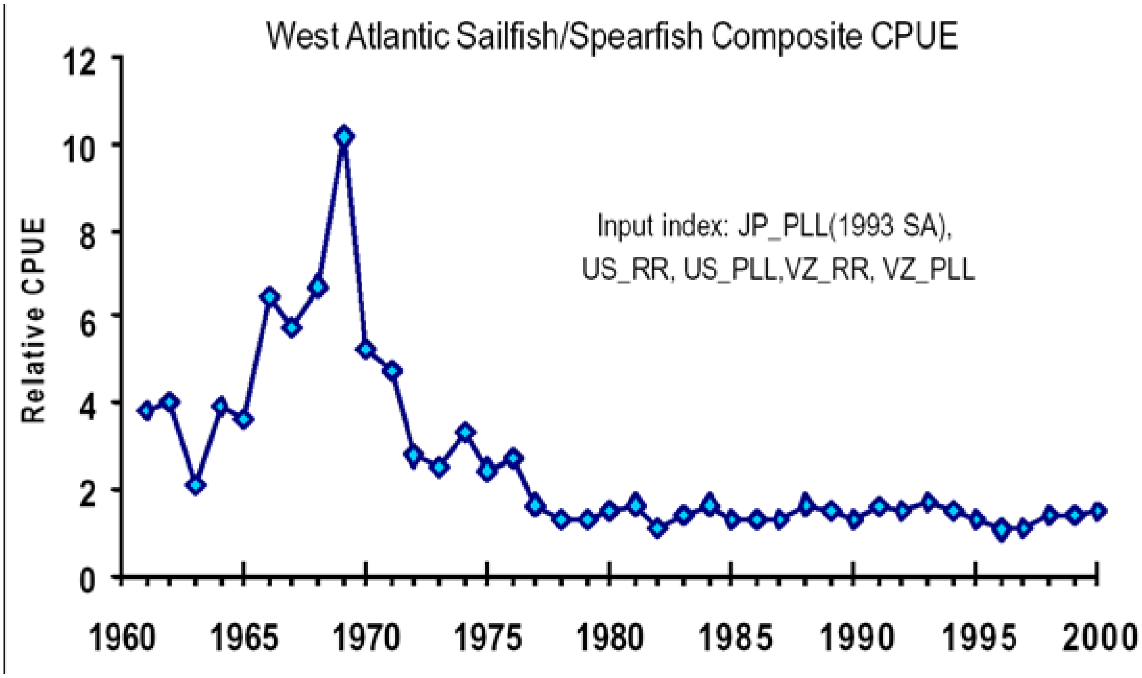


Figure 4.2-25b. Available standardized CPUE for western Atlantic sailfish/spearfish for the period 1967-2000, including Japanese, U.S., and Venezuelan time series data. Source: SCRS, 2005.

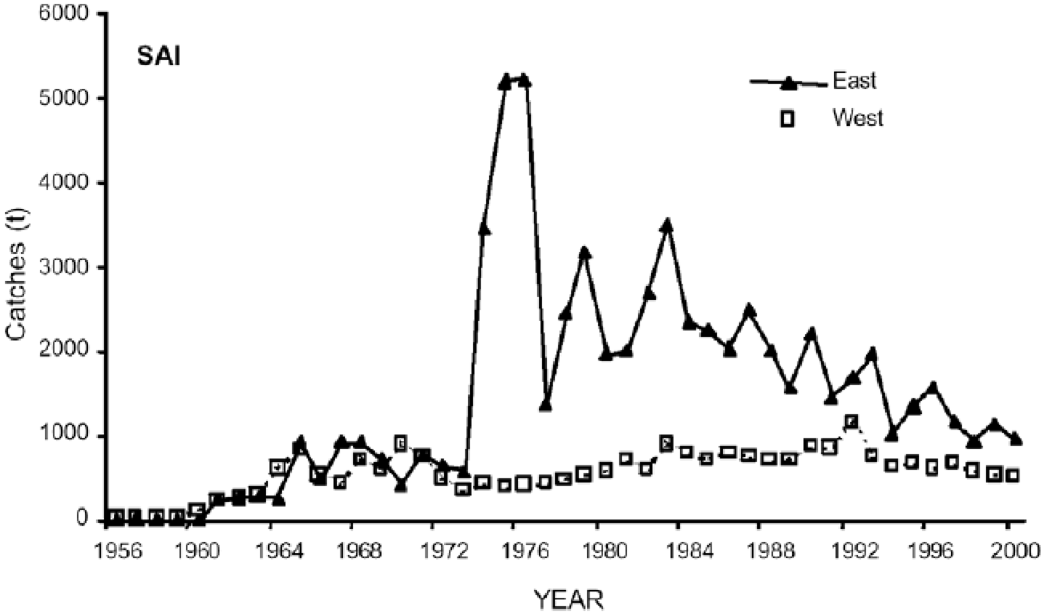


Figure 4.2-25c. Estimated sailfish "only" catches based on the new procedure for splitting combined sailfish and longbill spearfish catches from 1956-2000. Weights are in metric tons, whole weight. Source: SCRS, 2005.

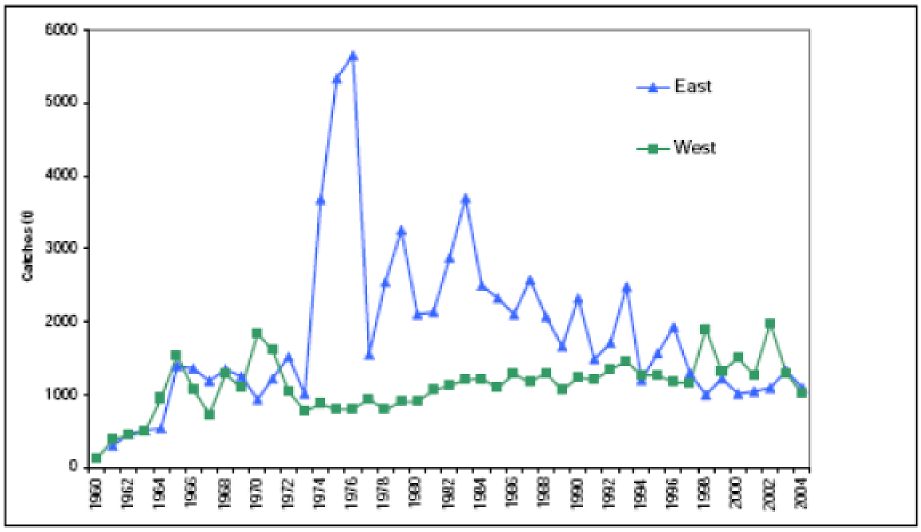


Figure 4.2-25d. Evolution of estimated sailfish/spearfish catches in the Atlantic (landings and dead discards, reported and carried over) in the ICCAT Task I database during 1956-2004 for the east and west stocks. Source: SCRS, 2005.

Longbill Spearfish

Initial stock assessments conducted on spearfish aggregated these landings with sailfish. As mentioned in the Sailfish section, the 2001 assessment included a 'sailfish only' in addition to an aggregate sailfish/spearfish assessment. West Atlantic catch levels for sailfish/spearfish combined seem sustainable because, over the past two decades, CPUE and catch levels have remained constant, however, MSY is unknown. As a result, it is unknown whether or not spearfish are experiencing overfishing or are overfished. Spearfish catch levels are shown in Figure 4.2-26. The SCRS recommends implementing measures to reduce or keep fishing mortality levels constant and evaluating new methods to split sailfish and spearfish indices of abundance (SCRS, 2004).

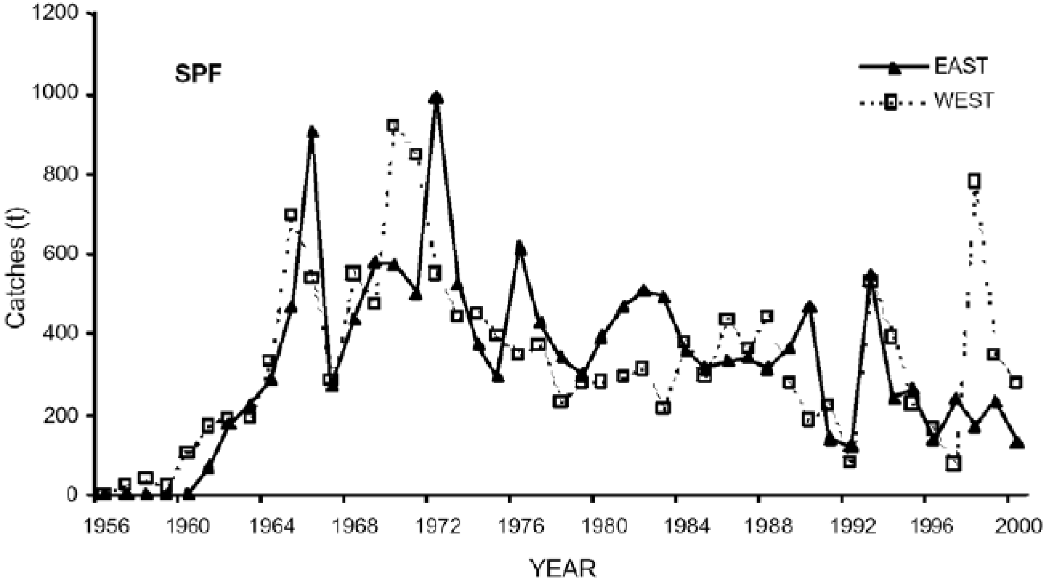


Figure 4.2-26. Estimated spearfish "only" catches in the Atlantic based on the new procedure for splitting combined sailfish and spearfish catches from 1956-2000. Weights are in metric tons, whole weight. Source: SCRS, 2005.

Atlantic Sharks

Life History and Biology

Sharks belong to the class Chondrichthyes (cartilaginous fishes) that also includes rays, skates, and deepwater chimaeras (ratfishes). From an evolutionary perspective, sharks are an old group of fishes characterized by skeletons lacking true bones. The earliest known sharks have been identified from fossils from the Devonian period, over 400 million years ago. These primitive sharks were small creatures, about 60 to 100 cm long, that were preyed upon by larger armored fishes that dominated the seas. The life span of all shark species in the wild is not known, but it is believed that many species may live 30 to 40 years or longer.

Relative to other marine fish, sharks have a very low reproductive potential. Several important commercial species, including large coastal carcharhinids, such as sandbar (*Carcharhinus plumbeus*) (Casey and Hoey, 1985; Sminkey and Musick, 1995; Heist et al., 1995), lemon (*Negaprion brevirostris*) (Brown and Gruber, 1988), and bull sharks (Branstetter and Stiles, 1987), do not reach maturity until 12 to 18 years of age. Various factors determine this low reproductive rate: slow growth, late sexual maturity, one to two-year reproductive cycles, a small number of young per brood, and specific requirements for nursery areas. These biological factors leave many species of sharks vulnerable to overfishing.

There is extreme diversity among the approximately 350 species of sharks, ranging from tiny pygmy sharks of only 20 cm (7.8 in) in length to the giant whale sharks, over 12 meters (39 feet) in length. There are fast-moving, streamlined species such as mako (*Isurus* spp.) and thresher sharks (*Alopias* spp.), and sharks with flattened, ray-like bodies, such as angel sharks (*Squatina dumerili*). The most commonly known sharks are large apex predators including the white (*Carcharadon carcharias*), mako, tiger (*Galeocerdo cuvier*), bull (*Carcharhinus leucas*), and great hammerhead (*Sphyrna mokarran*). Some shark species reproduce by laying eggs, others nourish their embryos through a placenta. Despite their diversity in size, feeding habits, behavior and reproduction, many of these adaptations have contributed greatly to the evolutionary success of sharks.

The most significant reproductive adaptations of sharks are internal fertilization and the production of fully developed young or "pups." These pups are large at birth, effectively reducing the number of potential predators and enhancing their chances of survival. During mating, the male shark inseminates the female with copulatory organs, known as claspers that develop on the pelvic fins. In most species, the embryos spend their entire developmental period protected within their mother's body, although some species lay eggs. The number of young produced by most shark species in each litter is small, usually ranging from two to 25, although large females of some species can produce litters of 100 or more pups. The production of fullydeveloped pups requires great amounts of nutrients to nourish the developing embryo.

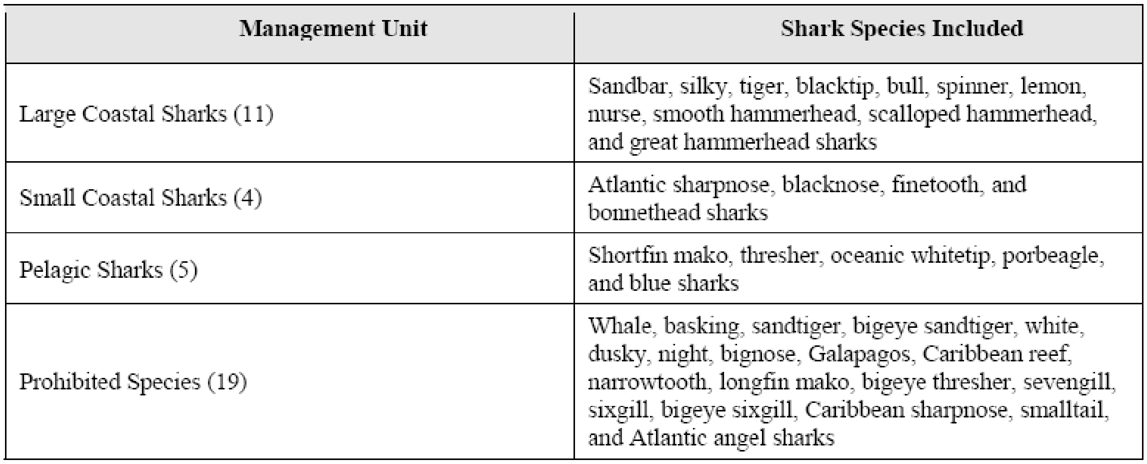
Traditionally, these adaptations have been grouped into three modes of reproduction: oviparity (eggs hatch outside body), ovoviviparity (eggs hatch inside body), and viviparity (live birth).

Adults usually congregate in specific areas to mate and females travel to specific nursery areas to pup. These nurseries are discrete geographic areas, usually in waters shallower than those inhabited by the adults. Frequently, the nursery areas are in highly productive coastal or estuarine waters where abundant small fishes and crustaceans provide food for the growing pups. These areas also may have fewer large predators, thus enhancing the chances of survival of the young sharks. In temperate zones, the young leave the nursery with the onset of winter; in tropical areas, young sharks may stay in the nursery area for a few years.

Shark habitat can be described in four broad categories: (1) coastal, (2) pelagic, (3) coastal-pelagic, and (4) deep-dwelling. Coastal species inhabit estuaries, the nearshore and waters of the continental shelves, e.g., blacktip (*Carcharhinus limbatus*), finetooth, bull, lemon, and sharpnose sharks (*Rhizoprionondon terraenovae*). Pelagic species, on the other hand, range widely in the upper zones of the oceans, often traveling over entire ocean basins. Examples include shortfin mako (*Isurus oxyrinchus*), blue (*Prionace glauca*), and oceanic whitetip (*Carcharhinus longimanus*) sharks. Coastal-pelagic species are intermediate in that they occur both inshore and beyond the continental shelves, but have not demonstrated mid-ocean or transoceanic movements. Sandbar sharks are examples of a coastal-pelagic species. Deepdwelling species, e.g., most cat sharks (*Apristurus* spp.) and gulper sharks (*Centrophorus* spp.) inhabit the dark, cold waters of the continental slopes and deeper waters of the ocean basins.

Seventy-three species of sharks are known to inhabit the waters along the U.S. Atlantic coast, including the Gulf of Mexico and the waters around Puerto Rico and the U.S. Virgin Islands. Thirty-nine species are managed by HMS; spiny dogfish also occur along the U.S. coast, however management for this species is under the authority of the Atlantic States Marine Fisheries Commission as well as the New England and Mid-Atlantic Fishery Management Councils. Deep-water sharks were removed from the management unit in 2003. Based on the ecology and fishery dynamics, the sharks have been divided into four species groups for management: (1) large coastal sharks, (2) small coastal sharks, (3) pelagic sharks, and (4) prohibited species (Table 4.2-17).

Table 4.2-17. Common names of shark species included within the four species management units under the purview of the HMS management division.



Management Unit	Shark Species Included
Large Coastal Sharks (11)	Sandbar, silky, tiger, blacktip, bull, spinner, lemon, nurse, smooth hammerhead, scalloped hammerhead, and great hammerhead sharks
Small Coastal Sharks (4)	Atlantic sharpnose, blacknose, finetooth, and bonnethead sharks
Pelagic Sharks (5)	Shortfin mako, thresher, oceanic whitetip, porbeagle, and blue sharks
Prohibited Species (19)	Whale, basking, sandtiger, bigeye sandtiger, white, dusky, night, bignose, Galapagos, Caribbean reef, narrowtooth, longfin mako, bigeye thresher, sevengill, sixgill, bigeye sixgill, Caribbean sharpnose, smalltail, and Atlantic angel sharks

Abundance and status of stocks

NMFS is responsible for conducting stock assessments for the Large and Small Coastal Shark complexes (LCS and SCS) (Cortes, 2002; Cortes et al., 2002). ICCAT and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) have recently conducted assessments of three pelagic shark species. Stock assessments were conducted for the LCS and SCS in 2002. NMFS is conducting stock assessments for LCS and SCS in 2006 and 2007, respectively. NMFS also recently released a stock assessment for dusky sharks (May 25, 2006, 71 FR 30123). Species-specific assessments for blacktip and sandbar sharks within the LCS complex and finetooth sharks, Atlantic sharpnose sharks, blacknose sharks (*Carcharhinus acronotus*), and bonnethead sharks (*Sphyrna tiburo*) within the SCS complex, were also conducted in 2002. The conclusions of these assessments are summarized in Table 4.2-18 and Table 4.2-19 and are fully described in Amendment 1 to the 1999 Atlantic Tunas, Swordfish, and Sharks FMP. Summaries of recent stock assessments and reports on several species of pelagic sharks (blue sharks, shortfin mako sharks, and porbeagle sharks (*Lamna nasus*) by Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and ICCAT are also included in this section.

Large Coastal Sharks

The last LCS stock assessment was held in June 2002, however, results from a new stock assessment should be released in 2006. Discussions of the 2002 stock assessment focused on the availability of four additional years worth of catch estimates, biological data, catch rate series, and the types of models that should be used. The modeling itself was performed after the Shark Evaluation Workshop and incorporated new catch and effort estimates for the years 1998 – 2001 as well as over 20 catch-per-unit-effort (CPUE) series for the LCS complex, sandbar, and blacktip sharks (Table 3.17).

A variety of stock assessment models were used to investigate the population dynamics of LCS including: (1) a non-equilibrium Schaefer biomass dynamic model using the sampling/importance re-sampling (SIR) algorithm (Bayesian SPM) and several weighting schemes; (2) a non-equilibrium Schaefer state-space surplus production model (SSSPM) using a Markov Chain Monte Carlo (MCMC) method for numerical integration; (3) a lagged recruitment, survival, and growth (SSLRSG) state-space model; (4) the maximum likelihood estimation model (MLE); and (5) a fully age-structured, state-space population dynamic model (ASPM).

General descriptions of these models can be found in the stock assessment. The use of multiple approaches in evaluating stock status can reduce uncertainty in the best available data and can balance individual model strengths and weaknesses. Due to concerns that catch series may underestimate mortality from the commercial fishery, four separate catch scenarios were considered to evaluate catch histories: updated, baseline, and the alternative scenarios. The updated catch scenario was comprised of catches used in the 1998 SEW, including data through 1997, and additional catches for 1998 – 2001. The baseline catch scenario included similar information and discards from the menhaden fishery, and Mexican catches, bottom longline discards back to 1981, and commercial and recreational catches back to 1981. The alternative scenario reconstructed historical catches back in time (calendar years 1960 – 2001) and applied to the LCS complex only.

The age-structured models for sandbar and blacktip shark included both updated and baseline scenarios in which specific catch series were linked to specific catchability and selectivity parameters. The alternative scenarios were used for sandbar and blacktip shark catch history evaluation.

Catch rates were also analyzed for other species included in the LCS complex such as tiger, hammerhead, dusky, and silky shark. Generally, commercial data indicate increasing catch rates for tiger shark (Brown and Cramer, 2002; Cortes et al., 2002) as well as decreasing trends for dusky shark, sand tiger shark, and hammerhead shark (Brown, 2002; Cortes et al., 2002; Brown and Cramer, 2002). Recreational catch data for hammerhead and bull shark point towards declining trends for both species (Cortes et al., 2002).

Considering the outputs of all model analyses combined, the assessment results were considerably more pessimistic for the LCS aggregate as compared to those for individual species within the complex (i.e., sandbar and blacktip sharks). While results illustrate improvements in the LCS complex since 1998, all of the models and catch scenarios described above, with the exception of the Bayesian SPM scenario which used only fishery-independent CPUE series, indicate that overfishing may be occurring and that the LCS complex may be overfished. Table 4.2-18 provides biomass and fishing mortality estimates used to make these determinations.

As such, the stock assessment finds that at least a 50-percent reduction in 2000 catch levels for the complex could be required for the biomass to reach maximum sustainable yield (MSY) in 10, 20 or 30 years. Furthermore, a 20-percent reduction in 2000 catch levels for the complex would result in less than a 50-percent probability of achieving MSY even after 30 years of implementation under those catch levels. Overall, the stock assessment found that the LCS complex as a whole is overfished and overfishing is occurring (Cortes et al., 2002).

The assessment acknowledges that the results between the complex and sandbar and blacktip sharks may be considered conflicting, given that sandbar and blacktip sharks comprise the majority of LCS commercial harvests. Specifically, sandbar and blacktip sharks make up approximately 44 percent of the total commercial catch (Burgess and Morgan, 2003) and over 70 percent of the landings (Cortes and Neer, 2002). The remainder of the catch is comprised mostly of tiger, scalloped hammerhead, silky, and sand tiger, with catch composition varying by region (Burgess and Morgan, 2003). These species are less marketable and are often released, so they are reflected in the overall catch but not the landings. Nonetheless, the complex represents a variety of species beyond sandbar and blacktip shark, some of which are in apparent decline.

In December 2002, the peer review process of the 2002 LCS stock assessment was completed as required by a court settlement agreement. The peer reviews were conducted by three separate non-NMFS reviewers who were asked to respond to five questions regarding the appropriateness of specific modeling approaches and the selection there of, consideration of available data and the quality of data sets, application of available data in selected models, reliability of projections, and the effects of various catch scenarios on stock trajectories. Peer review findings were generally positive in that reviewers agreed that a state-of-the-art assessment was performed and that the best available science was employed. Reviewers noted assessment strengths including (1) compilation of several indices of abundance, (2) consideration of multiple stock assessment models, including Bayesian analyses, (3) discussion of myriad alternative harvest policies, and (4) analytical changes to address concerns raised by previous reviewers.

Further investigation of catch series indices, assessment of individual species within the LCS complex, investigation of age and age-sex-area assessment models, consideration of alternative harvest policies in contrast to the current constant-catch policy, and NMFS support for observer programs to obtain fishery independent estimates of abundance were among the recommendations offered for improvements to future stock assessment for LCS.

The 2005/2006 stock assessment for LCS follows the Southeast Data, Assessment, and Review (SEDAR) process. This process is a cooperative program designed to improve the quality and reliability of the stock assessments. The SEDAR process emphasizes constituent and stakeholder participation in the assessment development, transparency in the assessment process, and a rigorous and independent scientific review of the completed stock assessment. The Data Workshop for the stock assessment, which documented, analyzed, reviewed, and compiled the data for conducting the assessment, was held from October 31 to November 4, 2005, in Panama City, FL (September 15, 2005, 70 FR 54537; correction October 5, 2005, 70 FR 58190). The Assessment Workshop, which developed and refined the population analyses and parameter estimates, was held from February 6 to February 10, 2006, in Miami, FL (December 22, 2005, 70 FR 76031). At the time of writing this Final HMS FMP, the last workshop, the Review Workshop, had not yet occurred. At the Review Workshop, independent scientists should review the assessment and data. This Workshop should be held on June 5 to June 9, 2006, in Panama City, FL (March 9, 2006, 71 FR 12185). The final results should be released after the review workshop. All reports are posted on SEDAR webpage when complete (http://www.sefsc.noaa.gov/sedar/).

Recently, the SEFSC released the first dusky shark stock assessment (May 25, 2006, 71 FR 30123). Results from all of the models used were similar with all models indicating that the stock is heavily exploited. The stock assessment summarizes relevant biological data, discusses the fisheries affecting the species, and details the data and methods used to assess the stock. At the time of writing this Final HMS FMP, NMFS is reviewing the stock assessment and considering implications for management.

Small Coastal Sharks

A stock assessment for small coastal sharks (SCS) was also conducted in 2002. This was the first assessment since 1992 and as such the assessment included new information regarding SCS age and growth, reproduction, and population dynamics. Additional information relative to commercial and recreational catches as well as extended bycatch estimates for the shrimp trawl fishery were also considered.

Trends in catch were analyzed for the SCS complex as well as the four species comprising this aggregate grouping (Table 4.2-19). Overall, SCS commercial landings exceeded recreational harvest in all years since 1996, with the exception of 2000. Of the four species of SCS analyzed, bonnetheads contributed to over 50 percent of all SCS commercial landings in 1995, but Atlantic sharpnose and finetooth sharks each accounted for over 30 percent of the commercial landings in years 1996 – 1999 and 1998 – 2000 respectively. Atlantic sharpnose dominated recreational catch in all years between 1995 and 2000.

Also, in 2002, researchers at the Mote Marine Laboratory and the University of Florida, conducted a stock assessment for SCS using similar data but different models. The results were similar to the NMFS assessment in that current biomass levels for Atlantic sharpnose, bonnethead, and blacknose were at least 69 percent of the biomass in 1972 while the current biomass level for finetooth sharks was only nine percent the level in 1972 (Simpfendorfer and Burgess, 2002). Both stock assessments note that the data used for finetooth sharks is not as high a quality as the data used for Atlantic sharpnose due to shorter catch-per-unit-effort (CPUE) and catch series, lack of bycatch estimates, and no catches reported in some years.

NMFS intends to conduct a new stock assessment for SCS starting in 2007. The new stock assessment would follow the SEDAR process.

Finetooth Sharks

Additional information on finetooth sharks and the results specific to this species from the 2002 SCS stock assessment are provided in this section because finetooth sharks were the only exception to the results of the assessment, in that fishing mortality in the final five years of data considered was above the mortality level associated with producing MSY. As such, finetooth sharks are not overfished, however, overfishing is occurring (Table 4.2-20a and Table 4.2-20b).

Finetooth sharks inhabit shallow coastal waters to depths of 10 m (32.8 feet) near river mouths in the Gulf of Mexico and South Atlantic Ocean between Texas and North Carolina. These fish often form large schools and migrate to warmer waters when water temperatures drop below 20°C (68°F). Finetooth sharks are relatively productive compared to other sharks as fish are sexually mature at 3.9 (TL = 118 cm (46 inches)) and 4.3 (TL = 123 cm (48 inches)) years for males and females, respectively (Carlson et al., 2003). Reproduction in finetooth sharks is viviparous with yolk sac placenta and embryos nourished through a placental connection. Females move into the nursery areas in late May and gestation is approximately 12 months. Each litter can have 1 – 6 pups with individuals measuring 51 – 64 cm (20 – 25 inches) in length.

The finetooth shark feeds primarily on mullet, Spanish mackerel, spot, Atlantic menhaden, cephalopods, and crustacean (Bester and Burgess, 2004).

In 2002, NMFS conducted a stock assessment for all SCS, including finetooth sharks. Five catch rate series were used, including fishery-independent and -dependent data. The fisheryindependent data sources included the NMFS Pascagoula and Panama City Laboratory longline surveys (NMFS SE LL and NMFS LL PC), and the NMFS Panama City Laboratory Gillnet Survey (NMFS GN). Fishery-dependent catch series data were included from the combined recreational series and the Directed Shark Gillnet Fishery Observer Program (DSGFOP). This catch rate series data were combined with life history information for finetooth sharks and evaluated with several stock assessment models. There were four models utilized for the assessment and numerous scenarios within each model, producing a range of point estimates for fishing mortality, relative fishing mortality, biomass, relative stock biomass, maximum fishing mortality threshold, minimum stock size threshold, and other parameters.

Of the catch series data used in the analysis, three of the five showed a positive trend (i.e., had positive slopes) in catch over time, suggesting an increase in finetooth shark abundance. The catch series data showing positive trends were DSGFOP (0.03), NMFS SE LL (0.34), and NMFS LL PC (0.04); however only the slope for the DSGFOP catch series data was statistically significant different from zero (P = 0.03). However, it should be noted that data were missing from some years in the NMFS SE LL and the DSGFOP catch series data; therefore, one cannot necessarily assume that finetooth sharks are increasing in abundance. The other two datasets, NMFS LL PC and NMFS GN PC, had negative trends in catch over time as indicated by their negative slopes (-0.24 and -0.11, respectively) but neither trend was statistically significant from zero. Overall, the slopes for the small coastal shark (SCS) complex as a whole and other individual species were relatively flat, indicating that the relative abundance of the stocks remained fairly stable during the exploitation phase (Cortés, 2002).

Four different stock assessment models were used to evaluate the status of SCS using Bayesian statistical techniques. Results of both surplus production models and the Lagged Recruitment Survival and Growth State Space model (LRSG) (using several different scenarios) indicate that the current level of removals is sustainable for the SCS aggregate and the individual species within the complex. Relative stock biomass and fishing mortality trajectories obtained with the Bayesian state-space Schaefer surplus production model (SPM) for the small coastal aggregate and the Atlantic sharpnose sharks followed similar trends, since the catches were dominated by these species. The model predicted that the stock biomass for the small coastal shark complex in any given year from 1972 – 2000 exceeded the biomass producing MSY.

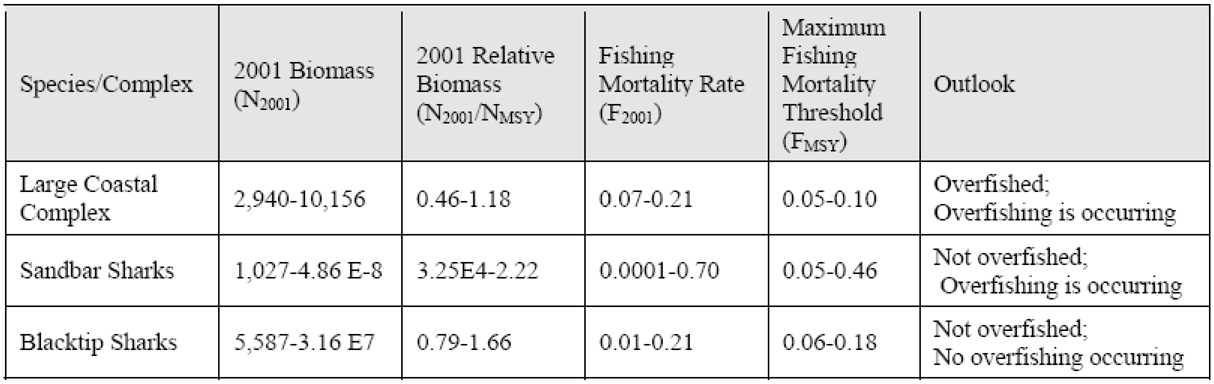
Relative fishing mortality (F/FMSY) was generally below one for the SCS complex, but for finetooth sharks, the final five values of F in the series (1996 – 2002) estimated by the model were above the level of F corresponding to MSY.

Results for finetooth sharks were directly influenced by the catch series used, which did not include any bycatch estimates, and this, in turn, influenced certain parameters of the

Bayesian models (specifically, the priors chosen for K, which describes uncertainty in assessment models) (Cortés, 2002). The lack of bycatch data in the catch series data lead to low values of MSY predicted for finetooth sharks in the SCS stock assessment (especially those obtained through the SPM models). This lack of bycatch data and shorter catch and catch per unit effort (CPUE) series, coupled with no catches reported in some years, led to some uncertainty in the stock assessment for finetooth sharks. In the case of finetooth sharks, model estimates of recent F levels are above FMSY, indicating that recent levels of effort directed at this species, if continued, could result in an overfished status in the relatively near future. The various stock assessments models used and sensitivity analyses run support these general conclusions (Cortés, 2002). Future work should continue to monitor the status of this individual species (Cortés, 2002).

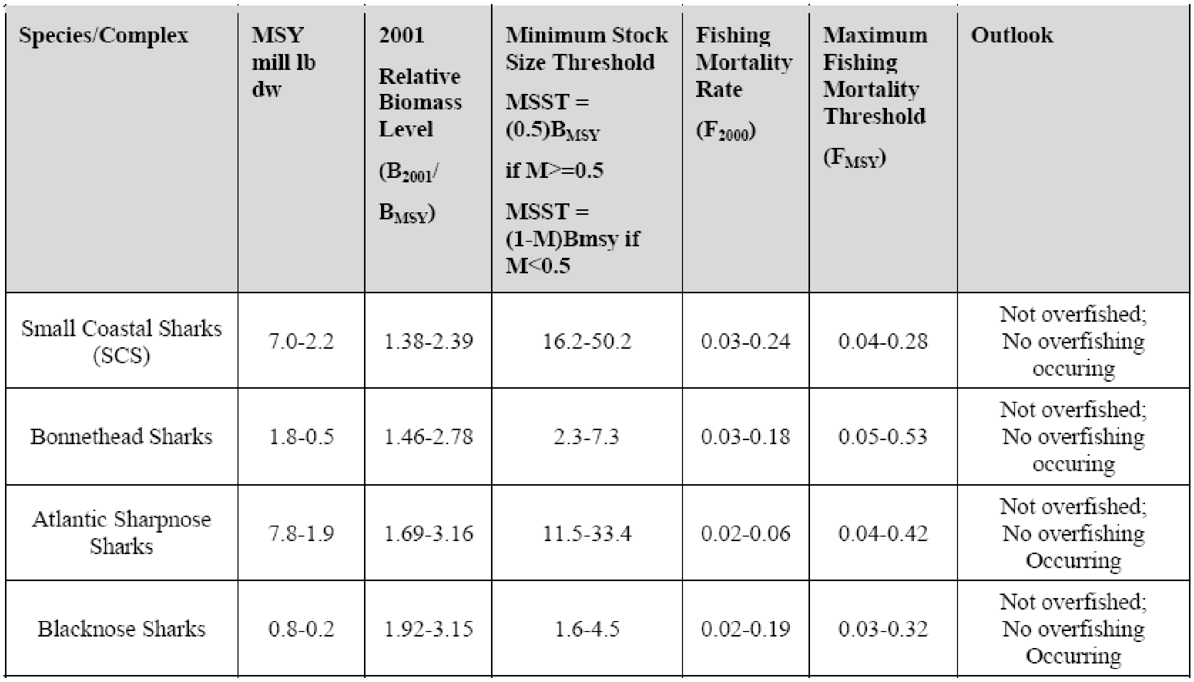
Landings of finetooth sharks in other fisheries are extensive; however, catch series data from these fisheries are currently unavailable. The inclusion of such data in future stock assessments will provide better information on both fishing effort and estimates of MSY. Thus, it may be prudent to develop a plan to prevent overfishing that first investigates other sources of fishing mortality before initiating a particular set of management actions. In order to capture additional catch series data on fisheries contributing to finetooth fishing mortality, NMFS is expanding observer programs to include DSGFOP observers on all boats that have directed or incidental shark permits to determine if these gillnet vessels in the South Atlantic are contributing to the majority of fishing mortality. A continuation of a pilot program initiated in the spring of 2005 that placed observers on board additional gillnet vessels targeting other fish species will improve data collection efforts. Furthermore, contacting Regional Fishery Management Councils and Interstate Marine Fisheries Commissions to determine sources of mortality occurring under other fishery management plans, and having finetooth sharks included as a select species for sub-sampling of bycatch in the Gulf of Mexico Shrimp Trawl Observer Program will provide additional landings data necessary for appropriate management and conservation actions in the future.

Table 4.2-18. Summary Table of Biomass and Fishing Mortality for Large Coastal Sharks (LCS). Source: Cortes et al., 2002.



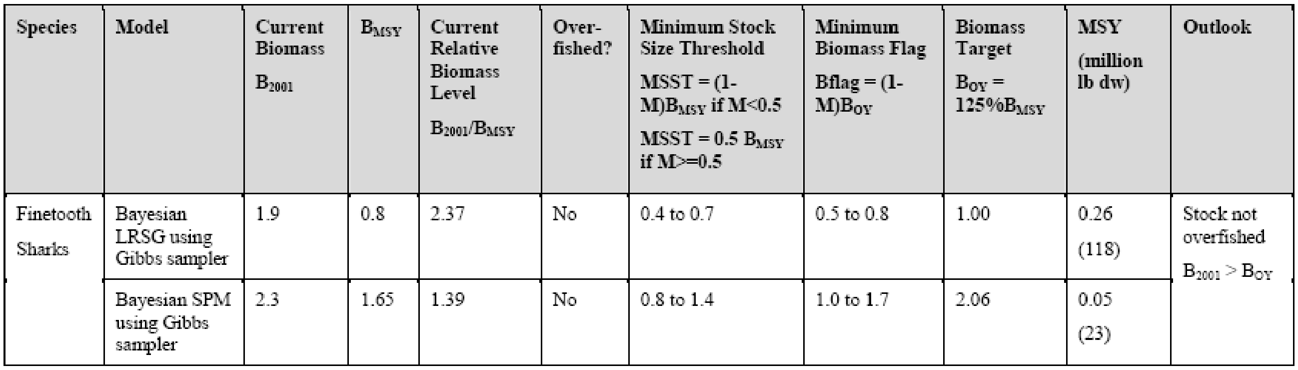
Species/Complex	2001 Biomass (N_{2001})	2001 Relative Biomass (N_{2001}/N_{MSY})	Fishing Mortality Rate (F_{2001})	Maximum Fishing Mortality Threshold (F_{MSY})	Outlook
Large Coastal Complex	2,940-10,156	0.46-1.18	0.07-0.21	0.05-0.10	Overfished; Overfishing is occurring
Sandbar Sharks	1,027-4.86 E-8	3.25E4-2.22	0.0001-0.70	0.05-0.46	Not overfished; Overfishing is occurring
Blacktip Sharks	5,587-3.16 E7	0.79-1.66	0.01-0.21	0.06-0.18	Not overfished; No overfishing occurring

Table 4.2-19. Summary Table of Biomass and Fishing Mortality for Small Coastal Sharks (SCS) Source: Cortes, 2002.



Species/Complex	MSY mill lb dw	2001 Relative Biomass Level (B_{2001}/ B_{MSY})	Minimum Stock Size Threshold MSST = $(0.5)B_{MSY}$ if M>=0.5 MSST = (1-M)Bmsy if M<0.5	Fishing Mortality Rate (F_{2000})	Maximum Fishing Mortality Threshold (F_{MSY})	Outlook
Small Coastal Sharks (SCS)	7.0-2.2	1.38-2.39	16.2-50.2	0.03-0.24	0.04-0.28	Not overfished; No overfishing occuring
Bonnethead Sharks	1.8-0.5	1.46-2.78	2.3-7.3	0.03-0.18	0.05-0.53	Not overfished; No overfishing occuring
Atlantic Sharpnose Sharks	7.8-1.9	1.69-3.16	11.5-33.4	0.02-0.06	0.04-0.42	Not overfished; No overfishing Occurring
Blacknose Sharks	0.8-0.2	1.92-3.15	1.6-4.5	0.02-0.19	0.03-0.32	Not overfished; No overfishing Occurring

Table 4.2-20a. Summary table of the status of the biomass of finetooth sharks. Sources: 2002 SCS stock assessment; E. Cortes, personal communication. LRSG=lagged recruitment, survival, and growth model; SPM=surplus production model.



Species	Model	Current Biomass B_{2001}	B_{MSY}	Current Relative Biomass Level B_{2001}/B_{MSY}	Over-fished?	Minimum Stock Size Threshold MSST = $(1-M)B_{MSY}$ if M<0.5 MSST = 0.5 B_{MSY} if M>=0.5	Minimum Biomass Flag Bflag = $(1-M)B_{OY}$	Biomass Target B_{OY} = 125%B_{MSY}	MSY (million lb dw)	Outlook
Finetooth Sharks	Bayesian LRSG using Gibbs sampler	1.9	0.8	2.37	No	0.4 to 0.7	0.5 to 0.8	1.00	0.26 (118)	Stock not overfished $B_{2001} > B_{OY}$
	Bayesian SPM using Gibbs sampler	2.3	1.65	1.39	No	0.8 to 1.4	1.0 to 1.7	2.06	0.05 (23)	

Table 4.2-20b. Summary table of the status of the fishing mortality of finetooth sharks. Sources: 2002 SCS stock assessment; E. Cortes, personal communication. LRSG=lagged recruitment, survival, and growth; SPM=surplus production model.

Species	Model	Current F F_{2000}	Maximum Fishing Mortality Threshold MFFT = F_{MSY}	Current Relative fishing Mortality Rate F_{2000}/F_{MSY}	Over-fishing?	Fishing Mortality Target $F_{OY} = 0.75F_{MSY}$	Management Measures to Reduce Fishing Mortality Required? $F_{2000} > F_{OY}$	Outlook
Finetooth Sharks	Bayesian LRSG using Gibbs sampler	1.50	0.44	3.42	YES	0.33	YES	OVERFISHING
	Bayesian SPM using Gibbs sampler	0.13	0.03	4.13	YES	0.02	YES	

Pelagic Sharks

Pelagic sharks are subject to exploitation by many different nations and exhibit transoceanic migration patterns. As a result, ICCAT's SCRS Subcommittee on Bycatch has recommended that ICCAT take the lead in conducting stock assessments for pelagic sharks.

An ICCAT meeting was held in September 2001 to review available statistics for Atlantic and Mediterranean pelagic sharks. Newly available biological and fishery information presented for review included age and growth, length/weight relationships, species identification, species composition of catch, catch per unit effort, mortality (both natural and fishing estimates for blue sharks), bycatch, and tagging and migration studies. Landings estimates, which incorporated data for both the Atlantic and Mediterranean populations of blue shark, suggested that landings declined in 2000 (3,652 mt) following a peak of 32,654 mt in 1999. Landings of porbeagles peaked in 1997, with an estimated total of 1,450 mt, and have slowly declined each year since that time period (1998 – 2000). Similarly, landing estimates for Shortfin mako also peaked in 1997 (5,057 mt) and have declined by 83 percent (863 mt in 2000) since that time. Meeting participants expressed concern regarding the lack of information pertaining to the number of fleets catching sharks, landing statistics, and dead discards for sharks.

The SCRS decided to conduct an assessment of Atlantic pelagic sharks beginning in 2004. Emphasis was placed on blue sharks and shortfin mako sharks. Several models such as nonequilibrium production and statistical age/length-structured models will be considered to analyze the population dynamics of pelagic shark species.

ICCAT Stock Assessment on Blue and Shortfin Mako Sharks

At the 2004 Inter-Sessional Meeting of the ICCAT Subcommittee on bycatch, stock assessments for Atlantic blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*) were conducted. This work included a review of their biology, a description of the fisheries, analyses of the state of the stocks and outlook, analyses of the effects of current regulations, and recommendations for statistics and research. The assessment indicated that the current biomass of North and South Atlantic blue shark seems to be above MSY (B>BMSY), however, these results are conditional and based on assumptions that were made by the committee. These assumptions indicate that blue sharks are not currently overfished, again, this conclusion is conditional and based on limited landings data. The committee estimates that between 82,000 and 114,000 mt ww (180,779,054 – 251,326,978 lb) of blue shark are harvested from the Atlantic Ocean each year.

The North Atlantic shortfin mako population has experienced some level of stock depletion as suggested by the historical CPUE trend and model outputs. The current stock may be below MSY (B<BMSY), suggesting that the species may be overfished. Overfishing may also be occurring as between 13,000 and 18,000 mt ww (28,660,094 – 39,683,207 lb) of shortfin mako are harvested in the Atlantic Ocean annually. South Atlantic stocks of shortfin mako shark are likely fully exploited as well, but depletion rates are less severe than in the North Atlantic.

The results of both of these assessments should be considered preliminary in nature due to limitations on quality and quantity of catch data available (SCRS, 2004). The subcommittee stated that catch data currently being reported to ICCAT does not represent the total catch actually landed, and are very limited with regard to size, age, and sex of shark harvested or caught incidentally. In order to attain a more accurate estimate of total landings, and improve future stock assessments, the committee made several recommendations, including: increase the infrastructure investment for monitoring the overall catch composition of sharks, standardize catch per unit effort (CPUE) from major fishing fleets, expand use of trade statitistics (fins) to extend historical time series, and include scientists from all Contracting Parties with significant blue and shortfin mako catches in future assessments (SCRS, 2004).

COSEWIC Stock Assessment on Porbeagle
The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) conducted a species report and assessment for porbeagle in 2004. They suggest that significant declines in porbeagle abundance have occurred as a result of overexploitation in fisheries. In 2001, porbeagle biomass was estimated at 4,409 mt ww (9,720,181 lb), a decline of 89 percent from the pre-fishing biomass in 1961 (COSEWIC, 2004). The model employed predicts that populations declined precipitously after the fishery was developed in 1961, recovered slightly in the 1980s, and then declined again to the current level. Porbeagle quotas have been reduced significantly for Canadian fisheries. NMFS is interested in working with the Canadian government to address concerns raised by the COSEWIC report. Currently, NMFS has a species-specific quota of 92 mt dw (202,823 lb) for porbeagle. These fish are generally harvested incidentally in the pelagic longline fisheries. Between 2000 and 2003, landings of porbeagle were approximately 3.4 mt dw for the four fishing years, combined (0.85 mt dw/year). NMFS is currently reviewing the latest Canadian stock assessment in terms of the overfishing and overfished thresholds defined in the FMP. At this time, the status of porbeagle sharks is unknown; however, if the stock is found to meet the thresholds, the status would be redefined.

4.3 Protected Species

4.3.1 Marine Mammals

(all text in this section submitted by A. Herndon on June 4, 2007)
There are 32 cetacean and one sirenian species that may occur in the South Atlantic region (Table 4.3-1). All of these species are protected under the Marine Mammal Protection Act. Ten of those species are considered rare within the region or too little data are available to effectively evaluate their presence. Twelve species occur occasionally within the region and are generally found in the waters at or seaward of the continental shelf (‘offshore’). All 22 species noted above rarely, if ever, interact with fishers participating in fisheries managed by the South Atlantic Fishery Management Council due to depth preferences and/or infrequency of

occurrence. The remaining eleven species are common within the region or have additional regulatory protection under the Endangered Species Act (ESA). Below is a brief discussion regarding the species found rarely or infrequently within the South Atlantic and those species found primarily seaward of the areas of operations for SAFMC managed fisheries. A more comprehensive discussion of the marine mammal species commonly found in the South Atlantic region and/or those with additional protection under the ESA is also provided. Much of the information presented below regarding species occurrence in the South Atlantic can be found in Wynne and Schwartz (1999) and Waring et al. (2007).

Table 4.3-1. Marine mammal species that may occur in the South Atlantic.

Rare Species	
False Killer Whale	*Pseudorca crassidens*
Pygmy Killer Whale	*Feresa attenuate*
Cuvier's Beaked Whale	*Ziphius cavirostris*
Killer Whale	*Orcinus orca*
Harbor Porpoise	*Phocoena phocoena*
Melon-Headed Whale	*Peponocephala electra*
Rough-Toothed Dolphin	*Steno bredanensis*
Fraser’s Dolphin	*Lagenodelphis hosei*
Spinner Dolphin	*Stenella longirostris*
Striped Dolphin	*Stenella coeruleoalba*
Occasional/Offshore Species	
Dwarf Sperm Whale	*Kogia sima*
Pygmy Sperm Whale	*Kogia breviceps*
Long-Finned Pilot Whale	*Globicephala melas*
Short-Finned Pilot Whale	*Globicephala macrorhynchus*
Risso's Dolphin	*Grampus griseus*
Common Dolphin	*Delphinus delphis*
True's Beaked Whale	*Mesoplodon mirus*
Gervais' Beaked Whale	*Mesoplodon europaeus*
Blainville's Beaked Whale	*Mesoplodon densirostris*
Sowerby's Beaked Whale	*Mesoplodon bidens*
Pantropical Spotted Dolphin	*Stenella attenuata*
Clymene Dolphin	*Stenella clymene*
Common/ESA Protected Species	
Blue Whale*	*Balaenoptera musculus*
Fin Whale*	*Balaenoptera physalus*
Humpback Whale*	*Megaptera novaeangliae*
Northern Right Whale*	*Eubalaena glacialis*
Sei Whale*	*Balaenoptera borealis*
Sperm Whale*	*Physeter macrocephalus*
West Indian Manatee (Florida Stock)**	*Trichechus manatus latirostris*
Atlantic Spotted Dolphin	*Stenella frontalis*
Bottlenose Dolphin (Coastal Stock)	*Tursiops truncatus*

Bottlenose Dolphin (Offshore Stock)	*Tursiops truncatus*
Minke Whale	*Balaenoptera acutorostrata*

*ESA-listed species
**The U.S. Fish and Wildlife Service have ESA jurisdiction for manatees.

Marine Mammals Considered Rare in the South Atlantic Region

Nine of the thirty-three marine mammal species listed above are seen only rarely in the South Atlantic region. These species either occur in low numbers naturally, or occur in the waters adjacent to the South Atlantic (i.e., Gulf of Mexico or waters off the northeastern U.S.) but only occasionally, if ever, appear in the South Atlantic. The false killer whale, pygmy killer whale, killer whale (Katona et al. 1998), melon-headed whale, rough-toothed dolphin, Fraser's dolphin, and spinner dolphin are examples of these species. The harbor porpoises and spinner dolphins (CeTAP 1982, Mullin and Fulling 2003, Palka et al. unpub. Ms) may also occur the in South Atlantic region when they travel to the southernmost portions of their ranges. However, sightings of these species north of Cape Hatteras, North Carolina are far more common. Cuvier's beaked whale is a species that may occur within the region but very little is known about its distribution (Leatherwood et al. 1976).

Marine Mammals Occurring Occasionally or Offshore in the South Atlantic Region
The range of the long-finned pilot whale, Risso's dolphin, common dolphin, and Clymene dolphin includes the northern portions of the South Atlantic region. These species occur in the waters from Cape Hatteras, North Carolina, north. When these four species and the short-finned pilot whale, striped dolphin, dwarf sperm whale, pygmy sperm whale and the four beaked whale species (Mesoplodon spp.) occur in the South Atlantic, they are generally found at or beyond the continental shelf (≥ 200 m). The areas where these species are commonly found are generally deeper and further offshore than those utilized by fishers participating in fisheries managed by the SAFMC (volume III of this document). Waring et al. (2007) noted no interactions between these species and SAFMC managed fisheries.

Marine Mammals Common to South Atlantic Region or with Additional ESA Protection

Blue Whale

Description and Distribution

Blue whales, *Balaenoptera musculus*, are long bodied and slender. The dorsal fin is proportionately smaller than those of other balaenopterid whales. It is also set far back, nearer to the tail flukes than to the middle of the body. Viewed from above, the blue whale has a broad, flat rostrum. Blue whales have a mottled gray color pattern which appears light blue when seen through the water. The background color can be dark gray, interrupted by irregular light gray markings, with dark gray splotches (NMFS 1998).

The blue whale is a cosmopolitan species of baleen whale (Gambell 1979, Yochem and Leatherwood 1985, Mead and Brownell 1993). The overall range of blue whales in the North Atlantic extends from the subtropics north to Baffin Bay and the Greenland Sea (Jongsård 1955, Yochem and Leatherwood 1985). The species was regularly hunted from land stations in Newfoundland and Labrador, the Gulf of St. Lawrence, West Greenland, Iceland, Norway, Ireland, and the islands of Shetland, the Hebrides and the Faroes (True 1904, Thompson 1928, Sergeant 1953, 1966; Jonsgård 1955, 1977; Kapel 1979, Sigurjónsson and Gunnlaugsson 1990).

Blue whales are rare in the shelf waters of the eastern U.S. Individuals have occasional been sighted off Cape Cod, Massachusetts, in summer and fall (Wenzel et al. 1988). Farther north in Canadian waters, a few sightings have been made on the Scotian Shelf (CeTAP 1982, Sutcliffe and Brodie 1977), and two blue whales were sighted in August 1995 in the lower Bay of Fundy (newspaper reports). A stranding at Ocean City, Maryland, in October 1891 (True 1904) is the southernmost confirmed record on the east coast. Several records (pre-1970) of blue whale strandings in the Gulf of Mexico (J. G. Mead, pers. comm., 27 October 1997) suggest occasional straying into that area. A large blue whale was killed at Cristobal, Panama, in the Caribbean Sea entrance to the Panama Canal in January 1922 (Harmer 1923).

Reproduction

The gestation period for the blue whale is approximately 10-12 months, and calves are nursed for about 6-7 months. Most reproductive activity, including births and mating, takes place in the winter season. Weaning probably occurs on, or en route to, the summer feeding areas. The average calving interval is estimated at two to three years. The age of sexual maturity is uncertain but is thought to be 5-15 years (Mizroch et al. 1984, Yochem and Leatherwood 1985).

Only nine blue whales classified as "calves" were observed during 19 seasons of observations along the north shore of the Gulf of St. Lawrence (R. Sears, pers. comm., October 1997). Either blue whale populations are segregated in such a way that lactating females reside mainly in areas other than those in which observations have been made, or weaning occurs prior to their arrival in these areas. R. Sears (pers. comm. October 1997, in NMFS 1998) also suggested the lack of calf observations could be because this population is producing relatively few calves.

Ecological Relationships

Diet, Development, and Growth

Based on stomach content analysis, the food of blue whales in the North Atlantic has been reported to consist entirely of "krill," (i.e., relatively large euphausiid crustaceans [Jonsgård 1955, Sergeant 1966, Christensen et al. 1992b]). The species Thysanoessa inermis and Meganyctiphanes norvegica are particularly important in the eastern North Atlantic (Hjort and Ruud 1929, Christensen et al. 1992b). The species Thysanoessa raschii and M. norvegica are said to represent important food sources of blue whales in the Gulf of St. Lawrence, based on observations of feeding whales and sampling of the nearby water column (Sears et al. 1987). Some other prey species, including fish and copepods, have been mentioned in the literature (e.g., see the review by Kawamura 1980), but these are not likely to contribute significantly to the diet of blue whales. Sears et al. (1987) suggested that the whales' apparent preference for the 100 m contour during daylight hours along the north shore of the Gulf of St. Lawrence is explained by krill concentrations found regularly at depths of 90-120 m.

The blue whale is the largest animal ever known to have lived on Earth. Adults in the Antarctic have reached a maximum body length of about 110 ft. (33 m) and can weigh more than 330,000 lbs. (150,000 kg). Blue whales in the Northern Hemisphere are generally smaller than those in the Southern Ocean. Although a 92 ft [28.1 m] blue whale is reported in whaling statistics from Davis Strait (R. Sears pers. comm., October 1997, in NMFS 1998). The largest blue whales reported from the North Pacific are a female that measured 88 ft (26.8 m) taken at Port Hobron in 1932 (Reeves et al. 1985) and a 89 ft (27.1 m) female taken by Japanese pelagic whaling operations in 1959 (J. Gilpatrick, pers. comm., June 1998). As is true of other baleen whale species, female blue whales are somewhat larger than males (Ralls 1976).

The question of whether blue whales are food-limited in the Northern Hemisphere has not been addressed. All baleen whale species that are sympatric with the blue whale eat euphausiids to some extent and are, therefore, potential competitors (Nemoto 1970). However, there is currently little or no direct evidence for interspecific competition involving blue whales anywhere (Clapham and Brownell 1996), and it seems unlikely that resource competition would be an important factor in preventing the recovery of blue whale stocks. The high mobility of blue whales should enable them to take advantage of transitory concentrations of prey over a very large area.

Migration and Movement

Blue whales are present in the Gulf of St. Lawrence for most of the year (records are for March to February according to R. Sears, pers. comm., October 1997), but most leave by early winter to avoid ice entrapment and do not return until the ice breaks up in spring. Two peaks or pulses of sightings occur in most years along the north shore of the Gulf: one in April to early June, the other from August into at least late October (R. Sears, pers. comm., August 1995, in NMFS 1998). Blue whales are especially common along the north shore during the summer and fall feeding season, with a peak in sightings from June to November (Sears et al. 1987, R. Sears, pers. comm., October 1997). Whaling records suggest that the occurrence of blue whales is seasonal in most areas, but the lack of whaling effort during the period from late fall to spring may explain the lack of records in those seasons (e.g., see Thompson 1928).

In the Gulf of St. Lawrence, individual blue whales rarely spend more than about ten days in a particular area, and they have been described as "very nomadic, with generally low local resident times" (Sears et al. 1990). Four individuals were documented to have traveled more than 400 km in a two-week period during the summer and fall (Sears et al. 1990). However, some individuals have been documented as remaining in the same area for a month or more (R. Sears pers. comm., August 1995, in NMFS 1998). The main sighting areas are off the Gaspé Peninsula, along the Quebec north shore of the Gulf, around Anticosti Island, and in the St. Lawrence River estuary to as far upriver as Tadoussac (R. Sears pers. comm., October 1997, in NMFS 1998).

Abundance and Status of Stock

Little is known about the population size of blue whales except for in the Gulf of St. Lawrence area. Here, 308 individuals have been catalogued (Sears et al. 1987), but the data were deemed to be unusable for abundance estimation (Hammond et al. 1990). However, this figure of 308 individuals is considered to be a minimum population estimate for the western North Atlantic stock (Waring et al. 2007). Mitchell (1974) estimated that the blue whale population in the western North Atlantic may number only in the low hundreds. R. Sears (pers. comm., in Warning et al. 2007) suggests that no present evidence exists to refute this estimate.

There are insufficient data to determine population trends for this species and the status of this stock relative to the optimum sustainable population in the U.S. Atlantic EEZ is unknown (Waring et al. 2007). Off western and southwestern Iceland, an increasing trend of 4.9% a year was reported for the period 1969-1988 (Sigurjónsson and Gunnlaugsson 1990), although this estimate should be treated with caution given the effort biases underlying the sightings data on which it was based.

Fin Whale

Description and Distribution

Fin whales, *Balaenoptera physalus*, are the second-largest whale species by length. They are long-bodied and slender, with a prominent dorsal fin set about two-thirds of the way back on the body. The basic body color of the fin whale is dark gray dorsally and white ventrally, but the pigmentation pattern is complex. The lower jaw is gray or black on the left side and creamy white on the right side. This asymmetrical coloration extends to the baleen plates as well, and is reversed on the tongue. Individually distinctive features of pigmentation, along with dorsal fin shapes and body scars, have been used in photo-identification studies (Agler et al. 1990).

The fin whale has an extensive distribution in the North Atlantic, occurring from the Gulf of Mexico (Jefferson and Schiro 1997) and Mediterranean Sea, northward to the edges of the arctic pack ice (Jonsgård 1966a, 1966b; Sergeant 1977, IWC 1992). In general, fin whales are more common north of approximately 30°N latitude, but considerable confusion arises about their occurrence south of 30°N latitude, because of the difficulty in distinguishing fin whales from Bryde’s whales (Mead 1977). Extensive ship surveys led Mitchell (1974) to conclude that the summer feeding range of fin whales in the western North Atlantic was mainly between 41°20'N and 51°00'N, from shore seaward to the 1,000-fathom contour.

The local distribution of fin whales during much of the year is probably governed largely by prey availability (Ingebrigtsen 1929, Jonsgård 1966a, 1966b). For example, the positions off southwestern Iceland where fin whales were caught correlated well with the known distribution of spawning krill (Meganyctiphanes norvegica), their preferred prey in that area (Rørvik et al. 1976). In general, fin whales in the central and eastern North Atlantic tend to occur most abundantly over the continental slope and on the shelf seaward of the 200 m isobath (Rørvik et al. 1976). In contrast, off the eastern U.S. they are centered along the 100 m isobath but with sightings well spread out over shallower and deeper water, including submarine canyons along the shelf break (Kenney and Winn 1987, Hain et al. 1992). Fin whales accounted for 46% of the large whales and 24% of all cetaceans sighted over the continental shelf during aerial surveys between Cape Hatteras and Nova Scotia during 1978-82 (CeTAP 1982).

Segregation seems to occur at least in summer, with the larger (mature) whales arriving at feeding areas earlier, and departing later, than the smaller individuals (Rørvik et al. 1976). Within the Gulf of Maine, lactating females and their calves primarily occupy, or at times are the only ones occupying, this southern portion of their summer feeding range (Agler et al. 1993).

Fin whales are locally common in the River and Gulf of St. Lawrence during the summer and fall, especially on the north shore shelf (Edds and Macfarlane 1987, Borobia et al. 1995, Kingsley and Reeves 1998). Sergeant (1977) suggested that they associate with steep contours of the Laurentian Channel, either because tidal and current mixing along such gradients drives high biological production or because changes in depth aid their navigation.

Reproduction

The gestation period is probably somewhat less than a year, and fin whale calves are nursed for 6-7 months (Haug 1981, Gambell 1985). Most reproductive activity, including births and mating, takes place in the winter season (November to March; peak December/January) (Haug 1981; Mitchell 1974), although "out-of-season" births do occur off the eastern U.S. (Hain et al. 1992).

The average calving interval has been estimated at about two years, based on whaling data (Christensen et al. 1992b). In unexploited populations, the interval may be somewhat longer. Agler et al. (1993) used photo-identification data to estimate an average interval of 2.7 years for fin whales in the Gulf of Maine although they acknowledged that this value was probably biased upward by incomplete sighting histories. If certain females calved in "missed" years (i.e., years in which they were not photo-identified in the study area), the mean interval could have been as low as 2.24 years (Agler et al. 1993). Breiwick (1993) found that the annual pregnancy rate (defined as the percentage of mature females that are pregnant in a given year) was significantly lower in the population hunted from Blandford, Nova Scotia, than in the population hunted from Williamsport and South Dildo, Newfoundland. Among the hypotheses that could explain this difference is that fin whales show a density-dependent response by shortening the birth interval (and/or the time to sexual maturity) and that the Nova Scotia population was less depleted than the Newfoundland population, at the time of sampling.

Fin whales in populations near carrying capacity may not attain sexual maturity until ten years of age or older, whereas those in exploited populations can mature as early as six or seven years of age (Gambell 1985). It should be noted, however, that the question of whether whaling data from the Southern Hemisphere do or do not demonstrate density-dependent responses in the reproductive cycle of fin whales is controversial (Mizroch and York 1984, Sampson 1989).

The gross annual reproductive rate of fin whales in the Gulf of Maine (calves as a percentage of the total population) was about 8% during the 1980s (Agler et al. 1993). Sigurjónsson (1995) gave the range of pregnancy rates for the species (proportion of adult females pregnant in a given year) as 0.36-0.47.

Ecological Relationships

Diet, Development, and Growth

Fin whales in the North Atlantic eat pelagic crustaceans (mainly euphausiids or krill, including Meganyctiphanes norvegica and Thysanoessa inermis) and schooling fish such as capelin (Mallotus villosus), herring (Clupea harengus), and sand lance (Ammodytes spp.) (Hjort and Ruud 1929, Ingebrigtsen 1929, Jonsgård 1966a, Mitchell 1974, Sergeant 1977, Overholtz and Nicolas 1979, Christensen et al. 1992b, Borobia et al. 1995). The availability of sand lance, in particular, is thought to have had a strong influence on the distribution and movements of fin whales along the east coast of the U.S. (Kenney and Winn 1986, Payne et al. 1990, Hain et al. 1992).

Although there may be some degree of specialization, most individuals probably prey on both invertebrates and fish, depending on availability (Watkins et al. 1984, Edds and Macfarlane 1987, Borobia et al. 1995). Sergeant (1977) suggested that euphausiids were the "basic food" of fin whales and that they took advantage of fish when sufficiently concentrated, "particularly in the pre-spawning, spawning, and post-spawning adult stages on the Continental Shelf and in coastal waters."

Migration and Movement

Fin whale populations exhibit differing degrees of mobility, presumably depending on the stability of access to sufficient prey resources throughout the year. Most groups are thought to migrate seasonally, in some cases over distances of thousands of kilometers. They feed intensively at high latitudes in summer and fast, or at least greatly reduce their food intake, at lower latitudes in winter. Some groups apparently move over shorter distances and can be considered resident to areas with a year-round supply of adequate prey. The fin whale is a cosmopolitan species with a generally anti-tropical distribution centered in the temperate zones. Two subspecies, a large Southern Hemisphere form and a smaller Northern Hemisphere form, have been recognized by some authorities (Tomilin 1946, 1967; Sokolov and Arsen'ev 1994, Rice 1998).

Although fin whales are certainly migratory, the overall migration pattern is confusing and likely complex (Christensen et al. 1992a). Regular mass movements along well-defined migratory corridors, with specific end-points, have not been documented by sightings. However, acoustic recordings from passive-listening hydrophone arrays, indicate a southward "flow pattern" occurs in the fall from the Labrador-Newfoundland region, south past Bermuda, and into the West Indies (Clark 1995). Fin whales occur year-round in a wide range of latitudes and longitudes, but the density of individuals in any one area changes seasonally. Thus, their aggregate movements are patterned and consistent, but movements of individuals in a given year may vary according to their energetic and reproductive condition, climatic factors, etc. In some parts of their range, such as the Gulf of St. Lawrence and the Newfoundland shelf, ice formation in winter forces fin whales offshore, and its disintegration in spring, allows them to move back inshore (Jonsgård 1966a, Sergeant 1977). One or more "populations" of fin whales were thought by Norwegian whalers to remain year-round in high latitudes, actually moving offshore, but not southward, in late autumn (Hjort and Ruud 1929, Jonsgård 1966a). These observations were recently reinforced by acoustic evidence that fin whales occur throughout the winter in the Norwegian and Barents Seas, apparently in considerable numbers (Clark 1995).

While much remains unknown, the magnitude of the ecological role of the fin whale is impressive (Waring et al. 2007). In the U.S. Atlantic Exclusive Economic Zone (EEZ), fin whales are probably the dominant large cetacean species during all seasons, having the largest standing stock, the largest food requirements, and therefore the largest impact on the ecosystem of any cetacean species (Kenney et al. 1997, Hain et al. 1992).

Abundance and Status of Stock

Two estimates of fin whale abundance are available. A 1995 sighting survey, covering the waters from Virginia to the mouth of the Gulf of St. Lawrence, estimated 2,200 individuals

(CV=0.24) (Palka 1995). A more recent estimate of 2,814 (CV=0.21) fin whales was derived from a 1999 sighting survey, covering waters from Georges Bank to the mouth of the Gulf of St. Lawrence (NMFS unpublished data, Palka 2006). The 1999 estimate is considered the best available for the western North Atlantic fin whale stock because it is relatively recent. However, this estimate must be considered extremely conservative (Waring et al. 2007).

The status of this stock relative to the optimum sustainable population in the U.S. Atlantic EEZ is unknown, but the species is listed as endangered under the ESA. There are insufficient data to determine the population trend for fin whales. This is a strategic stock because the fin whale is listed as an endangered species under the ESA (Waring et al. 2007).

Humpback Whale

Description and Distribution

Humpback whales, Megaptera novaengliae, have uncommonly long flippers, with a more robust body, fewer throat grooves, and more variable dorsal fin than other Balaenopterid whales. Their vocalizations are also longer and more complex than other whales Balaenopterid whales (NMFS 1991a). Their overall length varies slightly depending on geographic location, but the maximum length recorded was 60 ft. (Winn and Reichley 1985). Humpbacks are generally dark on the back, their flippers, underside, and flukes generally have substantial areas of white pigmentation (NMFS 1991a).

Humpbacks are distributed worldwide but are less common in arctic waters. During the winter months, humpbacks are most common in temperate and tropical waters (10°N-23°N latitude). In the summer, they will frequently head to more biological productive waters in the higher latitudes (35°N-65°N) (Winn and Reichley 1985). Humpbacks are generally thought to inhabit the waters over continental shelves and around some oceanic islands (Balcomb and Nichols 1978, Whitehead 1987).

Reproduction

Humpbacks reach sexual maturity between the ages of four and six (NMFS 1991a) and the mean length at sexual maturity for humpbacks off California was 48 ft. (14.5 m) for females and 44 ft. (13.5 m) for males (National Marine Mammal Laboratory, unpublished data). Mating and birthing is thought to occur during the migration to over-wintering areas. Sexually mature females give birth approximately every two to three years, although annual and multi-year (five years or more, Baker et al. 1988) have been observed (Chittleborough 1965, Glockner-Ferrari and Ferrari 1984, 1985; Clapham and Mayo 1987, 1990; Perry et al. 1988); gestation and lactation last 10-12 months (Nishiwaki 1959, NMML unpublished data, Rice 1963).

Ecological Relationships

Diet, Development, and Growth

In the western North Atlantic, humpback whales feed during spring, summer, and fall over a geographic range encompassing the eastern coast of the U.S. (including the Gulf of Maine), the Gulf of St. Lawrence, Newfoundland/Labrador, and western Greenland (Katona and Beard 1990). Humpback whales are frequently piscivorus when in New England waters, feeding on herring (Clupea harengus), sand lance (Ammodytes spp.), capelin (Mallotus villosus) and other small fishes. Atlantic mackerel (Scomber scombus), small pollock (Pollachius virens) and haddock (Melanogrammus aeglefinus) are also occasionally preyed upon (NMFS 1991a). In the northern Gulf of Maine, euphausiids are also frequently taken (Paquet et al. 1997). Humpbacks may dive as deep as 650 ft. (200 m) in pursuit of food (NMFS 1991a), though shallower dives are more common.

Humpbacks also use a wide variety of feeding methods, more so than any other baleen whale. Known humpback feeding behaviors are: (1) the use of columns, clouds or nets of expelled bubbles to concentrate krill or fish; (2) herding/disabling prey by pounding or flicking their flukes and flippers; (3) using the water surface as a barrier against which they can trap and concentrate prey; (4) feeding in formation ("echelon feeding"); (5) using acoustic cues to synchronize feeding lunges; (6) apparent short- and long-term cooperation between individuals (Ingebritsen 1929, Jurasz and Jurasz 1979, Watkins and Schevill 1979, Hain et al. 1982, Weinrich 1983, Baker and Herman 1985, Baker 1985, Hays et al. 1985, Winn and Reichley 1985, D'Vincent et al. 1985). There are also reports of humpbacks approaching fishing vessels in the process of hauling gear to take fish concentrated by the net (W.A. Watkins, J. Sigurjonsson pers. comm. in NMFS 1991a) or feeding on portions of catch that escaped through the trawl mesh (D.E. Sergeant pers. comm. in NMFS 1991a). Humpbacks also appear to feed off prey stirred up from the bottom during shrimping operations (von Ziegesar 1984).

Migration and Movement

Humpbacks exhibit two general types of migration and movement: (1) in season movement throughout portions of their summer range and (2) long distance migrations between summering and wintering areas (NMFS 1991a).

During winter, whales from most identified Atlantic feeding areas (including the Gulf of Maine) mate and calve in the West Indies, where spatial and genetic mixing among subpopulations occurs (Clapham et al. 1993, Katona and Beard 1990, Palsbøll et al. 1997, Stevick et al. 1998). A few whales of unknown northern origin migrate to the Cape Verde Islands (Reiner et al. 1996). In the West Indies, the majority of whales are found in the waters of the Dominican Republic, notably on Silver Bank, Navidad Bank, and in Samana Bay (Balcomb and Nichols 1982, Whitehead and Moore 1982, Mattila et al. 1989, 1994). Seawater temperatures in these locations can reach 28°C, which is among the highest experienced by any balaenopterid (NMFS 1991a). Humpback whales are also found at much lower densities throughout the remainder of the Antillean arc, from Puerto Rico to the coast of Venezuela (Winn et al. 1975, Levenson and Leapley 1978, Price 1985, Mattila and Clapham 1989).

Not all whales migrate to the West Indies every winter, and significant numbers of animals are found in mid and high-latitude regions at this time (Clapham et al. 1993, Swingle et al. 1993). An increased number of sightings of humpback whales near the Chesapeake and Delaware Bays occurred in 1992 (Swingle et al. 1993). Wiley et al. (1995) reported 38 humpback whale strandings occurred during 1985-1992 in the U.S. mid-Atlantic and southeastern states. Humpback whale strandings increased, particularly along the Virginia and North Carolina coasts, and most stranded animals were sexually immature. In addition, the small size of many of these whales strongly suggested that they had only recently separated from their mothers. Wiley et al. (1995) concluded that these areas were becoming an increasingly important habitat for juvenile humpback whales and that anthropogenic factors may negatively affect whales in this area.

There have also been a number of wintertime humpback sightings in coastal waters of the southeastern U.S. (NMFS unpublished data, New England Aquarium unpublished data, Florida DEP unpublished data). Whether the increased sightings represent a distributional change, or are simply due to an increase in sighting effort and/or whale abundance, is unknown.

Abundance and Status of Stock

Current data suggest that the Gulf of Maine humpback whale stock is steadily increasing in size. This is consistent with an estimated average trend of 3.1% (SE=0.005) in the North Atlantic population overall for the period 1979-1993 (Stevick et al. 2003), although there are no feeding-area-specific estimates. Although these estimates of abundance indicate continued population growth, the size of the humpback whale stock may be below optimum sustainable population in the U.S. Atlantic EEZ (Waring et al. 2007). There are insufficient data to determine current population trends for humpback whales in the North Atlantic overall.

A new large-scale assessment called More of North Atlantic Humpbacks (MoNAH) project is currently underway. This two-year study will attempt to estimate abundance and refine knowledge of population structure with extensive sampling in the Gulf of Maine/Scotian Shelf region and on the primary wintering ground on Silver Bank; additional research will focus on the U.S. mid-Atlantic states (Waring et al. 2007).

Northern Right Whale

Description and Distribution

The right whale, *Eubalaena glacialis*, is a large baleen whale. Adults are generally between 45 ft and 55 ft (13.7-16.8 m) in length and can weigh up to 70 tons (63.5 metric tons). Females are larger than males. The distinguishing features of right whales include a stocky body, generally black coloration (although some individuals have white patches on their undersides), lack of a dorsal fin, large head (about 1/4 of the body length), strongly bowed margin of the lower lip, and callosities on the head region. Two rows of long (up to about eight feet (2.4 m) in length), dark baleen plates hang from the upper jaw, with about 225 plates on each side. The tail is broad, deeply notched, and all black with smooth trailing edge (NMFS 2005).

Individuals of the western Atlantic northern right whale population range from wintering and calving grounds in coastal waters of the southeastern U.S. to summer feeding and nursery grounds in New England waters and northward to the Bay of Fundy and the Scotian Shelf. For much of the year, their distribution is strongly correlated to the distribution of their prey, which appears to be primarily calanoid copepods in the Northern Hemisphere.

Five areas of “high use” were identified in the previous Recovery Plan for the Northern Right Whale (NMFS 1991b), and they are still key habitat areas for right whales: (1) Coastal Florida and Georgia (Sebastian Inlet, Florida to the Altamaha River, Georgia), (2) The Great South Channel (east of Cape Cod), (3) Massachusetts Bay and Cape Cod Bay, (4) The Bay of Fundy, and (5) The Scotian Shelf, including Browns and Baccaro Banks, Roseway Basin and areas to the east. The first three of these areas were designated as Northern right whale critical habitat in June 1994. Right whales occur off New England at various times of the year, with a peak occurrence in winter/spring (Hamilton and Mayo 1990). Peak abundance occurs in the Great South Channel in spring (Kenney et al. 1995, Kenney 2001). In summer and fall, much of the population is found in Canadian waters (i.e., the Bay of Fundy and Scotian Shelf, with the former area being a major summer nursery ground) (Mitchell et al. 1986, Winn et al. 1986, Stone et al. 1990). Whales seen in the Roseway Basin/Browns Bank region were primarily juvenile and adult males (Brown et al. 2001), whereas most of the summer/autumn sightings of mother/calf pairs have been in the Bay of Fundy (Kenney et al. 2001). However, the former area appears to have been largely abandoned in 1993, and the population composition in the Bay of Fundy has recently been much more mixed than it was previously.

Records from the Gulf of Mexico (Moore and Clark 1963, Schmidly et al. 1972) represent either geographic anomalies or a more extensive historic range beyond the sole known calving and wintering ground in the waters of the southeastern U.S. Whatever the case, the location of most of the population is unknown during the winter. Offshore (greater than 30 miles) surveys flown off the coast of northeastern Florida and southeastern Georgia from 1996 to 2001 had 3 sightings in 1996, 1 in 1997, 13 in 1998, 6 in 1999, 11 in 2000 and 6 in 2001 (within each year, some were repeat sightings of previously recorded individuals). The frequency with which right whales occur in offshore waters in the southeastern U.S. remains unclear.

Critical Habitat

As noted above, there are five well-known habitats used annually by western North Atlantic right whales: 1) coastal Florida and Georgia, 2) the Great South Channel, east of Cape Cod, 3) Cape Cod and Massachusetts Bays, 4) the Bay of Fundy, and 5) Browns and Baccaro Banks, south of Nova Scotia. The first three areas occur in U.S. waters and were designated by NMFS as critical habitat in June 1994 (59 FR 28793).

Actions authorized, funded, or carried out by Federal agencies that may have an impact on critical habitat must be consulted upon in accordance with Section 7 of the ESA, regardless of the presence of right whales at the time of impacts. Impacts on these areas that may affect primary constituent elements such as prey availability and the quality of nursery areas must be considered when analyzing whether habitat may be adversely modified.

Reproduction

Females give birth to their first calf at an average age of 9 years (Best et al. 2001, Hamilton et al. 1998). Calves are 18 to 19 ft (5.5 m to 6.0 m) in length at birth (Best 1994). Gestation lasts from 357 to 396 days in southern right whales (Best 1994), and it is likely to be similar in the northern species. Standard reproductive rates for the western North Atlantic population have yet to be calculated.

The calving interval for right whales is between 2 and 7 years, with means ranging from 3.12 (95 percent confidence interval (CI) 3.05–3.17) to 3.67 years (95 percent CI 3.3–4.1) (Knowlton et al. 1994, Best et al. 2001, Burnell 2001, Cooke et al. 2001). In the western North Atlantic, there was a significant increase in the calving interval from 3.67 years for the period 1980 to 1992 (Knowlton et al. 1994) to 5.8 years for the period 1990 to 1998 (Kraus et al. 2001). The increase in the calving interval is of particular concern and, together with other perplexing biological parameters, may suggest the population is under rather unusual biological, energetic, or reproductive stress. Most recently (2001–2005), a dramatic increase in North Atlantic right whale calving (23 calves per year) may have decreased the interval to levels more similar to that of the southern right whale (Kraus et al., in press).

The waters south of Cape Cod and north of the Georgia/Florida winter calving ground are not considered "high use" areas, yet the whales clearly move through these waters, especially waters off New York/New Jersey and the "mid-Atlantic" states, regularly (Reeves et al. 1978, Reeves and Mitchell 1986, Winn et al. 1986, Reeves et al. 1999). Most calving takes place off Georgia and Florida, but limited surveys recently conducted along the mid-Atlantic suggest some mother-calf pairs use the area from Cape Fear, North Carolina, to South Carolina as a wintering/calving area as well.

Ecological Relationships

Diet, Development, and Growth

Weaning seems to be variable, and has been reported as 8 to 17 months in North Atlantic right whales (Hamilton and Marx 1995). In the western North Atlantic, right whales feed primarily on copepods, with Calanus finmarchicus believed to be the primary prey (Kraus et al. 1988, Wishner et al. 1988, Murison and Gaskin 1989). However, other zooplankters are also taken, including Pseudocalanus spp., Centropages spp., and even cyprids (Mayo and Marx 1990). There is no evidence for consumption of euphausiids although, given the inclusion of this taxon in the diet of right whales elsewhere, it would be surprising if North Atlantic right whales were different in this regard. Unlike balaenopterid whales, right whales are skimmers; they feed by continuously filtering prey through their baleen while moving, mouth agape, through a patch of zooplankton. Feeding occurs from spring through fall, and also in winter in certain areas (e.g., Cape Cod Bay; Mayo and Marx 1990). Oceanographic and bathymetric features, such as relatively cooler water temperatures and 100-200 m depths adjacent to steeply sloping bottom topography, also seem to be related to the utilization of certain areas for feeding (Winn et al. 1986, Clapham 1999).

Migration and Movement

In summer and fall, much of the population is found in Canadian waters (i.e., the Bay of Fundy and Scotian Shelf, with the former area being a major summer nursery ground) (Mitchell et al. 1986, Winn et al. 1986, Stone et al. 1990). Knowlton et al. (1992) reported several long-distance movements as far north as Newfoundland, the Labrador Basin, and southeast of Greenland; in addition, recent resightings of photographically identified individuals have been made off Iceland, arctic Norway and in the old Cape Farewell whaling ground east of Greenland.

Known wintering areas for this population are along the southeastern U.S. coast, where calving occurs from December through March (Winn 1984, Kraus et al. 1986, International Whaling Commission (IWC) 1986), and in Cape Cod Bay where, in 1998, whales were sighted from mid January to mid May (Brown and Marx 1998). However, a majority of the population is unaccounted for in winter (Kraus et al. 1986). Other wintering areas have been suggested, based upon sparse data; these include the Gulf of St. Lawrence (Lien et al. 1989), Newfoundland (Beamish 1981, Lien et al. 1989), New York and New Jersey coastal waters (Mead 1986), Bermuda (Payne and McVay 1971), and the Gulf of Mexico (Mead 1986) (see Reeves 2001 for a review).

Telemetry studies have revealed movement patterns of considerable length and duration (Mate et al. 1997, Slay et al. 1998). They may also feed, at least opportunistically, while migrating. Successful efforts to protect the whales in areas where they linger for long periods and/or aggregate in relatively high densities could be offset if the animals were to be exposed to serious risks, such as collision or entanglement, while in transit between such areas.

Information on residency times of individual whales at specific sites is ambiguous, especially in light of recent satellite transmitter results indicating right whales tagged in the Bay of Fundy may travel long distances in the few days or weeks between sightings (Mate et al. 1997). Schevill et al. (1986) reported individual right whales residing in Cape Cod waters for no more than a few days. In 1976, they observed a cow and calf over a 7-week period, the longest residence time documented during observations between 1955 and 1981. Prior to 1986, Hamilton and Mayo (1990) reported observations of individual whales up to 12 times in a year, with the longest apparent residency being 89 days. Fifty percent of individual right whales sighted by Hamilton and Mayo (1990) were seen in more than one year.

It has been suggested that interspecific competition with either sei whales (*Balaenoptera borealis*) or planktivorous fish may limit Northern right whale prey consumption (Mitchell 1975a, Kraus et al. 1988, Payne et al. 1990). In the North Atlantic, sei whales are sympatric with the right whales, and because both species feed on small zooplankton species, they may compete (Mitchell 1975a).

There is also speculation about competition with certain species of fish in the Gulf of Maine, including sand lance (*Ammodytes* spp.), herring (*Clupea* spp.), Atlantic mackerel (*Scomber scombrus*), river herrings (shad, blueback; *Alosa* spp.), menhaden (*Brevoortia tyrannus*), and basking sharks (*Cetorhinus maximus*). However, as noted by Clapham and Brownell (1996), assertions regarding interspecific competition are rarely well defined or ecologically based. While the potential for interference competition exists for right whales, direct evidence is essentially absent.

Abundance and Status of Stock

Based on a census of individual whales identified using photo-identification techniques and an assumption of mortality of whales not seen in seven years, the western North Atlantic stock size was estimated to be 295 individuals in 1992 (Knowlton et al. 1994). An updated analysis using the same method gave an estimate of 299 animals in 1998 (Kraus et al. 2001). A review of the photo-id recapture database in October 2005 indicated that 306 individually recognized whales were known to be alive during 2001. Because this was a nearly complete census, it is assumed that this estimate represents a minimum population size. However, no estimate of abundance with an associated coefficient of variation has been calculated for the population (Warning et al 2007).

The size of this stock is considered to be extremely low relative to optimum sustainable population in the U.S. Atlantic EEZ, and this species is listed as endangered under the ESA. The North Atlantic right whale is considered one of the most critically endangered populations of large whales in the world (Clapham et al. 1999). There has been no apparent sign of recovery in the last 15 years and the species may be rarer and more endangered than previously thought.

Because the right whale is a long-lived species, extinction may not occur in the near future, but the possibility of biological extinction in the next century is very real (NMFS 2005).

Sei Whale

Description and Distribution

Sei whales, *Balaenoptera borealis*, are generally 45 to 55 feet in length, though some may reach 65 feet and weigh 14 to 17 tons. Sei whales, like other rorquals species, have slim and streamlined bodies with a blueish-gray body and white undersides. They also possess a single ridge running from the tip of the snout to the blowhole. Sei whales have 32 to 60 throat grooves. They have relavitively short pectoral fins and a tall, falcate dorsal fin. The dorsal fin is located about one-third of the body length anterior from its relatively small fluke (Balcomb and Minasian 1984, Ellis 1980, Leatherwood and Reeves 1983, American Cetacean Society Fact Sheet 2007).

Indications are that, at least during the feeding season, a major portion of the Northwest Atlantic sei whale population is centered in northerly waters, perhaps on the Scotian Shelf (Mitchell and Chapman 1977). The southern portion of the species' range during spring and summer includes the northern portions of the U.S. Atlantic Exclusive Economic Zone (EEZ) - the Gulf of Maine and Georges Bank. The period of greatest abundance there is in spring, with sightings concentrated along the eastern margin of Georges Bank and into the Northeast Channel area, and along the southwestern edge of Georges Bank in the area of Hydrographer Canyon (CeTAP 1982). NMFS aerial surveys in 1999, 2000, and 2001 found concentrations of sei and right whales along the Northern Edge of Georges Bank in the spring.

The sei whale is often found in the deeper waters characteristic of the continental shelf edge region (Hain et al. 1985), and NMFS aerial surveys found substantial numbers of sei whales in this region, south of Nantucket, in the spring of 2001. Similarly, Mitchell (1975b) reported that sei whales off Nova Scotia were often distributed closer to the 2,000 m depth contour than were fin whales.

Reproduction

Sei whales reach sexual maturity around ten years of age. Males generally reach sexual maturity when they reach 40 ft. in length, while females mature when they reach about 50 ft. The gestation period is between 11.5 and 12 months, with a calving interval of approximately two years. At birth, sei whales range from 14 to 15 ft in length and weigh approximately 2,000 pounds (Balcomb and Minasian 1984, Ellis 1980, Leatherwood and Reeves 1983, American Cetacean Society Fact Sheet 2007).

Ecological Relationships

Diet

Although known to take piscine prey, sei whales (like right whales) are largely planktivorous, feeding primarily on euphausiids and copepods. In years of reduced predation on copepods by other predators, and thus greater abundance of this prey source, sei whales are reported in more inshore locations, such as the Great South Channel (in 1987 and 1989) and Stellwagen Bank (in 1986) areas (R.D. Kenney, pers. comm.; Payne et al. 1990).

Migration and Movement

Based on analysis of records from the Blandford, Nova Scotia, whaling station, where 825 sei whales were taken between 1965 and 1972, Mitchell (1975b) described two "runs" of sei whales, in June-July and in September-October. He speculated that the sei whale population migrates from south of Cape Cod and along the coast of eastern Canada in June and July, and returns on a southward migration again in September and October; however, such a migration remains unverified.

Abundance and Status of Stock

There are insufficient data to determine the population trends for this species and the total number of sei whales in the U.S. Atlantic EEZ is unknown (Waring et al. 2007). However, an abundance of 280 sei whales was estimated from an aerial survey program conducted from 1978 to 1982 on the continental shelf and shelf edge waters between Cape Hatteras, North Carolina and Nova Scotia (CeTAP 1982). Though, this estimate is more than 20 years out of date and almost certainly does not reflect the current true population size; in addition, the estimate has a high degree of uncertainty (i.e., it has a large CV), and it was estimated just after cessation of extensive foreign fishing operations in the region. There are no recent abundance estimates for the sei whale (Waring et al. 2007).

Sperm Whale

Description and Distribution

The sperm whale, *Physeter macrocephalus* (Linnaeus, 1758), is a truly cosmopolitan species, whose distribution is thought to be more extensive than that of any other marine mammal, except the killer whale (*Orcinus orca*) (Rice 1989). Male sperm whales can reach lengths of more than 18 meters (m), while females can reach lengths of up to 12.5 m. They can weigh up to 57 and 24 metric tons, respectively (Rice 1989).

The sperm whale has a disproportionately large head, one quarter to one third of its total body length (Rice 1989). Its rod-shaped lower jaw is narrow and underslung, with 20-26 pairs of well-developed teeth in the mandibles, but the maxillary teeth are vestigial. Its dorsal fin is low in profile, thick, and not pointed or recurved. Sperm whales are generally dark gray in color, with white lips and often white areas on the belly and flanks. Photographs of distinctive markings on the dorsal fins and flukes of sperm whales are used in studies of life history and behavior (Whitehead and Gordon 1986, Whitehead 1990).

The distribution of sperm whales extends to all deep ice-free marine waters from the Equator to the edges of polar pack ice (Rice 1989). Sperm whales are present in many warm-water areas throughout the year, and such areas may have discrete “resident” populations (Watkins et al. 1985, Gordon et al. 1998, Drout 2003, Engelhaupt 2004, Jaquet et al. 2003). While their aggregate distribution is certainly influenced by the patchiness of global marine productivity (Jaquet and Whitehead 1996), no physical barriers, apart from landmasses, appear to obstruct their dispersal (Berzin 1972, Jaquet 1996).

Two of the major 19th century whaling grounds for sperm whales, the Southern Ground and the Charleston Ground, are situated directly off the eastern United States (Townsend 1935). The sperm whalers also visited the northern Gulf of Mexico and the West Indies regularly.

Mitchell (1972) found the highest densities of sperm whales, by far, in the "North Sargasso Sea Region" (30-40°N, 50-70°W) and the "Gulf Stream Region" (two discrete offshore areas between 40°N and 50°N - one over the Grand Banks of Newfoundland and the other over the North Atlantic Ridge). This result is consistent with the observation by Townsend (1935) and Waring et al. (1993), that the Gulf Stream has an important influence on sperm whale distribution.

The overall distribution along the U.S. east coast is centered along the shelf break and over the slope (CETAP 1982, Waring et al. 2005). Very high densities occur in inner slope waters north of Cape Hatteras, North Carolina, seaward of the 1000-m isobath during summer months (Mullin and Fulling 2003; Southeast Fisheries Science Center unpublished data; Waring et al. 2005). Sperm whales are also known to move onto the continental shelf in waters less than 100 m deep on the southern Scotian Shelf and south of New England, particularly between late spring and autumn (Whitehead et al. 1992a-b, Waring et al. 1997, Scott and Sadove 1997).

The sperm whale is the most common large cetacean in the northern Gulf of Mexico, where it occurs in greatest density along and seaward of the 1000 m contour (Mullin et al. 1991, 1994; Jefferson and Schiro 1997, Davis et al. 1998, Weller et al. 2000, Würsig et al. 2000, Mullin and Fulling 2004). They appear to prefer steep rather than shallow depth gradients (Davis et al. 1998). The spatial distribution of sperm whales within the Gulf of Mexico is strongly correlated with mesoscale physical features such as loop current eddies that locally increase primary production and prey availability (Biggs et al. 2005). Several satellite tags used in conjunction with the Sperm Whale Seismic Study (SWSS) indicate sperm whale movements generally along the shelf break (700-1000 m depth) throughout the Gulf of Mexico, with some animals using deeper oceanic waters (Jochens and Biggs 2004).

Reproduction

Sperm whales mature slowly. Females usually begin ovulating at 7-13 years of age. Maturation in males usually begins in this same age interval, but most individuals do not become fully mature until their twenties. Prime bulls, in their late twenties and older, rove among groups of females on the tropical breeding grounds. A male's association with a female group can be as brief as several hours. Since females within a group often come into estrus synchronously, the male need not remain with them for an entire season to achieve maximal breeding success (Best and Butterworth 1980).

The peak breeding season for sperm whales in the North Atlantic occurs during the spring (March/April to May), with some mating activity taking place earlier or later, from December to August. Gestation lasts well over a year, with credible estimates of the normal duration ranging from 15 months to more than a year and a half. Lactation lasts at least two years, and the inter-birth interval is 4-6 years for prime-aged females and apparently, much longer for 40+ year-olds.

Two particular aspects of the sperm whale's reproductive biology are relevant to management. First, the maximal rate of increase in reproduction is very low, perhaps no more than one or two percent per year. Second, selective killing of large males by whalers could have had the residual effect of reducing reproductive rates (Whitehead et al. 1997).

Ecological Relationships

Diet, Development, and Growth

Sperm whales are deep and prolonged divers and can therefore use the entire water column, even in very deep areas. However, they seem to forage mainly on or near the bottom, often ingesting stones, sand, sponges, and other non-food items (Rice 1989; Whitehead et al. 1992a-b). As far as is known, sperm whales feed regularly throughout the year. Lockyer (1981) estimated that they consumed about 3.0-3.5% of their body weight per day.

A large proportion of the sperm whale's diet consists of low-fat, ammoniacal, luminescent squids (Clarke 1980, 1996; Martin and Clarke 1986). In some areas of the North Atlantic, however, males prey heavily on the oil-rich squid *Gonatus fabricii*, a species frequently also eaten by bottlenose whales (*Hyperoodon ampullatus*) (Clarke 1997). A giant squid (*Architeuthis* sp.) as large as 12 m long and weighing 200 kg has been found in a sperm whale's stomach (Berzin 1972). While sperm whales feed primarily on large and medium-sized squids, the list of documented food items is fairly long and diverse. Prey items include other cephalopods, such as octopuses, and medium- and large-sized demersal fishes, such as rays, sharks, and many teleosts (Berzin 1972; Clarke 1977, 1980; Rice 1989). The diet of large males in some areas, especially in high northern latitudes, is dominated by fish (Rice 1989). Lumpsuckers (*Cyclopterus lumpus*), for example, are frequently taken in Denmark Strait (Martin and Clarke 1986).

Stable, long-term associations among related and unrelated females (Christal 1998) form the core units of sperm whale societies (Christal et al. 1998). Up to about a dozen females usually live in such groups, accompanied by their female and young male offspring. Males start leaving these family groups at about six years of age, after which they live in "bachelor schools." The cohesion among males within a bachelor school declines as the animals age. During their breeding prime and old age, male sperm whales are essentially solitary (Christal and Whitehead 1997).

Migration and Movement

A striking feature of the sperm whale's life history is the difference in migratory behavior between adult males and females. Only adult males move into high latitudes, while all age classes and both sexes range throughout tropical and temperate seas. At least some individuals are present year-round in the higher latitudes (Mellinger et al. 2004). A combination of factors, including wide dispersal by males, ontogenetic changes in association patterns, and female pod fidelity and cohesion complicates any evaluation of population structure. An initial examination of global matrilineal population structure suggests that interoceanic dispersal of female lineages is limited (Dillon 1996, Lyrholm and Gyllensten 1998). However, studies of allelic variation in nuclear markers are needed to reveal the extent to which male dispersal might cause genetic mixing between oceanic populations (Lyrholm et al. 1999, Bond 1999).

In a review of the evidence for interspecific competition in baleen whales, Clapham and Brownell (1996) found it to be extremely difficult to prove that inter-specific competition comprises an important factor in the population dynamics of large whales. May et al. (1979) used a relatively simple example, using male sperm whales, squid, and krill in the Antarctic, to show how complex the dynamics could be. According to their model, yield in the krill fishery is a function of both fishing effort on krill and the abundance of sperm whales. Sperm whales prey on cephalopods, which in turn, prey on krill. According to the model, the largest sustainable krill fishery in the Southern Ocean would be attained when sperm whales were not exploited there.

There is no evidence that competition for prey resources is a factor limiting the abundance of sperm whales in the North Atlantic. Adult male sperm whales have been observed to aggregate near trawl nets targeting Greenland halibut (*Reinhardtius hippoglossoides*) in one area of the western North Atlantic, but they are not known to take fish from the nets (Leaper and Karpouzli 1998). Two of the squid species eaten by sperm whales in the North Atlantic - *Gonatus fabricii* and *Todarodes sagittatus* - are known to be important in the diets of northern bottlenose whales (Gonatus only), long-finned pilot whales (*Globicephala melas*, both subspecies recognized in the North Atlantic and Southern Hemisphere), and short-finned pilot whales (*G. macroryhncus*); (Clarke 1997). However, there is no basis for assuming that competition for food among these three cetacean species is a factor in determining their population trend and abundance.

Abundance and Status of Stock

Total numbers of sperm whales off the U.S. or Canadian Atlantic coast are unknown, although several estimates from selected regions of the habitat do exist for select time periods. Currently, the best abundance estimate for sperm whales is the sum of the estimates from the two 2004 U.S. Atlantic surveys, 4,804 (CV =0.38), where the estimate from the northern U.S. Atlantic is 2,607 (CV =0.57), and from the southern U.S. Atlantic is 2,197 (CV =0.47). This joint estimate is considered the best available because together these two surveys have the most complete coverage of the species' habitat (Waring et al. 2007). Because these estimates were not corrected for dive-time, they are likely downwardly biased and an underestimate of actual abundance. The average dive-time of sperm whales is approximately 30 - 60 min (Whitehead et al. 1991, Watkins et al. 1993, Peter Madsen, Woods Hole Oceanographic Institution, pers. comm., in Waring et al. 2007), therefore, the proportion of time that they are at the surface and available to visual observers is assumed to be low. The density of sperm whales along the U.S. east coast (17.04 per 1000 km2) is the highest reported in a recent survey of sperm whale densities worldwide (Whitehead 2002).

The collective 1990- 2004 sperm whale abundance data suggest that, seasonally, at least several thousand sperm whales are occupying the waters of the northeastern U.S. Sperm whale abundance may increase offshore, particularly in association with Gulf Stream and warm-core ring features; however, at present there is no reliable estimate of total sperm whale abundance in the western North Atlantic.

West Indian Manatee

Description and Distribution

West Indian manatees, *Trichechus manatus latirostris*, are massive fusiform-shaped animals with skin that is uniformly dark grey, wrinkled, sparsely haired, and rubber-like. Manatees possess paddle-like forelimbs, no hind limbs, and a spatulate, horizontally flattened tail. Females have two axillary mammae, one at the posterior base of each forelimb. Their bones are massive and heavy with no marrow cavities in the ribs or long bones of the forearms (Odell 1982).

Adults average about 3.0 m (9.8 ft) in length and 1,000 kg (2,200 lbs) in weight, but may reach lengths of up to 4.6 m (15 ft) (Gunter 1941) and weigh as much as 1,620 kg (3,570 lbs) (Rathbun et al. 1990). Newborns average 1.2 to 1.4 m (4 to 4.5 ft) in length and about 30 kg (66 lbs) (Odell 1981). The nostrils, located on the upper snout, open and close by means of muscular valves as the animals surface and dive (Husar 1977, Hartman 1979). A muscular flexible upper lip is used with the forelimbs to manipulate food into the mouth (Odell 1982). Bristles are located on the upper and lower lip pads. Molars designed to crush vegetation form continuously at the back of the jaw and move forward as older ones wear down (Domning and Hayek 1986). The eyes are very small, close with sphincter action, and are equipped with inner membranes that can be drawn across the eyeball for protection. Externally, the ears are minute with no pinnae. Internally, the ear structure suggests that they can hear sound within a relatively narrow low frequency range, that their hearing is not acute, and that they have difficulty in localizing sound (Ketten et al. 1992). Gerstein (1995) suggested that manatees may have a greater low-frequency sensitivity than the other marine mammal species that have been tested.

Manatees are typically found in the temperate and equatorial waters of the southeastern U.S., the Caribbean basin, northern and northeastern South America, and equatorial West Africa. At present, manatees of the genus *Trichechus* are represented by three allopatric species: *T. senegalensis*, the West African manatee, *T. inunguis*, the Amazonian manatee, and *T. manatus*, the West Indian manatee. The West Indian species is subdivided into two subspecies, the Antillean manatee (*Trichechus manatus manatus*) and the Florida manatee (*Trichechus manatus latirostris*) (USFWS 1989).

Historically, the winter range of the Florida manatee (*Trichechus manatus latirostris*) was thought to focus on south Florida, with some animals ranging north of Charlotte Harbor on Florida's west coast and north of Sebastian on Florida's east coast. Extralimital movements occurred and were typically seasonal, with animals traveling north during warmer periods and traveling south as temperatures declined. While most manatees wintered in south Florida, some were known to winter in natural spring areas to the north (Hartman 1974). With the advent of artificial warm water refugia, the spread of exotic submerged aquatic vegetation, and increased protective measures, the manatee's winter range has expanded significantly (Beeler and O'Shea 1988). On the east coast, manatees are now known to winter as far north as southeastern Georgia and, on the west coast, as far north as Crystal River, Florida. Range extremes extend north to Virginia on the Atlantic coast and west to Louisiana on the Gulf coast. The number of sighting reports outside of Florida has increased in recent years.

Reproduction

Breeding takes place when one or more males (ranging from 5 to 22) are attracted to an estrous female to form an ephemeral mating herd (Rathbun et al. 1995). Mating herds can last up to 4 weeks, with different males joining and leaving the herd daily (Hartman 1979, Bengtson 1981, Rathbun et al. 1995 in Rathbun 1999). Permanent bonds between males and females do not form. During peak activity, the males in mating herds compete intensely for access to the female (Hartman 1979). Successive copulations involving different males have been reported. Some observations suggest that larger, presumably older, males dominate access to females early in the formation of mating herds and are responsible for most pregnancies (Rathbun et al. 1995), but males as young as three years old are spermatogenic (Hernandez et al. 1995). Although breeding has been reported in all seasons, Hernandez et al. (1995) reported that histological studies of reproductive organs from carcasses of males found evidence of sperm production in 94% of adult males recovered from March through November. Only 20% of adult males recovered from December through February showed similar production.

The length of the gestation period is uncertain but is thought to be between 11 and 14 months (Odell et al. 1995; Rathbun et al. 1995; Reid et al. 1995). The normal litter size is one, with twins reported rarely (Marmontel 1995; Odell et al. 1995; O'Shea and Hartley 1995; Rathbun et al. 1995). Newborns average 1.2 to 1.4 m (4 to 4.5 ft) in length and about 30 kg (66 lbs) (Odell 1981). Calving intervals vary greatly among individuals. They are probably often less than 2 to 2.5 years, but may be considerably longer depending on age and perhaps other factors (Marmontel 1995, Odell et al. 1995, Rathbun et al. 1995, Reid et al. 1995).

Ecological Relationships

Diet, Development, and Growth

Manatees are herbivores that feed opportunistically on a wide variety of submerged, floating, and emergent vegetation. Because of their broad distribution and migratory patterns, Florida manatees utilize a wider diversity of food items and may be less specialized in their feeding strategies, than manatees in tropical regions (Lefebvre et al. 2000).

Seagrasses appear to be a staple of the manatee diet in coastal areas (Ledder 1986, Provancha and Hall 1991, Kadel and Patton 1992, Koelsch 1997, Lefebvre et al. 2000). Packard (1984) noted two feeding methods in coastal seagrass beds: (1) rooting, where virtually the entire plant is consumed; and (2) grazing, where exposed grass blades are eaten without disturbing the roots or sediment. Manatees may return to specific seagrass beds to graze on new growth (Koelsch 1997, Lefebvre et al. 2000).

In the upper Banana River (located in Brevard County, Florida) Provancha and Hall (1991) found spring concentrations of manatees grazing in beds dominated by manatee grass (*Syringodium filiforme*). They also reported an apparent preference for manatee grass and shoalgrass (*Halodule wrightii*) over the macroalga *Caulerpa* spp. Along the Florida-Georgia border, manatees feed in salt marshes on smooth cordgrass (*Spartina alterniflora*) by timing feeding periods with high tide (Baugh et al. 1989, Zoodsma 1991).

Feeding rates and food preferences depend, in part, on the season and available plant species. Bengtson (1981, 1983) reported that the time manatees spent feeding in the upper St. Johns River was greatest (6 to 7 hrs/day) before winter (August to November), least (3 to 4 hrs/day) in spring and summer (April to July), and intermediate (about 5 hrs/day) in winter (January to March). He estimated annual mean consumption rates at 33.2 kg/day/manatee or about 4 to 9% of their body weight per day depending on season (Bengtson 1983). At Crystal River, Etheridge et al. (1985) reported cumulative daily winter feeding times from 0 to 6 hrs. 10 min. based on observations of three radio-tagged animals over seven 24-hour periods. The estimated daily consumption rates by adults, juveniles, and calves eating hydrilla (*Hydrilla verticillata*) were 7.1, 9.6, and 15.7% of body weight per day, respectively.

Females appear to reach sexual maturity by about age five but have given birth as early as four (Marmontel 1995, Odell et al. 1995, O'Shea and Hartley 1995, Rathbun et al. 1995), and males may reach sexual maturity at 3 to 4 years of age (Hernandez et al. 1995). Manatees may live in excess of 50 years (Marmontel 1995), and evidence for reproductive senescence is unclear (Marmontel 1995, Rathbun et al. 1995). Catalogued Florida manatee CR 28, a wild manatee that overwinters in Crystal River, was last documented with a calf in 1998, at which time she was estimated to be at least 34 years of age (USGS-Sirenia, unpublished data). A captive animal, MSTm-5801, gave birth to a calf in 1990, at which time she was estimated to be 43 to 48 years of age (FWS, unpublished data).

Migration and Movement

When ambient water temperatures drop below 20° C (68°F) in autumn and winter, manatees aggregate within the confines of natural and artificial warm-water refuges (Lefebvre et al. 2001) or move to the southern tip of Florida (Snow 1991). Most artificial refuges are created by warm-water outfalls from power plants or paper mills. The largest winter aggregations (maximum count of 100 or more animals) are at refuges in Central and Southern Florida. The northernmost natural warm-water refuge used regularly on the west coast of Florida is at Crystal River and at Blue Springs in the St. Johns River on Florida's east coast. Most manatees return to the same warm-water refuges each year; however, some use different refuges in different years and others use two or more refuges in the same winter (Reid and Rathbun 1984, 1986; Rathbun et al. 1990, Reid et al. 1991, 1995). Many lesser known, minor aggregation sites are used as temporary thermal refuges. Most of these refuges are canals or boat basins where warmer water temperatures persist as temperatures in adjacent bays and rivers decline.

During mild winter periods, manatees at thermal refuges move to nearby grassbeds to feed, or even return to a more distant warm season range (Deutsch et al. 2000). For example, manatees using the Riviera Power Plant feed in adjacent Lake Worth and in Jupiter and Hobe Sounds, 19 to 24 km (12 to 15 mi) to the north (Packard 1981). Animals at Blue Spring leave the spring run to feed on freshwater aquatic plants along the St. Johns River and associated waters near the spring (Bengtson 1981, Marine Mammal Commission 1986).

As water temperatures rise manatees disperse from winter aggregation areas. While some remain near their winter refuges, others undertake extensive travels along the coast and far up rivers and canals. On the east coast, summer sightings drop off rapidly north of Georgia (Lefebvre et al. 2001) and are rare north of Cape Hatteras (Rathbun et al. 1982, Schwartz 1995); the northernmost sighting is from Rhode Island (Reid 1996).

Abundance and Status of Stock

The Florida manatee is listed as "endangered" under provisions of the ESA. The manatee is considered a "strategic stock" as defined in Section 12 of the Marine Mammal Protection Act. The basis for this designation is the high level of documented mortality (natural and human-related) relative to the estimated population level and continuing, severe threats to critical manatee habitats in the southeastern U.S.

Despite considerable effort in the early 1980s, scientists have been unable to develop a useful means of estimating or monitoring trends in the size of the overall manatee population in the southeastern U.S. (O’Shea 1988, O’Shea et al. 1992, Lefebvre et al. 1995). Thus, the exact population size for Florida manatees is unknown but the minimum population is estimated at 1,822 animals, based on intensive statewide winter aerial surveys at warm-water refuges coordinated by the Florida Department of Environmental Protection in early February of 1995 (FDEP 1995). Even though most, if not all, warm-water refuges are known, direct counting methods (i.e., by aerial and ground surveys) used to estimate manatee abundance at these refuges have limitations. They are unable to account for uncertainty in the number of animals that may be away from these refuges at any given time, the number of animals not seen because of turbid water, and other factors. The use of mark-resighting techniques to estimate manatee population size based on known animals in the manatee photo identification database has also been impractical, as the proportion of unmarked manatees cannot be estimated.

Manatee population trends are poorly known but, based on the results of a carcass recovery program, deaths have increased by an average of 5.9 percent per year in Florida from 1976 through 1992 (Ackerman et al. in press). Garrott et al.'s (1994) analysis of trends at winter aggregation sites suggest a mean annual increase of 7-12 percent in adjusted counts at sites on the east coast from 1978-1992. Reynolds and Wilcox (1994) reported a decline in the percentage and number of calves seen at power plant aggregation sites during recent winter aerial surveys. It is not clear at this time whether this is related to increases in perinatal mortality or to some other factor.

The health of the population in the Atlantic Region (the east coast of Florida, including all of the Florida Key), which represents almost one-half of the entire population, is unclear. Marmontel (1994) conducted a population viability analysis through computer simulations. This study yielded information on age-related aspects of mortality and reproduction for the Florida manatee population. A scenario, calculated from the data, having an initial population size of 2,000 individuals resulted in a gradually declining population ($r = -0.003$), a probability of persistence of 44 percent in 1,000 years, and a mean final population size of less than 10 percent of the original value. When adult mortality was reduced by 10 percent in the model, population growth improved considerably, but when adult mortality was increased by 10 percent the population quickly dwindled. These results clearly indicate that the Florida manatee population is still at high risk of extinction in the long term. Any negative change in the population parameters, caused by environmental changes or a catastrophe, might tip the balance towards greater risk of extinction.

Atlantic Spotted Dolphin

Description and Distribution

The Atlantic spotted dolphin, *Stenella frontalis*, occurs in two forms which may be distinct subspecies (Perrin et al. 1987, 1994; Rice 1998): the large, heavily spotted form which inhabits the continental shelf and is usually found inside or near the 200-m isobath; and the smaller, less spotted island and offshore form which occurs in the Atlantic Ocean but is not known to occur in the Gulf of Mexico (Fulling et al. 2003, Mullin and Fulling 2003, Mullin and Fulling 2004). The spotted dolphin's body is covered with spots and becomes more densely spotted with age. The spotted dolphin has a long slim beak containing 35 to 48 small conical teeth in each side of the upper jaw and 34 to 47 small, conical teeth in each side of the lower jaw. The dorsal fin is tall and curved; the flippers are small and pointed as are the flukes with a small median notch.

Length averages about 7 ft. (2.1 m) with an average weight of 220 pounds (100 kg). Calves measure 32 to 36 inches (80 to 90 cm) at birth (Balcomb and Minasian 1984, Leatherwood and Reeves 1983, Leatherwood et al. 1982, American Cetacean Society Fact Sheet 2007).

Atlantic spotted dolphins are distributed in tropical and warm temperate waters of the western North Atlantic (Leatherwood et al. 1976). Their distribution is from southern New England, south through the Gulf of Mexico and the Caribbean to Venezuela (Leatherwood et al. 1976, Perrin et al. 1994). The large, heavily spotted form of the Atlantic spotted dolphin along the southeastern and Gulf coasts of the United States, inhabits the continental shelf, usually being found inside or near the 200 m isobath (within 250-350 km of the coast) but sometimes coming into very shallow water adjacent to the beach (Waring et al. 2007). Off the northeast U.S. coast, spotted dolphins are widely distributed on the continental shelf, along the continental shelf edge, and offshore over the deep ocean south of 40° N (CETAP 1982). Atlantic spotted dolphins regularly occur in the inshore waters south of Chesapeake Bay and near the continental shelf edge and continental slope waters north of this region (Payne et al. 1984, Mullin and Fulling 2003). Sightings have also been made along the north wall of the Gulf Stream and warm-core ring features (Waring et al. 1992).

Reproduction

This species reaches maturity between 6 and 8 years of age. Most animals are approximately 6.5 ft (2 m) in length when they reach sexual maturity. Mating and calving take place throughout the year; the calving interval is believed to be about every two years. In stressed populations, mating takes place at an earlier age and the calving intervals are shorter. Gestation is 11 1/2 months and calves are nursed for 11 months (Balcomb et al. 1984, Leatherwood and Reeves 1983, Leatherwood et al. 1982, American Cetacean Society Fact Sheet 2007).

Ecological Relationships

Diet, Development, and Growth

Spotted dolphins feed on many varieties of fish and squid found near the surface of the water. In the eastern Pacific, pregnant females feed more on squid and nursing females tend to feed more on fish. The reason for this is unknown (Balcomb et al. 1984, Leatherwood and Reeves 1983, Leatherwood et al. 1982, American Cetacean Society Fact Sheet 2007).

Migration and Movement

Spotted dolphins consist of tropical and subtropical species and are widely distributed in all tropical and warm-temperate waters of the Atlantic, Pacific, and Indian Oceans (Balcomb et al. 1984, Leatherwood and Reeves 1983, Leatherwood et al. 1982, American Cetacean Society Fact Sheet 2007).

Abundance and Status of Stock

Total numbers of Atlantic spotted dolphins off the U.S. or Canadian Atlantic coast are unknown. The best 2004 abundance estimate for Atlantic spotted dolphins is the sum of the estimates from the two 2004 western U.S. Atlantic surveys, 50,978 (CV=0.42), where the estimate from the northern U.S. Atlantic is 3,578 (CV=0.48), and from the southern U.S. Atlantic is 47,400 (CV=0.45). However, this does not account for the potential for a mixed species herd, as has been recorded for several dolphin assemblages. Pending further genetic studies for clarification of this problem, a single species abundance estimate is considered the best estimate of abundance. This combines species-specific data from the northern as well as southern portions of the species' ranges. There are insufficient data to determine the population trends for this species, given that surveys prior to 1998 did not differentiate between species of spotted dolphins (Waring et al. 2007).

Bottlenose Dolphin (coastal stock)

Description and Distribution

This is a relatively robust dolphin with a usually short and stubby beak - hence the name "bottlenose." The bottlenose dolphin, *Tursiops truncatus*, has more flexibility in its neck than other oceanic dolphins, because five of the seven neck vertebrae are not fused together as in the other oceanic dolphins. There are 18-26 pairs of sharp, conical teeth in each side of its jaw. The color of the bottlenose dolphin varies considerably, but generally this dolphin is light gray to slate gray on the upper part of the body shading to lighter sides and pale, pinkish gray on the belly. The dorsal fin is high and falcate (curved) and located near the middle of the back. The flukes are broad and curved with a deep median notch. The flippers are of moderate length and pointed. Adult length is from 8-12 feet (2.5-3.8 m). These dolphins may weigh as much as 1,430 pounds (650 kg) off Great Britain, though most are much smaller in other parts of the world. Males are significantly larger than females (Wells and Scott 2000, 2002; Reynolds et al. 2000, Connor et al. 2000, American Cetacean Society Fact Sheet 2007).

The coastal morphotype of bottlenose dolphin is continuously distributed along the Atlantic coast south of Long Island, around the Florida peninsula and along the Gulf of Mexico coast. Based on differences in mitochondrial DNA haplotype frequencies, nearshore animals in the northern Gulf of Mexico and the western North Atlantic represent separate stocks (Curry 1997, Duffield and Wells 2002). Recent genetic analyses of samples from northern Florida, Georgia, central South Carolina (primarily the estuaries around Charleston), southern North Carolina, and coastal Virginia, using both mitochondrial DNA and nuclear microsatellite markers, indicate that a significant amount of the overall genetic variation can be explained by differences between these areas (NMFS 2001). These results indicate a minimum of five stocks of coastal bottlenose dolphins along the U.S. Atlantic coast (Waring et al. 2007). Photo-identification studies also support the existence of multiple stocks (NMFS 2001).

The movement patterns of animals outfitted with satellite-linked radio transmitters off Virginia Beach, VA, Beaufort, NC, Charleston, SC, and New Jersey, along with photo-identification of freeze-branded animals, indicate that a significant number of dolphins reside in North Carolina in summer and do not migrate. A dolphin tagged in Virginia Beach, VA, spent the winter between Cape Hatteras and Cape Lookout, NC, indicating seasonal migration between North Carolina and areas further north (NMFS 2001).

In summary, several stock identification techniques (i.e., genetic sampling, photo-identification, satellite telemetry, etc.) confirm a complex mosaic of coastal bottlenose dolphin stocks. Therefore, seven management units exist within the range of the coastal morphotype of western North Atlantic bottlenose dolphin (Figure 4.3-1).

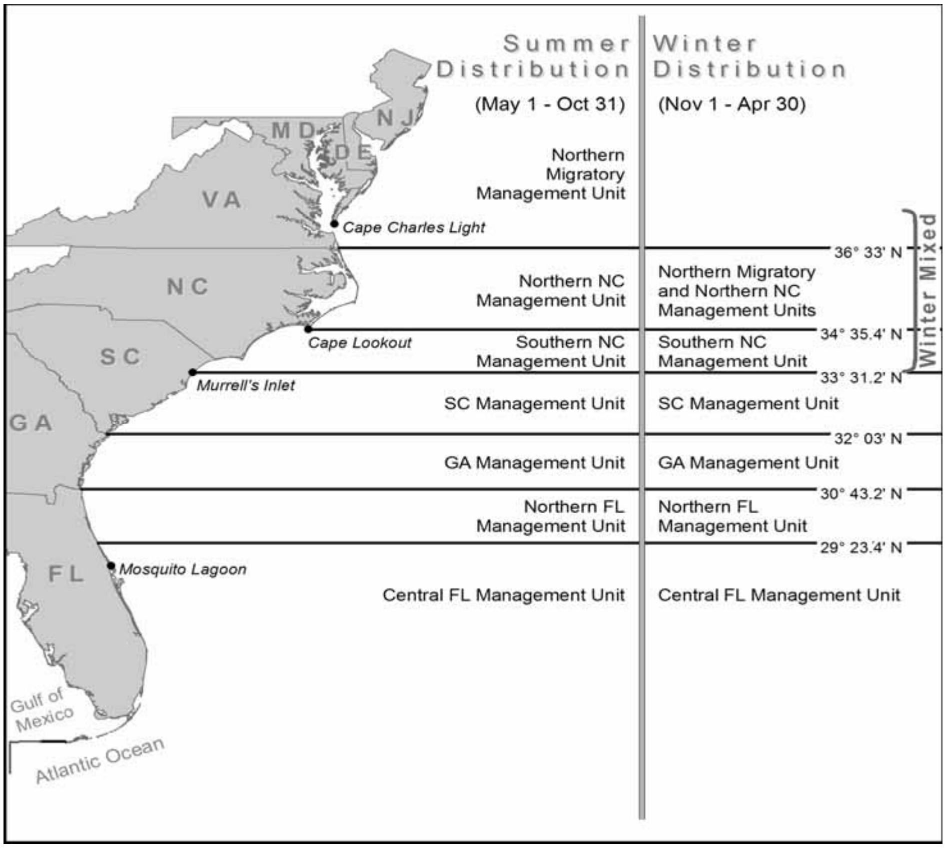


Figure 4.3-1. Management units of the coastal morphotype of bottlenose dolphin along the Atlantic coast of the U.S. as defined from genetic, stable isotope ratio, photo-identification, and telemetry studies (NMFS 2001).

Aerial surveys conducted between 1978 and 1982 (CeTAP 1982) north of Cape Hatteras, North Carolina identified two concentrations of bottlenose dolphins, one inshore of the 25 m isobath and the other offshore of the 50m isobath. The lowest density of bottlenose dolphins was observed over the continental shelf, with higher densities along the coast and near the continental shelf edge. It was suggested, therefore, that the coastal morphotype is restricted to waters < 25 m deep north of Cape Hatteras (Kenney 1990).

Genetic analysis of tissue samples collected during large vessel surveys the summers of 1998 and 1999 indicated that bottlenose dolphins within 7.5 km from shore were most likely of the coastal morphotype. These samples also suggested an area of extensive overlap between the coastal and offshore morphotypes located 7.5 and 34 km from shore south of Cape Hatteras, North Carolina (Torres et al. 2003).

Reproduction

Males reach sexual maturity at about 10 years. Females reach sexual maturity at about 5-10 years. The gestation period is 12 months. Calving can take place year-round with peaks in some areas during spring and fall. Calves nurse for over a year (12-18 months), and stay with their mothers for 3-6 years learning how to catch fish and other important tasks (Wells and Scott

2000, 2002; Reynolds et al. 2000, Connor et al. 2000, American Cetacean Society Fact Sheet 2007).

Ecological Relationships

Diet, Development, and Growth

Feeding behaviors are diverse, primarily involving individual prey capture, but sometimes involving coordinated efforts to catch food, feeding in association with human fishing, and chasing fish into mudbanks. An adult bottlenose dolphin may consume 15-30 pounds (8-15 kg) of food each day. Bottlenose dolphins eat a wide variety of food, including primarily fishes, and sometimes squid, and crustaceans (Wells and Scott 2000, 2002; Reynolds et al. 2000, Connor et al. 2000, American Cetacean Society Fact Sheet 2007).

Abundance and Status of Stock

There are insufficient data to determine the population trend for these stocks. However, the coastal migratory stock was designated as depleted under the MMPA. Table 4.3-2 outlines abundance estimates for each management unit. NMFS conducted abundance surveys during the summer and winter of 2002 in order to update previous abundance estimates from 1995. Current estimates are confounded somewhat by an overlap in distribution between the coastal and offshore bottlenose dolphin stocks, and the difficulty of distinguishing between the two stocks while surveying. However, these estimates are considered more robust than previous abundance estimates conducted in 1995 due to improved experimental design.

Table 4.3-2. Estimates of abundance and the associated CV, N_{min}, and PBR for each stock of WNA coastal bottlenose dolphins (Garrison et al. 2003 in Waring et al. 2007). The PBR for the Northern Migratory, Northern NC, and Southern NC management units are applied semi-annually. South of NC, the PBR is applied annually. Except where noted, abundance estimates and PBR values do not include estuarine animals. The recovery factor (Fr) used to calculate PBR for each stock is based upon the CV of the abundance estimate based on the guidelines in Wade and Angliss (1997).

Unit		Best Abundance		N_{min}	Recovery Factor (Fr)	PBR	
		Estimate	CV			Annual	½ Yr
SUMMER (May - October)							
Northern migratory		17,466	0.19	14,621	0.50	(146.2)	73.1
Northern NC							
	oceanic	6,160	0.52	3,255	0.48	(31.2)	15.6
	Estuary[d]	919	0.13	828	0.50	(8.2)	4.2
	BOTH	7,079	0.45	4,083	0.48	(39.2)	19.6
Southern NC							
	oceanic	3,645	1.11	1,863	0.40	(14.9)	7.5
	Estuary[d]	141	0.15	124	0.50	(1.2)	0.6
	BOTH	3,786	1.07	1,987	0.40	(15.9)	7.9
WINTER (November - April)							
NC mixed[a]		16,913	0.23	13,558	0.50	(135.6)	67.8
ALL YEAR							
South Carolina		2,325	0.20	1,963	0.50	19.6	unk
Georgia		2,195	0.30	1,716	0.50	17.2	unk

Northern Florida[b,c]	448	0.38	unk	unk	unk	unk
Central Florida[c]	10,652	0.46	unk	unk	unk	unk

a. NC mixed = northern migratory, Northern NC, and Southern NC
b. Northern Florida estimates are a weighted mean of abundance estimates from the winter 1995 survey and the summer 2002 survey. Due to the age of the winter abundance estimate, PBR cannot be calculated for this stock.
c. Northern and Central Florida estimates include data from the winter 1995 survey and cannot be used to determine PBR due to their age.
d. Read et al. 2003

Bottlenose Dolphin (offshore stock)

The bottlenose dolphin, *Tursiops truncatus*, offshore stock is distributed primarily along the outer continental shelf and continental slope in the Northwest Atlantic Ocean. North of Cape Hatteras, North Carolina, during summer months, there is a clear distinction between the coastal and offshore stocks of bottlenose dolphins across bathymetry (Waring et al. 2007). Torres et al. (2003) found a statistically significant break in the distribution of the coastal and offshore stocks at 34 km from shore based upon the genetic analysis. The offshore morphotype was found exclusively seaward of 34 km and in waters deeper than 34 m. Biopsy samples of the offshore morphotype have been collected as close as 7.3 km from shore in water depths of 13 m (Garrison et al. 2003).

Seasonally, bottlenose dolphins occur over the outer continental shelf and inner slope waters as far north as Georges Bank (CeTAP 1982, Kenney 1990). Sightings occurred along the continental shelf break from Georges Bank to Cape Hatteras during spring and summer (CeTAP 1982, Kenney 1990). Information from Wells et al. (1999) indicates that the range of the offshore bottlenose dolphin may include waters beyond the continental slope and that offshore bottlenose dolphins may move between the Gulf of Mexico and the Atlantic. Offshore morphotype bottlenose dolphins have stranded as far south as the Florida Keys (Waring et al. 2007).

Reproduction

Males reach sexual maturity at about 10 years. Females reach sexual maturity at about 5-10 years. The gestation period is 12 months. Calving can take place year-round with peaks in some areas during spring and fall. Calves nurse for over a year (12-18 months), and stay with their mothers for 3-6 years learning how to catch fish and other important tasks (Wells and Scott 2000, 2002; Reynolds et al. 2000, Connor et al. 2000, American Cetacean Society Fact Sheet 2007).

Ecological Relationships

Diet, Development, and Growth

Feeding behaviors are diverse, primarily involving individual prey capture, but sometimes involving coordinated efforts to catch food, feeding in association with human fishing, and chasing fish into mudbanks. An adult bottlenose dolphin may consume 15-30 pounds (8-15 kg) of food each day. Bottlenose dolphins eat a wide variety of food, including primarily fishes, and sometimes squid, and crustaceans (Wells and Scott 2000, 2002; Reynolds et al. 2000, Connor et al. 2000, American Cetacean Society Fact Sheet 2007).

Abundance and Status of Stock

During the summer (June - July) of 2002, aerial surveys were conducted along the U.S. Atlantic coast between Florida and New Jersey. The resulting coastwide abundance estimate for the offshore morphotype in waters < 40 m depth was 26,849 (CV = 0.193)(Buckland et al. 2001, Palka 1995, Garrison et al. 2003, Waring et al. 2007).

Another abundance estimate of 9,786 (CV = 0.56) for offshore morphotype bottlenose dolphins was derived from a June 12 to August 4, 2004 ship and plane survey. The survey covered 10,761 km of track line in waters north of 38° N (Palka unpubl., Palka 1995, Palka and Hammond 2001, Hiby 1999, Waring et al. 2007).

An additional survey of the U.S. Atlantic outer continental shelf and continental slope (water depths > 50m) between 27.5 – 38ºN latitude was conducted during June-August, 2004. Survey effort was stratified to include increased effort along the continental shelf break and Gulf Stream front in the Mid-Atlantic. The survey included 5,659 km of trackline; there were 473 cetacean sightings. Sightings were most frequent in waters North of Cape Hatteras, North Carolina along the shelf break (Palka 1995, Buckland et al. 2001). The resulting abundance estimate for offshore morphotype bottlenose dolphins between Florida and Maryland was 44,953 (CV = 0.26) (Waring et al. 2007).

The best available estimate for offshore morphotype bottlenose dolphins is the sum of the estimates from the summer 2002 aerial survey covering the continental shelf, the summer 2004 vessel survey south of Maryland, and the summer 2004 vessel and aircraft surveys north of Maryland. This joint estimate provides complete coverage of the offshore morphotype habitat from Florida to Georges Bank during summer months. The combined abundance estimate from these surveys is 81,588 (CV = 0.17) (Waring et al. 2007).

The status of this stock relative to its optimum sustainable population in the U.S. Atlantic EEZ is unknown. The western North Atlantic offshore bottlenose dolphin is not listed as threatened or endangered under the ESA. There are insufficient data to determine the population trends for this species. Average 1999-2003 annual fishery-related mortality and serious injury does not exceed the PBR therefore this is not a strategic stock. The total fishery-related mortality and serious injury for this stock is less than 10% of the calculated PBR and, therefore, can be considered to be insignificant and approaching zero mortality and serious injury rate.

Minke Whale

Description and Distribution

The minke whale, *Balaenoptera acutorostrata*, is the smallest member of the rorqual family of whales. One of its most distinctive features is the narrow, triangular rostrum (upper jaw), which is proportionally shorter than in other rorquals. A single ridge extends from the tip of the rostrum to the blowhole. Its body is slender and streamlined. Like all rorquals, the minke has a series of 50 to 70 ventral grooves, or pleats, that expand during feeding. The minke is counter-shaded-black to dark gray on top, white below. Some minkes have a light-colored chevron on the back behind the head. Two areas of lighter gray appear on each side: one behind the flippers and another below and forward of the dorsal fin. Distinctive to minke whales outside of the Antarctic is a white band on each flipper. The dorsal fin of the minke is tall and falcate (curved), and is located two-thirds of the way back on the body. Its flippers are slender and pointed at the tips. Flukes are broad, up to one-fourth of the body length, pointed at the tips, and notched in the center. Adult males average about 26 ft (8 m) with a maximum length of 31 ft (9.4 m), while adult females average 27 ft (8.2 m) with a maximum length of 33 ft (10.2 m). Both males and females weigh about 10 tons. Both sexes are slightly larger in the southern hemisphere (Balcomb and Minasian 1984, Ellis 1980, Leatherwood and Reeves 1983, American Cetacean Society Fact Sheet 2007).

Minke whales have a cosmopolitan distribution, being distributed in polar, temperate and tropical waters. In the North Atlantic, there are four recognized populations — Canadian East Coast, west Greenland, central North Atlantic, and northeastern North Atlantic (Donovan 1991). Minke whales off the eastern coast of the U.S. are considered to be part of the Canadian East Coast stock, which inhabits the area from the eastern half of the Davis Strait (45ºW) to the Gulf of Mexico. The relationship between this stock and the other three stocks is uncertain. It is also uncertain if there are separate stocks within the Canadian East Coast stock (Waring et al. 2007).

The minke whale is common and widely distributed within the U.S. Atlantic Exclusive Economic Zone (EEZ) (CeTAP 1982). There appears to be a strong seasonal component to minke whale distribution. Spring and summer are times of relatively widespread and common occurrence, and when the whales are most abundant in New England waters. During fall in New England waters, there are fewer whales, while during winter, the species appears to be largely absent. Like most other baleen whales, minke whales generally occupy the continental shelf proper, rather than the continental shelf edge region. Records summarized by Mitchell (1991) hint at a possible winter distribution in the West Indies, and in the mid-ocean south and east of Bermuda. As with several other cetacean species, the possibility of a deep-ocean component to the distribution of minke whales exists but remains unconfirmed (Waring et al. 2007).

Reproduction

Sexual maturity is reached at 7 or 8 years in the northern hemisphere. Breeding peaks in summer months. The gestation period is 10 to 11 months, and calving is thought to occur once every two years on average. Calves are 10 ft (3 m) at birth and weigh 1000 pounds (450 kg). Minke calves nurse for approximately 6 months (Balcomb and Minasian 1984, Ellis 1980, Leatherwood and Reeves 1983, American Cetacean Society Fact Sheet 2007).

Ecological Relationships

Diet, Development, and Growth

Minke whales feed primarily on krill in the southern hemisphere and on small schooling fish (capelin, cod, herring, pollock) or krill in the northern hemisphere. They will also eat copepods in certain areas (Balcomb and Minasian 1984, Ellis 1980, Leatherwood and Reeves 1983, American Cetacean Society Fact Sheet 2007).

Migration and Movement

Minkes tend to be solitary animals, though sometimes they are seen traveling in pairs or in small groups of 4 to 6. They are found in all oceans, though they are rarely observed in the tropics.

They seem to prefer icy waters, and are found right up to the edge of the icepack in polar regions, and have actually become entrapped in the ice fields on occasion (Balcomb and Minasian 1984, Ellis 1980, Leatherwood and Reeves 1983, American Cetacean Society Fact Sheet 2007).

Abundance and Status of Stock
The total number of minke whales in the Canadian East Coast population is unknown (Waring et al 2007). The best available current abundance estimate for minke whales is 2,998 animals (CV=0.19). This estimate obtained from a July to August 1999 sighting survey conducted by a ship and airplane covering waters from Georges Bank to the mouth of the Gulf of St. Lawrence (NMFS unpublished data, Palka 2006). The status of minke whales, relative to optimum sustainable population, in the U.S. Atlantic EEZ is unknown. However, the minke whale is not listed under the Endangered Species Act (ESA) (Waring et al. 2007).

4.3.2 Sea Turtles

Description and distribution

(from draft SNG Amendment 14)
The following section offers a brief overview of the general life history characteristics of the sea turtles found in the South Atlantic region. Several volumes exist that cover more thoroughly the biology and ecology of these species (i.e., Lutz and Musick (eds.) 1997; Lutz et al. (eds.), 2002).

The ESA status of sea turtles in the South Atlantic was recently evaluated in a section 7 consultation on the continued authorization of snapper grouper fishing under the South Atlantic Snapper Grouper Fishery Management Plan and Amendment 13C (NMFS 2006).

Green sea turtle, *Chelonia mydas*, hatchlings are thought to occupy pelagic areas of the open ocean and are often associated with Sargassum rafts (Carr, 1987; Walker, 1994). Pelagic stage green sea turtles are thought to be carnivorous. Stomach samples of these animals found ctenophores and pelagic snails (Frick 1976, Hughes 1974). At approximately 20 to 25 cm carapace length, juveniles migrate from pelagic habitats to benthic foraging areas (Bjorndal 1997). As juveniles move into benthic foraging areas a diet shift towards herbivory occurs. They consume primarily seagrasses and algae, but are also know to consume jellyfish, salps, and sponges (Bjorndal 1980, 1997; Paredes, R.P. 1969; Mortimer 1981, 1982). The diving abilities of all sea turtles species vary by life stage. The maximum diving depth of green sea turtles is estimated at 110 m (360 ft) (Frick 1976), but they frequently make dives of less than 20 m (65 ft.)(Walker 1994). The time of these dives also varies by life stage. The maximum dive length is estimated at 66 minutes with most dives lasting from 9 to 23 minutes (Walker 1994).

The hawksbill's, *Eretmochelys imbricata*, pelagic stage lasts from the time they leave the nesting beach as hatchlings until they are approximately 22-25 cm in straight carapace length (Meylan 1988, Meylan and Donnelly 1999). The pelagic stage is followed by residency in developmental habitats (foraging areas where juveniles reside and grow) in coastal waters. Little is known about the diet of pelagic stage hawksbills. Adult foraging typically occurs over coral reefs, although other hardbottom communities and mangrove-fringed are occupied occasionally. Hawksbills show fidelity to their foraging areas over several years (van Dam and Diéz 1998). The hawksbill's diet is highly specialized and consists primarily of sponges (Meylan 1988). Gravid females have been noted ingesting coralline substrate (Meylan 1984) and calcareous algae (Anderes Alvarez and Uchida 1994), which are believed to be possible sources of calcium to aid in eggshell production. The maximum diving depths of these animals are not known, but the maximum length of dives is estimated at 73.5 minutes. More routinely dives last about 56 minutes (Hughes 1974).

Leatherbacks, *Dermochelys coriacea,* are the most pelagic of all ESA-listed sea turtles and spend most of their time in the open ocean; although they will enter coastal waters and are seen over the continental shelf on a seasonal basis to feed in areas where jellyfish are concentrated.

Leatherbacks feed primarily on cnidarians (medusae, siphonophores) and tunicates. Unlike other sea turtle species, leatherbacks' diets do not shift during their life cycles. Because leatherbacks' ability to capture and eat jellyfish is not constrained by size or age, they continue to feed on these species regardless of life stage (Bjorndal 1997). Leatherbacks are the deepest diving of all sea turtles. It is estimated that this species can dive in excess of 1000 m (Eckert et al. 1989) but more frequently dive to depths of 50 m to 84 m (Eckert et al.. 1986). Dive times range from a maximum of 37 minutes to more routines dives of 4 to 14.5 minutes (Standora et al. 1984, Eckert et al. 1986; Eckert et al. 1989; Keinath and Musick 1993). Leatherbacks may spend 74% to 91% of their time submerged (Standora et al. 1984).

Loggerhead, *Caretta caretta*, hatchlings forage in the open ocean and are often associated with Sargassum rafts (Hughes 1974, Carr 1987, Walker 1994, Bolten and Balazs 1995). The pelagic stage of these turtles are known to eat a wide range of prey including salps, jellyfish, amphipods, crabs, sygnathid fish, squid, and pelagic snails (Brongersma 1972).

Stranding records indicate that when pelagic immature loggerheads reach 40-60 cm straight-line carapace length they begin to live in coastal inshore and nearshore waters of the continental shelf throughout the U. S. Atlantic (Witzell 2002) where they forage over hard- and soft-bottom habitats (Carr 1986). Benthic foraging loggerheads eat a variety of invertebrates with crabs and mollusks being important prey sources (Burke et al. 1993).

Estimates of the maximum diving depths of loggerheads range from 211 m to 233 m (692-764ft) (Thayer et al.,1984; Limpus and Nichols, 1988). The lengths of loggerhead dives are frequently between 17 and 30 minutes (Thayer et al. 1984; Limpus and Nichols 1988; Limpus and Nichols 1994; Lanyan et al. 1989) and they may spend anywhere from 80 to 94% of their time submerged (Limpus and Nichols 1994; Lanyan et al. 1989).

Kemp's ridley, *Lepidochelys kempii*, hatchlings are also pelagic during the early stages of life and feed in surface waters (Carr, 1987; Ogren L.H., 1989). Once the juveniles reach approximately 20 cm carapace length they move to relatively shallow (less than 50m) benthic foraging habitat over unconsolidated substrates (Márquez-M. 1994). They have also been observed transiting long distances between foraging habitats (Ogren L.H. 1989).

Kemp's ridleys feeding in these nearshore areas primarily prey on crabs, though they are also known to ingest mollusks, fish, marine vegetation and shrimp (Shaver 1991). The fish and shrimp Kemp’s ridleys ingest may be scavenged opportunistically from bycatch discards and from discarded bait, and are not thought to be a primary prey item (Shaver 1991). Given their predilection for shallower water, Kemp’s ridleys most routinely make dives of 50 m or less (Soma 1985; Byles 1988). Their maximum diving range is unknown. Depending on the life stage a Kemp’s ridleys may be able to stay submerged anywhere from 167 minutes to 300 minutes, though dives of 12.7minutes to 16.7 minutes are much more common (Soma 1985; Mendonca and Pritchard 1986; Byles 1988). Kemp’s ridleys may also spend as much as 96% of their time underwater (Soma 1985, Byles 1988).

Reproduction

To be added.

Development, growth and movement patterns

Growth in all species of sea turtles is a relative unknown because direct measurements are not practical given the relatively long life span, specialized habitat requirements, and large spatial scale at which individuals operate, all of which precludes maintaining them in the laboratory or making direct observations in the field. Growth has been inferred from tagging studies (cites), and some bone histology (cites). In general growth rates in all species of sea turtles are hypothesized to be relatively slow. Maturity is though to be reached in as little as 6 years in Kemps or Leatherbacks, 10-15 years for greens and hawksbills, and 21 to 35 years for loggerheads. Considerable uncertainty exists in all of these estimates, in particular leatherbacks have been hypothesized to reach maturity in as little as 3 years (Pritchard, 19xx) and as many as 30 years (Avens, pers. comm.).

Most green turtles (*C. mydas*) exhibit particularly slow growth rates, which has been described as a consequence of their largely herbivorous (i.e., low net energy) diet (Bjorndal 1982). Growth rates of juveniles vary substantially among populations, ranging from <1 cm/year (Green 1993) to >5 cm/year (McDonald-Dutton and Dutton 1998), likely due to differences in diet quality, duration of foraging season (Chaloupka et al. 2004b), and density of turtles in foraging areas (Bjorndal et al. 2000, Seminoff et al. 2002c, Balazs and Chaloupka 2004b). Consistent with slow growth, age-to-maturity for the green turtles appears to be the longest of any sea turtle species (Chaloupka and Musick 1997, Hirth 1997).

A variety of studies have addressed growth rates and age to various life stages in Kemp's ridleys. Based on mark-recapture data, skeletal chronological analysis, and growth rates in captivity, it has been estimated that Kemp's ridleys require approximately 1.5 to 2 years to grow from a hatchling to a size of approximately 20 cm straight carapace length (SCL), at which size they are capable of making a transition to a benthic immature stage (B. Higgins, NMFS, personal communication, 2007; Caillouet et al. 1995; Schmid and Witzell 1997; Zug et al. 1997; Schmid 1998; Snover et al. 2007). However, variability in growth rates suggests that the actual time necessary to achieve a 20 cm SCL could range from approximately 1 to 4 years or more (Turtle Expert Working Group (TEWG) 2000).

The state of knowledge of sea turtles movements is increasing rapidly due to a number of factors which include the development and availability of telemetry equipment, and the cooperation and communication between various entities of tagging information. A growing body of literature is available documenting individual movements for many of the species, and some synthetic studies are becoming available that link turtle movements to environmental conditions. Recent examples include, for leatherbacks, the work of Hayes and colleagues (Hayes et al, 2006), and James and colleagues (James, 2006).

Green turtles are highly mobile and they undertake complex movements through geographically disparate habitats during their lifetimes (Musick and Limpus 1997, Plotkin 2003). While offshore, and sometimes while in coastal habitats, green turtles are not obligate herbivores as widely believed, and instead consume invertebrates such as jellyfish, sponges, sea pens, and pelagic prey (i.e., prey that occupy the water column) (Godley et al. 1998, Heithaus et al. 2002, Seminoff et al. 2002b, Hatase et al. 2006, Parker and Balazs in press).

Green turtles spend the majority of their lives in coastal foraging grounds. These areas include both open coastline and protected bays and lagoons. In addition to coastal foraging areas, oceanic habitats are used by oceanic-stage juveniles, migrating adults, and, on some occasions, by green turtles that reside in the oceanic zone for foraging. At nesting beaches, green turtles rely on safe and healthy beaches with intact dune structures, native vegetation, and normal beach temperatures for nesting (Ackerman 1997). Coastal areas denuded of vegetation or with coastal construction can impact thermal regimes on beaches and thus affect the incubation and resulting sex ratio of hatchling turtles.

For leatherback turtles, important nesting areas in the western Atlantic Ocean occur in Florida (USA); St. Croix, U.S. Virgin Islands; Puerto Rico; Costa Rica; Panama; Colombia; Trinidad and Tobago; Guyana; Suriname; French Guiana; and southern Brazil (Marquez 1990, Spotila et al. 1996; Bräutigam and Eckert 2006).

Four leatherbacks tagged on the beaches of Costa Rica and Panama were later found nesting in Cuba, Florida, St. Croix, and Grenada, thereby weakening the concept of a distinct Western Caribbean leatherback population. Among leatherbacks fitted with transmitters in Florida, most remained along the North American continental shelf for three seasons and in winter moved off the shelf. In February 2008, scientists tracked a leatherback turtle that swam from Indonesia to the U.S. coast, an estimated 13,000 mile journey (Associated Press, 2008. Avaialble at www.seaturtle.org).

Ecological relationships

All sea turtles species in the Atlantic impact nearshore terrestrial beach habitats (supralittoral) and a variety of neritic and oceanic habitats. Some stages of nearly all sea turtle species inhabit neritic zones, including benthic and pelagic use, while oceanic zone use is typically epipelagic but some stages of some species (e.g. leatherbacks) are pelagic oceanic for nearly their entire lives (see Bolten 2003). Energy exchange between habitats, and the impact of species specific foraging ecology within habitats may have been substantial historically but due to the hypothesized massive declines in sea turtle populations the impact and potential alterations to these ecosystems could be, in part, responsible for large shifts in ecosystem function (Bjorndal and Jackson, 2003). Unfortunately many of the ecological relationships for most species and stages of sea turtles are based on inference and anecdotal information, thus most of this section is conjecture.

All species of sea turtles come ashore to nest, typically depositing large numbers of eggs. The total biomass deposited into these terrestrial habitats can be large, both from adult female mortality and eggs. Nest failure and partial hatching can leave large quantities of biomass in nutrient poor ecosystems that make up most beach habitat, in addition to transfer of biomass through direct predation on eggs and hatchlings by a variety of terrestrial predators.

After emergence from nests and entering the ocean, all species of sea turtle hatchlings are thought to be pelagic. Little is known about the habitats and foraging ecology, and thus the ecological relationships, of hatchlings after the first few days since entering the sea, and much of this was reviewed above. Most are thought to remain pelagic, passively drifting with some active swimming and inhabiting weed lines or sargassum for many years (Bolten 2003). After this stage leatherbacks become oceanic pelagic, likely eating gelatinous organisms until adult females return to the terrestrial zone for nesting and use the neritic zone as internesting habitat. The remaining species in the Atlantic are thought to move to the oceanic zone and remain pelagic until they reach the large juvenile stage when they return to the neritic zone. Loggerheads are thought to become benthic at this point, inhabiting a wide range of benthic habitat and feeding primarily on hard shelled invertebrates.

Coral reef ecosystems and sea turtles

Sea turtles, particularly Hawksbill and Green sea turtles, impact coral reef ecosystems through selective grazing and predation, and direct disturbance to corals. Loggerheads, and possibly some Kemp’s ridleys are known to use coral reefs as resting or hiding spots.

Hawksbill turtles affect the evolution and maintenance of reef structure and dynamics because they prey upon sponges that compete with coral for space on reefs (León and Bjorndal 2002; Meylan 1988). Green turtles primarily forage on seagrass beds (nursery grounds for many reef species) and occasionally on sponges. Green turtles are also known to use coral reefs as ‘scratching posts’ causing erosions, breaks, and larger scale structural shears and collapses (Bennet and Balaz 2002). Both green turtles and hawksbills use their flippers to pry corals out of the way to access sponges, with green turtles foraging on the periphery of reefs, and hawksbills foraging throughout the reef system. Both of these species can have substantial impacts on the habitats they exploit (see Bjorndal 1997 for review).

Hawksbill turtles diet of demosponges and corallimorpharians, aggressive competitors for space on reefs, makes them important predators, which play a significant role in reef structure and dynamics (León and Bjorndal 2002; Meylan 1988). In spongivore exclusion experiments, Hill (1998) found that the demosponge *Chondrilla nucula* would rapidly overgrow the majority of corals with which it interacts and caused >70% of all coral overgrowths in his Florida Keys study. Similar results have been found with *Ricodea florida*, a corallimorpharians (Vicente 1990). Hawksbills have been reported to positively select both of these species as forage (León and Bjorndal 2002).

Large juvenile and adult green turtles are primarily associated with seagrass beds, their primary forage, and may repeatedly graze patches of seagrass over time. Grazing has been found to substantially increase biomass and productivity without reducing growth rates of *Thalassia testudinum* seagrass beds (Moran et al. 2002). In addition, new growth of *T. testudinum* after grazing has a higher energy and nutrient content than seagrass that did not experience grazing. Grazing activity also has a significant effect on the physical structure of seagrass by decreasing blade length and width, detrital layer, blades/shoot, and above ground biomass (Moran et al. 2002).

While both green and hawksbills turtles are clearly integral components of the dynamics of seagrass and coral habitats, at current population sizes it seems unlikely that they are adequately fulfilling their ecological role in many habitats around the world. Since the arrival of Europeans in the Caribbean, sea turtles have declined drastically. Prior to Columbus' arrival, the population of green turtles may have numbered in the hundreds of millions with hawksbills in the tens of millions (Jackson 1997). Today, it is believed that these populations are at most 5 to 10% of historic levels. Clearly, the absence of these ecosystem engineers from seagrass and coral habitats could have a profound effect on the biodiversity, dynamics, function, and recovery of those habitats. This reduction in sea turtle abundance in seagrass and coral habitats could have a profound effect on the function and recovery of those habitats. Effective management of protected reef areas will require understanding sea turtle distribution and use of coral reefs and other marine habitats.

Abundance and status of stocks

All populations of all species of sea turtles in the North Atlantic are thought to be at fractions of their historic population sizes (Bjorndal and Jackson, 2003). No reliable historic or current estimates are available for any species, although a number of authors have made guestimates. For example Jackson (1997) argued that historical populations of green turtles may have numbered in the hundreds of millions with hawksbills in the tens of millions, and each is now thought to be at only 5 to 10% of previous levels.

By calculating populations based on the annual nests from 2001 to 2005, the abundance of Green turtles in Florida is approximately 5,055 (Meylan et al. 2006). The green turtle nesting population of Florida appears to be increasing based on 18 years (1989-2006) of index nesting data from throughout the state. Although in the last four years there are three 'low' years, this may be due to lesser reproductive effort as a result of environmental variability at foraging grounds rather than a decrease in the number of nesting females.

The most recent population size estimate for leatherbacks in the North Atlantic alone ranges between 34,000 and 94,000 adults (Turtle Expert Working Group 2007). In Florida, a Statewide Nesting Beach Survey (SNBS) program has documented an increase in leatherback nesting numbers from 98 nests in 1988 to between 800 and 900 nests per season in the early 2000s (Florida Fish and Wildlife Conservation Commission, unpublished data; Stewart and Johnson 2006). The estimated annual growth rate was approximately 1.17 with estimated confidence intervals of approximately 1.1-1.21 (Turtle Expert Working Group 2007).

There are increasing impacts to the nesting and marine environment that affect leatherback turtles. Leatherback nesting beaches are affected by development and tourism in several countries (e.g., Maison 2006, Hamann et al. 2006a, Santidrian-Tomillo et al. 2007, Hernandez et al. 2007). In addition, coastal development is usually accompanied by artificial lighting. The presence of lights on or adjacent to nesting beaches alters the behavior of nesting adults and is often fatal to emerging hatchlings as they are attracted to light sources and drawn away from the water (Witherington and Bjorndal 1991, Witherington 1992, Cowan et al. 2002, Deem et al. 2007).

In 2000, the Turtle Expert Working Group (TEWG), convened by the U.S. National Marine Fisheries Service, estimated between 53,000 and 92,000 loggerhead nests per year in the southeastern United States and the Gulf of Mexico, and estimated the total number of nesting females as 32,000-56,000. The Northern Nesting Subpopulation (occurring from North Carolina through northeastern Florida) had an average of 5,151 nests per year from 1989-2005 (Georgia Department of Natural Resources (GDNR), unpublished data; North Carolina Wildlife Resources Commission (NCWRC), unpublished data; South Carolina Department of Natural Resources (SCDNR), unpublished data).

The loggerhead turtle South Florida Nesting Subpopulation occurs from northeastern Florida through Pinellas County, Florida. A near complete census of this nesting subpopulation, undertaken from 1989 to 2006 reveals a mean of 65,460 loggerhead nests per year (approximately 15,966 females nesting per year) (Florida Fish and Wildlife Conservation Commission (FFWCC), unpublished data). During the majority of the 1990's, the South Florida Nesting Subpopulation showed an increase in numbers of nests of 3.6% annually from 1989-1998 (TEWG 2000) and the nesting assemblage was considered "stable or increasing" at that time (Witherington and Koeppel 2000).

However, the most recent and longer time series data from the Florida Index Nesting Beach Survey Program, administered by FFWCC, show a significant decline in nesting of loggerhead turtles. There has been a 22.3% decrease in the annual number of nests over the 17-year period from 1989-2005. In the past decade a decline of 39.5% has been reported (McRae 2006).

Approximately 60% of Kemp's ridley nesting occurs along an approximate 40-km stretch of beach near Rancho Nuevo, Tamaulipas, Mexico (FWS 2006). The Kemp's ridley, like the olive ridley, tends to nest in large aggregations or *arribadas* (Bernardo and Plotkin 2007). It has been speculated that the *arribada* phenomenon may be advantageous for a variety of reasons, including mate finding and enhancing the survival of eggs and hatchlings due to predator swamping (Bernardo and Plotkin 2007). The biological or physical factors that initiate an *arribada* are not clear, but a variety of potential cues have been suggested, including strong onshore wind, lunar and tidal cycles, social facilitation, and olfactory signals (Bernardo and Plotkin 2007).

Data suggest that in adult female Kemp's ridleys, approximately 20% nest every year, approximately 60% nest every 2 years, 15% nest every 3 years, and 5% nest every 4 years (Marquez Millan et al. 1989, TEWG 2000). These data indicate a remigration rate of female Kemp's ridleys from 1.8 (Rostal 2007) to 2.0 years (Marquez Millan et al. 1989, TEWG 2000), suggesting that the total number of adult females in the Kemp's ridley population during 2006 was approximately 7,000 to 8,000 turtles.

The Kemp's ridley occurs in the Gulf of Mexico and along the Atlantic coast of the U.S. There are documented cases of Kemp's ridleys captured in the Atlantic that migrated back to the nesting beach at Rancho Nuevo (Schmid and Witzell 1997, Schmid 1998, Witzell 1998). It is not known what proportion of the Kemp's ridley population migrates to U.S. Atlantic coastal waters.

Listing designations

(from Atlantic Croaker FMP Update 2005)
All sea turtles that occur in U.S. waters are listed as either endangered or threatened under the ESA. The Kemp's ridley (*Lepidochelys kempii*), leatherback (*Dermochelys coriacea*), and hawksbill (*Eretmochelys imbricata*) are listed as endangered. The loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) are listed as threatened, except for breeding populations of green turtles in Florida and on the Pacific coast of Mexico, which are listed as endangered. All five of these species inhabit the waters of the U.S. Atlantic and Gulf of Mexico.

NOAA Fisheries recognizes five loggerhead subgroups within the western Atlantic including two primary subpopulations: (1) a northern nesting subpopulation that occurs from North Carolina to northeast Florida, about 29EN (approximately 7,500 nests in 1998); (2) a south Florida nesting subpopulation, occurring from 29EN on the east coast to Sarasota, Florida on the west coast (mean of 73,751 nests each year). The status of the northern population based on the number of loggerhead nests has been classified as stable or declining (TEWG 2000). Data from all beaches within the south Florida subpopulation where nesting activity has been recorded indicate substantial increases when data are compared over the last 25 years. However, an analysis limited to nesting data from the statewide sea turtle Index Nesting Beach Survey program from 1989 to 2002, a period encompassing index surveys that are more consistent and more accurate than surveys in previous years, has shown no detectable trend (Blair Witherington, Florida Fish and Wildlife Conservation Commission (FFWCC), pers. comm., 2002).

The Kemp's ridley is one of the most endangered of the world's sea turtle species. The only major nesting site for ridleys is a single stretch of beach near Rancho Nuevo, Tamaulipas, Mexico. Estimates of the adult female nesting population reached a low of 300 in 1985. Conservation efforts by Mexican and U.S. agencies have aided this species by eliminating egg harvest, protecting eggs and hatchlings, and reducing at-sea mortality through fishing regulations. From 1985 to 1999, the number of nests observed at Rancho Nuevo, and nearby beaches increased at a mean rate of 11.3% per year (TEWG, 1998).
Current totals exceed 8,000 nests per year, allowing cautious optimism that the population is on its way to recovery.

Critical Habitat Designations

4.3.3 Birds

Birds are a part of the coastal and oceanic ecosystem of the southeastern United States, occupying roles from grazing herbivores to top predators on many types and sizes of aquatic life. This section on protected species addresses listed bird species occupying habitat from the open ocean and outer continental shelf to coastal wetlands in the Southeast Region of the United States from the Virginia-North Carolina border south to the Dry Tortugas, Florida (Table 4.3-3). These species do not necessarily breed within the area as some breed in Bermuda, the Bahamas, or the West Indies and others breed as far north as the Arctic or as far south as the Falklands.

Bird species are listed for protection in the Migratory Bird Treaty Act (MBTA), the Endangered Species Act (ESA), and the special provisions of state governments. The National Marine Fisheries Service, through the authority of the Magnuson-Stevens Fishery Conservation and Management Act and the High Seas Fishing Compliance Act, has a role in bird conservation. Federal and State governments and non-governmental organizations have joined in bird conservation partnerships and developed bird conservation plans. Those that cover coastal and oceanic birds of the Southeast Region of the U.S. include the North American Waterbird Conservation Plan (Kushlan et al. 2002), the Draft Southeastern United States Regional Waterbird Conservation Plan (Hunter et al. 2005), the North American Waterfowl Management Plan, the U.S. Shorebird Conservation Plan, the South Atlantic Migratory Bird Initiative Implementation Plan (Watson and McWilliams 2005). These plans were sources of information for this description. The U.S. Fish and Wildlife publication, Birds of Conservation Concern 2002, was another source of information. Publications by Lee (1999, 2000) and his recent report in progress (Lee, in prep.) are other major sources. Collier, N. J. and P. Andrew. 1988. Birds to watch: The ICBP World Checklist of Threatened Birds (Collier and Andrew 1988) is another potential information source.

Somewhere near 200 birds occupy habitats extending from the coastal wetlands to the ocean pelagic environment of the South Atlantic Council region. These birds are in 12 orders and 33 families. They fit into eight functional groups of the South Atlantic Council's ECOPATH model and occupy the following habitats: Open Ocean, Coastal Shelf, Beach and Dune, Estuaries, and Coastal Wetlands (marshes and mangroves). In this report, "open ocean" refers to the area at and beyond the shelf break, whereas coastal shelf refers to the area landward of the shelf break. The discussion of birds is organized by habitat, although some bird groups and even bird species occur in more than one habitat. Some species groups that we discuss fit into more than one habitat.

Many oceanic and coastal bird populations of the Southeast Region have declined and are listed as endangered, threatened, or species of concern. Species listed in Table 4.3-3 fit into the above groups. Their highest (most protected) Federal status, State status, and status in the South Atlantic Migratory initiative Implementation Plan (SAMBI) is shown (Table 4.3-3). Only three species, the Bermuda petrel, the roseate tern, and the piping plover, are federally listed as threatened or endangered (the Bermuda petrel listed by Bermuda and Canada, not U.S.), however SAMBI lists 27 of these species as highest priority requiring immediate management attention and another 57 as high priority needing management attention. All birds in Table 4.3-3 are listed by MBTA, and many of these are included on State lists of species of concern.

Table 4.3-3. Selected Bird Species with Protected Status in the Coastal Waters of the Southern United States Atlantic States.

Birds				
Open Ocean	Scientific Name	*Federal Status**	*State Status*	*SAMBI***
Bermuda petrel	Pterodrama cahow	E	NC-extremely high conservation concern	HSP
Black-capped petrel	*Pterodroma hasitata*	MBTA	NC-extremely high conservation concern	HP
Fea's petrel	*Pterodroma feae*	MBTA	NC-extremely high conservation concern	
Herald (Trinidade) petrel	*Pterodroma arminjoniana*	MBTA	NC-extremely high conservation concern	
Band-rumped storm-petrel	*Oceanodroma castro*	MBTA		HP
Audubon's shearwater	*Puffinus lherminieri*	MBTA	NC-high conservation concern	HSP
Greater shearwater	*Puffinus gravis*	MBTA		HP
Manx shearwater	*Puffinus puffinus*	MBTA		HP
Cory's shearwater	*Calonectris diomedea*	MBTA	NC-high conservation concern	HP
Sooty shearwater	*Puffinus griseus*	MBTA		H
Masked booby	*Sula dactylatra*	MBTA	FL-conservation concern	
Brown booby	*Sula leucogaster*	MBTA		
Northern gannet	*Morus bassanus*	MBTA		HP
White-tailed tropicbird	*Phaethon lepturus*	MBTA		HP
Red-tailed tropicbird	*Phaethon aethereus*	MBTA		
Razorbill	*Alca torda*	MBTA		HP
Bridled tern	*Sterna anaethetus*	MBTA	FL-conservation concern	HP
Sooty tern	*Sterna fuscata*	MBTA		
Red phalarope	*Phalaropus fulicaria*	MBTA		HP
Red-necked phalarope	*Phalaropus lobatus.*	MBTA		
Waterfowl	Scientific Name	*Federal Status**	*State Status*	*SAMBI***
Common loon	*Gavia immer*	MBTA	NC-moderate conservation concern; SC-conservation concern; FL-conservation concern	HP
Red-throated loon	*Gavia stellata*	MBTA		HP
Horned grebe	*Podiceps auritus*	MBTA	SC-conservation concern; FL-conservation concern	HP
Black scoter	*Melanitta nigra*	MBTA	SC-conservation concern	HSP
Tundra swan	*Cygnus colunbianus*	MBTA	SC-conservation concern	
Snow goose	*Chen caerulescens*	MBTA		HSP

Brant	*Branta bernicla*	MBTA		HSP
Wood duck	*Aix sponsa*	MBTA	SC-conservation concern	
Mallard	*Anas platyrhynchos*	MBTA	SC-conservation concern	HSP
American black duck	*Anas rubripes*	MBTA	SC-conservation concern	HSP
Gadwall	*Anas strepera*	MBTA		
Green-winged teal	*Anas crecca*	MBTA		
American wigeon	*Anas americana*	MBTA		HP
Northern pintail	*Anas acuta*	MBTA	SC-conservation concern; FL-conservation concern	HSP
Blue-winged teal	*Anas discors*	MBTA	SC-conservation concern	HP
Canvasback	*Aythya valisineria*	MBTA	SC-conservation concern	HSP
Redhead	*Aythya americana*	MBTA	SC-conservation concern	HSP
Ring-necked duck	*Aythya collaris*	MBTA	SC-conservation concern	
Greater scaup	*Aythya marila*	MBTA	SC-conservation concern	
Lesser scaup	*Aythya affinis*	MBTA	SC-conservation concern; FL-conservation concern	HSP
White-winged scoter	*Melanitta deglandi*	MBTA	SC-conservation concern	HP
Surf scoter	*Melanitta perspicillata*	MBTA	SC-conservation concern	
Common goldeneye	*Bucephala clangula*	MBTA		HP

Coastal/shorebirds	Scientific Name	*Federal Status**	*State Status*	*SAMBI***
Black skimmer	*Rynchops niger*	MBTA	NC-special concern; SC-conservation concern; FL-special concern	HP
Roseate tern	*Sterna dougalli*	E/T***; MBTA	NC-threatened; SC-endangered; GA-special concern; FL-threatened	HP
Least tern	*Sterna antillarum*	MBTA	NC-special concern; SC-conservation concern; GA-rare; FL-threatened	HP
Royal tern	*Sterna maxima*	MBTA	SC-conservation concern; FL-conservation concern	M
Common tern	*Sterna hirundo*	MBTA	NC-special concern; SC-conservation concern	HSP
Gull-billed tern	*Sterna nilotica*	MBTA	NC-threatened; SC-conservation concern; GA-threatened; FL-conservation concern	HP
Forster's tern	*Sterna forsteri*	MBTA	SC-conservation concern	M
Sandwich tern	*Sterna sandvicensis*	MBTA	SC-conservation concern; FL-conservation concern	HP
Black tern	*Chlidonias niger*	MBTA		HP
Bonaparte's gull	*Larus philadelphia*	MBTA		M
Laughing gull	*Larus atricilla*	MBTA	SC-conservation concern	N/D (where threatening stability of other waterbirds)
Brown pelican	*Pelecanus occidentalis*	MBTA	SC-conservation concern; FL-special concern	HP
American white pelican	*Pelecanus erythrorhynchos*	MBTA		HP

Double-crested cormorant	*Phalacrocorax auritus*	MBTA	SC-conservation concern (breeding populations)	N/D (non-breeding)
Magnificent frigatebird	*Fregata magnificens*	MBTA	FL-conservation concern	
Osprey	*Pandion haliaetus*	MBTA		
Bald eagle	*Haliaeetus leucocephalus*	MBTA	NC-threatened; SC-threatened; GA-endangered; FL-threatened	M
Willet	*Catoptrophorus semipalmatus*	MBTA	SC-conservation concern	HP
Black-necked stilt	*Himantopus mexicanus*	MBTA	SC-conservation concern	
American oystercatcher	*Haematopus palliatus*	MBTA	SC-conservation concern; GA-rare; FL-special concern	HP
Piping plover	*Charadrius melodus*	MBTA	NC-threatened; SC-threatened; GA-threatened; FL-threatened	HSP
Semipalmated plover	*Chardrius semipalmatus*	MBTA	SC-conservation concern	M
black-bellied piper	*Pluvialis squatarola*	MBTA	SC-conservation concern	M
American golden plover	*Pluvialis dominica*	MBTA	SC-conservation concern	HP
Wilson's plover	*Charadrius wilsonia*	MBTA	SC-conservation concern; GA-rare; FL-conservation concern	HP
Snowy plover	*Charadrius alexandrinus*	MBTA	FL-threatened	HSP
Spotted sandpiper	*Actitis macularia*	MBTA	SC-conservation concern	M
Buff-breasted sandpiper	*Tryngites subruficallis*	MBTA	SC-conservation concern	HSP
Upland sandpiper	*Bartramia longicauda*	MBTA	SC-conservation concern	HP
Semipalmated sandpiper	*Calidris pusilla*	MBTA	SC-conservation concern; FL-conservation concern	HP
Solitary sandpiper	*Tringa solitaria*	MBTA	SC-conservation concern	HP
Stilt sandpiper	*Calidris himantopus*	MBTA	SC-conservation concern	HP
Western sandpiper	*Calidris mauri*	MBTA	SC-conservation concern; FL-conservation concern	HP
Pectoral sandpiper	*Calidris melanotos*	MBTA	SC-conservation concern	M
Least sandpiper	*Calidris minutilla*	MBTA	SC-conservation concern	HP
White-rumped sandpiper	*Calidris fuscicollis*	MBTA	SC-conservation concern	
Purple sandpiper	*Calidris maritime*	MBTA	SC-conservation concern	
sanderling	*Calidris alba*	MBTA	SC-conservation concern; FL-conservation concern	HP
Red knot	*Calidris canutus*	MBTA	SC-conservation concern; GA-special concern; FL-conservation concern	HP
Ruddy turnstone	*Arenaria interpres*	MBTA		HP
American avocet	*Recurvirostra americana*	MBTA	SC-conservation concern; FL-conservation concern	HP
Lesser yellowlegs	*Tringa flavipes*	MBTA	SC-conservation concern	HP
Greater yellowlegs	*Tringa melanoleuca*	MBTA	SC-conservation concern	
Dunlin	*Calidris alpina*	MBTA	SC-conservation concern	HP
Short-billed dowitcher	*Limnodromus griseus*	MBTA	SC-conservation concern	HP
Long-billed dowitcher	*Limnodromus scolopaceus*	MBTA	SC-conservation concern	
Whimbrel	*Numenius phaeopus*	MBTA	SC-conservation concern; FL-conservation concern	HSP

Long-billed curlew	*Numenius americanus*	MBTA	SC-conservation concern	HSP
Marbled godwit	*Limosa fedoa*	MBTA	SC-conservation concern; FL-conservation concern	HP
Waders	Scientific Name	*Federal Status**	*State Status*	*SAMBI***
Anhinga	*Anhinga anhinga*	MBTA	SC-conservation concern	
Great blue heron	*Ardea herodias*	MBTA	SC-conservation concern	
Great white heron	*Ardea herodias occidentalis*	MBTA		HSP
Glossy ibis	*Plegadis falcinellus*	MBTA	NC-special concern; SC-conservation concern; GA-special concern; FL-conservation concern	HP
Snowy egret	*Egretta thula*	MBTA	NC-special concern; SC-conservation concern; FL-special concern	HP
Reddish egret	*Egretta rufescens*	MBTA	FL-special concern	HSP
Great egret	*Ardea alba*	MBTA	SC-conservation concern	M
Cattle egret	*Bubulcus ibis*	MBTA	SC-conservation concern	N/D (where replacing other species)
White ibis	*Eudocimus albus*	MBTA	SC-conservation concern; FL-special concern	HP
Little blue heron	*Egretta caerulea*	MBTA	NC-special concern; SC-conservation concern; GA-special concern; FL-special concern	HP
Tri-colored heron	*Egretta tricolor*	MBTA	NC-special concern; SC-conservation concern; FL-special concern	HP
Green heron	*Butorides virescens*	MBTA	SC-conservation concern	
Black-crowned night heron	*Nycticorax nycticorax*	MBTA	SC-conservation concern; FL-conservation concern	HP
Yellow-crowned night heron	*Nyctanassa violacea*	MBTA	SC-conservation concern; FL-conservation concern	HP
Roseate spoonbill	*Ajaia ajaja*	MBTA		M
Wood stork	*Mycteria americana*	MBTA	NC-endangered; SC-endangered; GA-endangered; FL-endangered	HSP
Sandhill crane	*Grus canadensis*	MBTA		HSP
Whooping crane	*Grus americana*	MBTA	FL-special concern	HSP
Marsh/Wetlands	Scientific Name	*Federal Status**	*State Status*	*SAMBI***
American woodcock	*Scolopax minor*	MBTA	SC-conservation concern	HSP
Clapper rail	*Rallus longirostris*	MBTA		M
Yellow rail	*Coturnicops noveboracensis*	MBTA	SC-conservation concern; FL-conservation concern	HP
King rail	*Rallus elegans*	MBTA	SC-conservation concern; FL-conservation concern	HP
Black rail	*Laterallus jamaicensis*	MBTA	SC-conservation concern; FL-conservation concern	HP
American bittern	*Botaurus lentiginosus*	MBTA	SC-conservation concern; FL-conservation concern	HP
Least bittern	*Ixobrychus exilis*	MBTA	SC-conservation concern; FL-conservation concern	HP
Pied-billed grebe	*Podilymbus podiceps*	MBTA	SC-conservation concern (breeding populations)	

American coot	*Fulica americana*	MBTA	SC-conservation concern (breeding populations)	HSP
Wilson’s snipe	*Gallinago gallinagodelicate*	MBTA	SC-conservation concern	HP
Purple gallinule	*Porphyrula martinica*	MBTA	SC-conservation concern	HSP
Limpkin	*Aramus guarauna*	MBTA	FL-special concern	HSP
Saltmarsh sharp-tailed sparrow	*Ammodramus caudacutus*	MBTA	GA-special concern	HSP
Seaside sparrow	*Ammodramus maritimus*	MBTA	GA-special concern	HP
Coastal plain swamp sparrow	*Melospiza georgiana*	MBTA		M
Nelson’s sharp-tailed sparrow	*Ammodramus nelsoni*	MBTA	GA-special concern	HP

Lee (1999) listed 17 birds of conservation concern with documented occurrences on the Outer Continental Shelf off North Carolina (Table 4.3-4). He divided them into two categories, critical species and species of concern. Most are oceanic pelagic species, but a few occur primarily in coastal shelf waters.

Table 4.3-4. Seabird species of conservation concern occurring at or near proposed oil exploration sites on the Outer Continental Shelf of North Carolina (from Lee 1999).

Critical Species
Black-capped Petrel
Bermuda Petrel
Herald Petrel
Madeiran or Fea's Petrel (‘mollis’ group)
Roseate Tern
Species of Concern
Common Loon
Bulwer's Petrel
Greater Shearwater
Sooty Shearwater
Audubon's Shearwater
Band-rumped Storm-Petrel
White-tailed Tropicbird
Red-billed Tropicbird
Masked Booby
Northern Gannet
Bridled Tern
Atlantic Puffin

The present status of Southeast Region oceanic and coastal birds listed for special protection or management attention is a result of a variety of factors, including fishing effort, habitat loss, disturbance at nesting sites, pollution, marine debris, disease, and change in food availability. Habitat loss has been a major cause of decline in population number. Introduction and expanding exotic or feral species (e.g., house cats and black rats on nesting islands) is another. In addition, certain native species such as Greater Black-backed, Herring, and Laughing Gulls that prey on the eggs and young of other bird species have greatly increased in number recently and pose a threat to other waterbird species, especially shorebirds. Many seabirds found in the southeast region nest outside the region, where substantial decreases in nesting number have occurred due to human disturbance and predation by both humans and introduced species (e.g., see Schreiber and Lee [2000]). Oil spills are one source of pollution damaging to seabirds. Direct or indirect interactions with fisheries also affects some population groups (i.e., open ocean and coastal shelf species), although these interactions are not well documented or understood in the Southeast Region, and the direct impacts (i.e., capture or entanglement in fishing gear) may be small. Climate change and over fishing, by changing the availability of food supplies may also affect coastal and oceanic bird populations of the Southeast Region.

This presentation will include a brief description and information on distribution, reproduction, development, growth, abundance, movement patterns, population dynamics, and ecological relationships of selected species or species groups. The following discussion starts with birds of the open ocean, followed by birds of coastal waters, then shorebirds, waterfowl, and wading birds, and finally other marsh and coastal wetland birds. Detailed descriptions are given only for a few seabirds, both oceanic and coastal.

Open Ocean Species

Many species of oceanic seabirds breed in the Southeast region or occur in the area regularly. These include boobies, fulmars, petrels, shearwaters, storm-petrels, skuas, jaguars, dovekies, and some species of terns. The Northern Gannet, more coastal than oceanic, is also included with this group in order to be discussed with its relatives, the boobies. The gannet is a boreal breeder. Others, such as the black-capped petrel, the boobies, and the tropicbirds, nest in Caribbean and Gulf of Mexico waters. In addition, some nest in the eastern Atlantic, and others nest in the South Atlantic. Island nesting is the norm. Population numbers range from several million Greater Shearwaters and Wilson's Storm Petrels to less than 100 Bermuda Petrels. This group is characterized by long-lived species in which several years are required to reach maturity and breeding. Movements of juveniles and sexes may be distinct from adults. Age or sex differences in migration routes and destinations may make these populations more vulnerable to disturbances such as oil spills or pollution than they would be if the segments of the population were mixed. The species of this group range in size from the tiny storm petrels (15-22 cm in total length) to the Northern Fulmar (45-51 cm in total length)

Seabirds are a special concern in managing marine fisheries because of their interactions with fishing gear and vessels in both coastal and distant fisheries. Mortalities resulting from fishing gear could complicate efforts to conserve seabird populations threatened with habitat loss or other human caused mortality.

The United States has developed a national plan of action for reducing the incidental catch of seabirds in U.S. longline fisheries (NPOA-S 2005) as a voluntary response to resolution 02-14 of the International Commission for the Conservation of Atlantic Tuna (ICCAT), of which it is a member. Development of the NPOA-S was a collaborative effort between the National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (FWS). Action items for continued cooperative effort between the two agencies include a detailed assessment of longline fisheries for seabird bycatch, annual reports on the status of seabird mortality for each longline fishery (in consultation with the appropriate Councils), and measures to reduce seabird bycatch if any problems are found. Such measures include data collection, prescription of mitigation measures, research and development of mitigation measures and methods, and outreach, education, and training about seabird bycatch.

Longline fisheries pose a significant threat to some seabird populations in some parts of the world. The seabird bycatch of U.S. Western North Atlantic (USWNA) longline fisheries is small by comparison. The seabird bycatch of USWNA pelagic longline fisheries has recently been estimated based on data from the observer program, which covers about 6% of the longline effort. From 2002 through 2004, observers recorded two northern gannet (live), one laughing gull (live), and 12 unidentified seabirds (all dead) caught in the South Atlantic Bight (SAB) region. Based on the observer bycatch and longline effort, Hata (2005) estimated an average annual bird bycatch of 27.39 per year in the SAB. Only six taxa have been identified in the USWNA longline bycatch. Besides the northern gannet and the laughing gull, these are the greater and Cory's shearwaters, the herring and great black-backed gulls, and an unknown species of storm petrel. The high percentage of unidentified birds in the bycatch and low observer coverage make estimation of impacts on seabird populations problematic. Population levels are so low for some species that they might be impacted even if catch rates were extremely low. Most seabirds are long-lived (e.g., 10 to >30 yrs) and have low reproductive potential, thus their populations are more sensitive and less resilient to increased mortality than short-lived species.

Eighteen species of open ocean seabird appear in Table 4.3-3. Sixteen of these are included in Lee's (1999) list of seabirds of concern occurring regularly on the Outer Continental Shelf off North Carolina (Table 4.3-4). A set of species profiles by Lee (in prep) is a further source of information on this group. The major component of this group is characterized by long-winged strong fliers that spend months of the year at sea out of sight of land. Most of these species nest outside of the Southeast Region and are in the regional waters during their non-nesting period, winter for northern-nesting species and summer for those that nest in the southern hemisphere. Others range as far north as North Carolina to feed during their nesting season in tropical latitudes, and they occur in the Southeast Region during the summer. Still others migrate through the region during the spring and fall. These birds are characteristically long-lived with extended adolescence, and they usually raise only one chick per season. This makes their populations especially vulnerable to increased mortality rates of nestlings, fledglings, or adults. Many of these species nest in colonies on islands, where they are especially vulnerable to human harvests and depredation by exploding populations of introduced predator species (e.g., rats, mongooses, and feral cats and pigs).

A set of taxonomic families aptly nicknamed "tubenoses" makes up the largest taxonomic group of open ocean seabirds listed in Table 4.3-3. Of these, the four petrels are of the highest conservation concern (Lee1999). Other tubenoses in Table 4.3-3 include Audubon, Cory, sooty, and greater shearwaters. The smallest tubenoses are the storm-petrels. Lee (1999) suggested that the Wilson's storm-petrel, common in waters of the Southeast Region, may be the most populous bird in the world's open oceans. The band-rumped storm-petrel, Leach's storm-petrel, and white-faced storm petrel also are found in the Western North Atlantic and are included on the MBTA list of protected birds. All four WNA storm-petrels occur on the Outer Continental Shelf off North Carolina (Lee 1999), but only one--the band-rumped storm-petrel--is included on Lee's (1999) list of species of concern.

Petrels nest in burrows on islands and have been subjected not only to predation by humans and introduced animals but also to disturbance of nesting sites by lights, lumbering, forest fires, and other habitat alteration. One egg is laid, and the time from hatching to maturity is 7 yrs and longer for many species. The vulnerability of petrels at their nesting sites has already caused at least three petrel species in the Western Atlantic to become extinct. The remaining four species are in severe jeopardy.

Bermuda Petrel, *Pterodroma cahow*

When first discovered in Bermuda in the 16th century, nesting Bermuda Petrels numbered in the hundreds of thousands. They do not nest anywhere else and were presumed extinct by 1620 as a result of human exploitation and introduced predators. After being considered extinct for over 300 years, 18 pairs were discovered in 1951 on five small islets off Bermuda (Lee, in prep.). Lee (1999) reported 53 pairs but hurricanes in the last decade have destroyed a number of nesting burrows. The Bermuda Government reported 29 pairs actively nesting in 2005 (Lee, in prep.). The only published records of at sea occurrence are for waters around Bermuda and from the Gulf Stream over the Outer Continental Shelf of North Carolina, which appears to be an important foraging area for this rare species. This is a federally listed endangered species and one of the most endangered birds in the world.

Black-capped Petrel, *Pterodroma hasitata*

This highly pelagic species is endemic to the Western North Atlantic. It breeds in the West Indies, where nesting is now confined to the mountains of southern Hispaniola, and forages regularly off the southeastern coast of Cuba and in the deep Gulf Stream waters off the southeastern United States, mostly from Cape Canaveral north to Cape Hatteras (Lee 2000). Nesting occurs in the winter (Lee 2000). This petrel was thought to be extinct until nesting colonies were discovered in Haiti in 1961, when population estimates were made of 2,000 to 20,000 pairs, the latter likely an overestimate. Subsequent habitat destruction may have reduced the population to a current 1,000 to 2,000 pairs (Lee, in prep.). Material in caves from Haiti suggest the birds were once much more abundant and widespread in Hispaniola than they are today, and human consumption and habitat alternation had probably already reduced their number by the time the Haitian colonies were discovered by Wingate (1964). This is one of the most threatened species in America.

Herald Petrel, *Pterodroma arminjoniana*

This is a rare, highly pelagic tropical petrel confined in the Atlantic to two breeding sites, South Trinidade Island and Martin Vas Rocks off Brazil (Lee, in prep.). This petrel disperses great distances from its breeding sites. Of several hundred sighting reports in the Western North Atlantic, most are from off Cape Hatteras, but the species has also been reported from Virginia, Puerto Rico, and the mid Atlantic. Most records are from summer along the Outer Continental Shelf and well within the Gulf Stream. This species is highly endangered in the Atlantic basin because of human disturbance and introduced house cats affecting nesting, and the population appears to continue to decline (Lee 2000). Evidence suggests that the Atlantic population is specifically different from ones nesting in the Indian Ocean and tropical Pacific, and the two color morphs nesting on South Trinidade Island may actually represent two different species (Lee 2000).

Fea's Petrel, *Pterodroma feae*

The Fea's petrel breeds in the Cape Verde Islands and Bugio, Desertas Islands off Maderia. A sister species Maderian petrel, P. maderia, breeds in remote high elevation sites on Maderia. These two species, known as soft-plumaged petrels, both occur in the North Atlantic and are so similar that even experts cannot agree on how to tell them apart. The population of Fea's petrels is only a few hundred pairs while the Madeira population is less than 50 pairs, possibly only 20 pairs. Both are extremely rare, declining, globally endangered species.

Shearwaters

The shearwaters are another group of tubenoses. In the Western North Atlantic, these include Audubon's, Greater, Manx, Cory's, and Sooty shearwaters. The shearwater species of greatest concern is Audubon's Shearwater, *Puffinus iherminieri*, a tropical species that occurs in the Atlantic as two subspecies. The current nominate population, *P. I. iherminieri*, consists of 3,000 to 5,000 pairs (Lee 2000), and the western Caribbean subspecies, *P. I. loyemilleri*, is close to extinction (van Halewyn and Norton 1984). Nesting site disturbance by rats and feral cats on islands is the greatest threat to this species.

The other shearwaters in Table 1 are obligate trans-equatorial migrants. In the western Atlantic, the sooty shearwater, *Puffinus griseus*, is limited to 1,000-10,000 pairs, although it also occurs in the Pacific. The greater shearwater, *Puffinus gravis*, is of conservation concern not because of low population numbers in the Atlantic basin (populations are estimated at over 5 million breeding pairs in Tristan de Cunha, Gough Island, and a single island in the Falklands [Williams 1984]) but because they aggregate for both nesting and feeding. The Cory's shearwater, *Calonectris diomedea*, is endemic to the Atlantic, where three subspecies exist, none of which are considered imperiled. Young disperse to the Western Atlantic, and two subspecies have been found in the area from Cape Hatteras south. Two shearwaters, the greater and Cory's, have been identified in the observed catch of the U.S. WNA longline fleet, where they usually are found dead on the line rather than being released alive. The greater shearwater is the most frequently identified species in the observed catch. The greater shearwater also is caught in gillnets in New England fisheries. Unexplained greater shearwater mortalities were observed along the Atlantic coast in June 2007, particularly in Florida. The strongest hypothesis for this mortality event is that these were young-of-the-year birds starving to death on their first migration (Lee, pers. comm.).

Gannets and Boobies

Gannets and boobies form another taxonomic group (Sulidae) included in Table 4.3-3. In all members of this group, different plumages are exhibited at different stages of maturity, at least four immature plumages and an adult plumage. The northern gannet and NWA boobies have similar physical characteristics; however the gannet is a boreal breeder whereas the boobies breed tropically.

The northern gannet, *Sula bassana*, is the most coastal of the WNA sulid species and, although it winters at sea, is rarely out of sight of land. In the NWA, the gannet breeds in Newfoundland, Labrador, and Quebec. Canadian waterbird sites list about 194,000 breeders as of 2005 (from data compiled by D. Forsell from Canadian wet sites (see note at end of this section). This estimate does not include Iceland. Since numbers are increasing, there may now be 200,000 breeders and maybe 50,000 -100,000 immatures and fledglings. The northern gannet is seen regularly off North Carolina and might be found anywhere along the South Atlantic coast. Adults winter from the Carolinas to Maryland and northward. The youngest birds winter further south (Florida, Cuba, and Upper Gulf of Mexico). New tracking data also shows some adults now going to the Florida Gulf coast. Gannets often concentrate around fishing vessels and may be vulnerable to various fishing gear. The northern gannet is an observed bycatch species of the WNA longline fishery, but usually is retrieved alive and released. This species has also been observed caught in both anchored and drift gillnets of several coastal and offshore fisheries and also is caught in paired trawls in the Gulf of Maine (D. Forsell, pers. comm). Large numbers of gannets have been found dead and dying off the Atlantic coast on several occasions (e.g., thousands died during the winter of 2002-2003). “Emaciation syndrome” is suggested by autopsies, implicating stress or starvation. Drowning in deep-set gill nets and disease have also been proposed as possible factors in the large mortalities. Despite the die-offs, population numbers are increasing (D. Forsell, pers. comm.).

The masked booby, *Sula dactylatra dactylatra*, is the least common booby species in the WNA, but it is the one most likely to be encountered away from nesting sites because individuals disperse great distances from their breeding grounds. Nesting is on remote islands lacking mammalian predators, often with other boobies. This is a deepwater, pelagic species occurring northward in the Gulf Stream to the Carolinas, where it is usually associated with *Sargassum*. Its diet is flying fish, jacks, and squid. The current NWA population consists of 550-650 pairs in eight known colonies in the West Indies, another 4,000 to 5,200 pairs nesting on islands off Venezuela and Mexico (Schreiber 2000), and a few pairs nesting in the Dry Tortugas. Although the species is pan tropical, it is rare everywhere, and the Atlantic population is considered endangered in the West Indies where over half the breeding stock occurs on a single island off Jamaica. Other WNA boobies are less likely to occur in the waters off the Southeast Region.

Oceanic Terns

The sooty tern, *Sterna fuscata*, and the bridled tern, *Sterna anaethetus melanoptera*, are more oceanic than coastal and so are included in this section on oceanic birds. Both species are found far at sea. Neither species is a plunge diver. Both feed by dipping prey from near the water surface.

The sooty tern is a common high-flying circum-tropical oceanic species. It does not dive nor land on the water, but scoops small fish from the surface of the water while in flight. It often occurs in large flocks; sometimes thousands are in a single flock. Feeding flocks form over foraging schools of surface feeding fishes. Flocks of Sooty Terns have been seen in association with schools of tuna that drive concentrations of small forage fish to the ocean surface where they are accessible to capture by the terns (A. Sprunt IV, pers. comm.). This species has a substantial nesting colony in the Dry Tortugas National Park off the Florida Keys, where carangids and clupeid fish, as well as squid make up the major part of the diet (Browder et al.

1996), and also breeds in the Bahamas and off Central and South America. Small groups occasionally nest along the Gulf coast and north to the Outer Banks. Young WNA sooty terns live primarily off the west coast of Africa after dispersing from their natal areas. Adults occur in tropical seas and, in summer, wander north in the Gulf Stream. This species is the most abundant seabird breeding in the tropical Atlantic. The total Greater Caribbean population is estimated at 230,000-500,000+ pairs (Lee, in prep.). This species occurs throughout the world's tropical seas.

The bridled tern is a pelagic tropical and subtropical species. This tern often is seen resting on boards, the backs of sea turtles, and other floating material far at sea, distinguishing them from sooty terns, which do not have this habit (Sibley 2003). Much of its foraging is in Sargassum, so it is frequently associated with large Sargassum mats. It occurs singly or in small flocks. The bridled tern is distributed throughout the Caribbean, but it is not a common species. Non-breeding birds occur in the Gulf of Mexico and regularly in the Gulf Stream north to the Carolinas. It nests in widely scattered, mostly unprotected sites. Several subspecies collectively form a composite circum-equatorial distribution. Nesting occurs primarily in the West Indies, but also on islands off the northern South American coast, and, minimally, in the Florida Keys. The total WNA population is estimated at 7,000 pairs (Lee, in prep.). This species is not of conservation concern globally or regionally, but individual breeding populations for some countries are quite small (Lee, in prep.), as is the WNA total.

Coastal, Shelf, Beach and Dune Species

Birds of these habitats form three groups: gulls and terns; loons, ducks, geese, and other waterfowl; and shorebirds. These species are listed in their three groups in Table 1. Many species in these groups also occur in estuaries and wetlands, but will be described only in this section. Most gulls and terns listed in Table 1 are in this coastal group. The sooty and bridled terns are discussed in the previous section with other oceanic birds. Other tern species are found far at sea occasionally. The northern gannet, although more coastal than oceanic, was included in the previous section to be discussed with its close relative, the masked booby.

Coastal avian species have a variety of feeding habits and food items, and the diets and feeding modes of some are more varied than others. Gulls are found along beaches and on mudflats of river mouths and estuaries where they may feed on mollusks and benthic infauna (small organisms that live in the sediment) as well as fish and the eggs of other waterbirds. Most gulls (in winter) are roosting along inlets because they are following fishing boats to feed on offal or discarded bait or bycatch or scavenging on beaches. The food of most tern species, cormorants, and brown pelicans is more confined to fish and squid. Most tern species feed on the wing by dipping prey from the water surface, however a few terns plunge dive.

These avian species also are varied in the degree of concern expressed for them and protection they are afforded. The roseate tern is the only coastal pelagic bird species Federally listed as endangered. Some other members of this group listed in Table 1—black skimmer and least, common, sandwich, Forester's, and gull-billed terns—are listed as "species of concern" in one or more of the southern east coast states where they nest. The black tern, although not listed anywhere as a species of concern, probably should be listed because it has been declining since the 1960s. Two other, primarily tropical, terns that nest in the southeast coastal region also are included in Table 1 and in the below discussion, although they are not listed as species of concern either by states or Federally. SAMBI classified three gull species—great-black-backed, herring, and laughing gulls—as "nuisance or depredating" (N/D) species because their expanding populations pose a threat to other birds, especially shorebirds. While the herring gull may be in the N/D category and expanding in the southern states, its population may be declining at about the same rate that the great- black-backed gull is increasing in the New England and Mid-Atlantic states (D. Forsell, pers. comm.) The laughing gull has been listed as a species of concern in South Carolina and, for this reason, is listed in Table 1. Observers have reported all three above-mentioned gull species in the bycatch of the WNA U.S. longline fishery. The Bonaparte gull is the only gull species listed by SAMBI as a priority species for conservation and also is listed in Table 1.

Roseate Tern, *Sterna dougalli dougalli*
The Roseate Tern is Federally listed as "endangered" in North Carolina and the Northeast Region and federally listed as "threatened" from South Carolina to Florida, as well as in Puerto Rico and the U.S. Virgin Islands. It also occurs in—and is listed as "endangered" by the governments of Bermuda and Canada (Newfoundland, Nova Scotia, and Quebec). Breeding areas are disjunct from Nova Scotia to the West Indies. This tern feeds over breaking surf, particularly over the backwash of outgoing tides of estuaries, and roosts on rocks rather than sand or mudflats. It dives on shoals of fish. In Massachusetts, where the principal food of both species is sand lance, the roseate tern feeds with common terns and captures food mainly by plunge-diving (diving from heights of 1-12 m above the surface and often submerging to ≥ 50 cm) (Mostello 2002). The breeding ecology of the roseate tern is closely linked with that of the common tern in Massachusetts; roseate tern nests form clusters inside larger common tern colonies, where the more aggressive species may reduce the overall level of predation (Mostello 2002). The total WNA population presently is probably less than 8,000 pairs (Lee, in prep.). The nominate subspecies, endemic to the North Atlantic, is in sharp decline. A population of the subspecies also exists in Europe.

Common Tern, *Sterna hirundo*
The common tern is a common and widespread tern found in both the eastern and western hemispheres. Nesting in the western hemisphere occurs on inland lakes and rivers and along the Atlantic seaboard from Canada to islands off the Gulf coast states and also in Bermuda, the Bahamas, the Virgin Islands, and islands off Venezuela (Harrison 1983). The common tern feeds by plunge diving (Harrison 1983). This species is found at sea in small to modest-sized flocks often associated with other tern species during migration and when wintering (Lee, in prep.). Off Massachusetts, it feeds closer to shore than the roseate tern (Mostello 2002). Based on independent estimates from the various regions of nesting, the population estimate for the WNA from Lee (in prep.) is 129,473 pairs.

Gull-billed Tern, *Sterna nilotica*
The gull-billed tern is another near-cosmopolitan species that breeds along the eastern seaboard, nesting locally from Long Island south through the Gulf coast states to Cuba and the West Indies. This species' feeding habits differ from that of other terns. According to Sibley (2003), it feeds mainly on insects and crabs, acquired by swooping to the surface, never plunge diving

and almost never foraging in water. According to Harrison (1983), it usually obtains prey by hawking over exposed mud flats, but it occasionally plunges into the water, although not from great height. It feeds along coasts, over marshes, lakes, mudflats and even fields, dipping swiftly to pluck prey from the surface or seize insects in mid air (Harrison 1983). Lee (in prep.) estimates the total Western North Atlantic population at: 3,100-3,500 pairs.

Forster's Tern, *Sterna forsteri*

The Forster's tern breeds only in North America and mostly at inland sites in the middle and western portion of the continent, but it also nests in marshes along south eastern Atlantic states north to New Jersey and upper Gulf coasts. These terns migrate and winter primarily inland and along the coast of the southeastern states, Mexico, the California coast, and in the upper Gulf of Mexico. Birds are found in the West Indies in winter indicating some at-sea migration, but this species is only rarely found at sea in the western North Atlantic. The WNA population, including Inland Canada, consists of about 30,000 pairs, most of which occur on the Gulf coast. This is listed as a species of conservation concern in South Carolina.

Sandwich Tern, *Sterna sandvicensis*

This species breeds in North America, Eurasia, and northern South America. Nesting occurs from Virginia southward and along the Gulf coast and also in the West Indies, islands off Central America, and on the coasts of northern and northeastern South America. This is a coastal foraging species and, excluding migration periods, it is almost never seen more than 12 miles from land. A subspecies, the Cayenne tern (*Sterna s. eurygnata*), is recognized that occurs along the South American coast and in the Caribbean. This is not a species of concern except for the Cayenne subspecies. The total WNA population of *Sterna s. sandvicensis* is estimated at 48,000 pairs, and the Cayenne tern population is estimated at 12,000 pairs (Lee, in prep.).

Least Tern, *Sterna antillarum*

The least tern is a cosmopolitan species. The subspecies *S. a. antillarum*, breeds along the eastern seaboard to the Gulf of Mexico and the Caribbean. This tern is coastal species and rarely seen out of sight of land even during migration. It nests on sand dunes just above the high-tide line among grass and debris, as well as on flat rooftops near water. Its habits are similar to common and other terns, and it mixes freely with other terns at roosting and foraging sites. Wintering birds are found along the South American coast south to Northern Brazil. It also occurs inland. Other subspecies breed in other parts of the Western Hemisphere and the world, however not in the South Atlantic. Protection in the United States has greatly increased the number of viable breeding colonies in the last several decades, and population estimates of 32,000+ pairs for the eastern seaboard group may not reflect the recent increase (Lee, in prep.).

Black Tern, *Chilidonias niger*

Black terns breed in inland freshwater marshes and feeds on insects. They migrate over land, along the coast, and out at sea. The terns nesting in North America winter primarily along the Pacific coast of Central and South America and in the Atlantic along the north coast of South America. The eastern Atlantic subspecies winters primarily along the coast of West Africa. Although not listed as a species of concern at this time, it probably should be; populations have been in sharp decline since the 1960s, and North American breeding bird survey data shows a sharp and significant decline, perhaps as much as 60%, between the 1970s and the late 1990s

(Lee, in prep.). Kushlan et al. (2002) estimate the total North American population at 500 to 2,500 adult pair.

Royal Tern, *Sterna maxima*

The royal tern is a large, crested, orange-billed tern second only in size to the Caspian tern, *Sterna caspia*, the largest tern in the world, which also has an orange bill. In the Western Hemisphere, the royal tern breeds on the Atlantic coast from Virginia to Texas and also in the West Indies, Central America, and on the Pacific coast. It also breeds in northern West Africa. This tern usually is found along ocean beaches. It forages by flying over the water to scout out prey and then diving below the water surface (Sibley 2003). It makes its nest scrape on the ground on low-lying natural islands or shoals or dredged-material islands. Royal terns nest in large colonies ranging from a few hundred to over 5,000 nesting pairs (NC Audubon Chapter 1998, (http://www.audubon.org/chapter/nc/nc/wb_07.html). Within a day of hatching, chicks leave the nest to become part of a group that can consist of thousands of chicks from 2 to 35 days old (Cornell Lab of Ornithology website http://www.birds.cornell.edu/AllAboutBirds/BirdGuide). Parent chicks feed only their own chick, which they are able to locate in the crowd (op. cit.). The North Carolina population consists of about 11,000 pairs and is declining (NC Audubon 1998). SAMBI (2005) estimates 5,500 in South Carolina, 8,000 in Georgia, and 2,500 in Florida. The major threats are human disturbances at nesting sites, loss of nesting habitat, fish kills, and discarded monofilament fishing line (op. cit.).

Black Skimmer, *Rynochops niger*

The black skimmer is a strictly coastal species in North America, although it lives along rivers in South America. Skimmers feed by skimming the water surface with their knife-like bills. They rest on mudflats and sandy beaches. They breed along the Atlantic coast from Massachusetts south through the Gulf of Mexico to northern Brazil (but not the Bahamas or West Indies). In winter northern populations migrate southward to Florida and the Gulf of Mexico. Several states with small numbers of colonies and declining populations (NC, SC, and FL) list this as a species of concern. Lee (in prep.) estimates that the total Atlantic population is in excess of 27,500 pairs.

Laughing Gull, *Larus atricilla*

The laughing gull is a small gull that breeds in the WNA from Maine south to Florida (including Florida Bay), throughout the Bahamas and West Indies, Gulf of Mexico, Mexico and the northern South American coast. It winters in coastal areas within its breeding range and at sea from the Carolinas southward. During the summer the species is restricted to coastal areas, but during the winter it often occurs in flocks in open ocean environments. Laughing gulls follow ships and form feeding flocks around fishing operations. There may at present be about 270,000 pairs of laughing gulls in the Southeast Region (Lee, in prep.).

Great Black-backed Gull, *Larus marinus*

The great black-backed gull is the largest gull in the world (total length 71-79 cm, with a wing span of 152-167 cm). It is confined to the North Atlantic and breeds in North America along coastal areas from Labrador and Quebec south to New York, with individual nesting as far south as North Carolina. Birds from North America and Greenland winter in marine environments from Labrador south to Florida. It is found mostly in coastal areas but can occur far at sea. This species currently is expanding in both distribution and numbers and is viewed (Hunter et al. 2005) as a species that may need to be controlled because of its predation on other beach-nesting bird species. Lee (in prep.) estimates abundance for the WNA is at least 40,000 pairs.

Herring Gull, *Larus argentatus*
The Herring Gull is another large gull of the WNA. It is common and widespread and is known to hybridize on a regular basis with greater black-backed gulls. Most of the breeding range is inland, but nesting occurs from southeastern Alaska east to Greenland and south along the coast to North Carolina. Wintering individuals are found along the coast to southern Florida. In some areas, immatures are more likely to be found far at sea than adults. Kushlan et al. (2002) estimate the North American breeding population at 132,000 pairs. More than 1,000 pairs nested along the NC coast by 1988 (Lee 1995), expanding south into areas where they had not nested prior to 1970. The population is increasing partly because of this gull's use of landfills as winter-feeding sites. In some areas this gull needs to be controlled because it is detrimental to breeding populations of roseate terns and other species of conservation concern (Hunter et al. 2005, Lee, in prep.). Although the herring gull may be expanding south, the herring gull population may be decreasing in New England and the Mid-Atlantic coast, where the great-black-backed gull is increasing (D. Forsell, pers. comm.).

Loons
Two loon species occur in coastal and inland waters of the south Atlantic states, the common loon (*Gavia immer*) and the red-throated loon (*Gavia stellata*). The common loon is the larger, and more oceanic, of the two. The Atlantic populations of common loon breeds in inland lakes of the mid-west and New England States to arctic Canada. According to Lee (in prep.), common loons winter primarily at sea, and some migrate as far south as Florida. Once on wintering grounds they completely molt their flight feathers and are flightless for an extended period. They are typically seen floating on the water surface and are more likely to dive to avoid approaching ships than to fly. They feed on fish that they capture on extended deep dives. Oil spills are a major problem for the birds at sea, but mortalities from oil spills are localized. Mass mortalities with loons washing up on coastal beaches all along the coast may result from drowning in nearshore gillnets D. Forsell, pers. comm.), although mercury-contamination picked up on their breeding lakes is another possible reason for these deaths (Lee, in prep.). Populations reportedly are declining, but currently still high overall. Haney (1990) estimated up to 200,000 (a significant portion of the total population) wintering off the Atlantic coast of North America between Latitudes 29° and 35°N. Common loons are the second most abundant North American breeding bird captured in gillnets in the Atlantic offshore waters (Forsell 1999).

The red-throated loon breeds in the northern hemisphere only in the High Arctic and winters in estuaries and coastal waters of the Atlantic coastal states. Nests are reportedly not only in Alaska but also in Canada, Greenland, and Russia. Canada and Greenland are the most likely sources of those that winter along the Atlantic coast., which Lee (in prep.) conservatively estimates at 50,000+. The actual population size may be much larger as the New Jersey (Avalon) Seawatch reported 51,645 seen at Cape May in 2004, http://www.njaudubon.org/Research/PDF/Avalon_totals.pdf , and many migrate overland to the coast south of there (D. Forsell, pers. comm.). This species is the most abundant North American breeding bird caught in mid-Atlantic coastal gillnet fisheries in both coastal and estuarine waters (Forsell 1999).

Shorebirds

Shorebirds, by number, form a major component of the WNA marine bird fauna. All but a few of the shorebirds listed in Table 4.3-3 are of conservation concern in one or more of the southeastern states. There is much concern for these species because of loss and disturbance of habitat and predation by feral animals, raccoons, and certain gulls with expanding populations. Besides development, recreational activities on beaches and dunes have affected both breeding and feeding habitat. High quality breeding habitat is viewed as the key to protecting shorebird populations. An immediate SAMBI objective is to maintain the habitat supporting the present breeding populations of 900 pairs of American oystercatchers, 45 pairs of snowy plovers, 850 pairs of Wilson's plovers, and 55 pairs of piping plovers. The piping plover is now Federally listed as an endangered species. The SAMBI goal is to double the breeding population size for each of these shorebird species in the southern coastal plain states or, through population analyses, to determine the population levels needed to ensure the long-term viability of breeding populations. Another immediate SAMBI objective is to provide high quality managed habitat to support successful migration through, and over-wintering within, the southern coastal states, particularly during fall migration. This means maintaining wash-overs, sand flats, and mudflats, especially on barrier islands created by hurricanes. Another emphasis is on reducing the populations of great black-backed gulls, which prey on shorebirds.

Waterfowl

Ducks, geese, and swans make up the other major component of the coastal avifauna. Most members of this group migrate, following various migration pathways. Some reach only to the northern part of North Carolina and others reach the southern tip of Florida and even into the Caribbean. There are three major groups of ducks: dabbling ducks, bay ducks, and sea ducks. Both the bay ducks and the sea ducks are divers.

Of all the waterfowl groups, the greatest conservation concern is for the sea ducks and greater and lesser scaup. Included in this group called sea ducks are scoters, eiders, harlequin ducks, mergansers, long-tailed ducks, goldeneyes and buffleheads (Bellrose 1976), not all of which occur along the southeastern seaboard. The 15 species of sea ducks constitute 42% of the ducks breeding in North America, yet these are the least known waterfowl (Sea Duck Joint Venture, SDJV). Our knowledge of most sea ducks was very limited until the past decade when new emphasis on estuaries and declining sea duck populations began to focus interest of scientists and managers. Unfortunately most studies have been conducted on breeding grounds or in Canada or waters north of the Carolinas. Little is known about their distribution and habitat requirements during their winter at sea off the southeastern states. There are few reliable population estimates or indices. They breed in low densities in remote parts of the continent, making population surveys logistically difficult, and discouraging the accumulation of even basic natural history information, much less information on life-history, population dynamics, and ecology. Sea ducks may represent no more than 5% of the continental waterfowl harvest, however surveys are not designed to accurately estimate the harvests of these species. Sea ducks have long life spans and, consistent with this, low reproductive rates. Unlike other ducks, most sea duck species are not sexually mature until they are 2 or 3 years old.

Population declines in 10 of the 15 sea duck species have been reported based on surveys conducted in the 1990s (SDJV). The eastern population of harlequin ducks has been listed as endangered in Canada (SDJV). Causes of population losses are unknown. Sea ducks spend about nine months in marine environments, where they occupy a range of habitats—bays, lagoons, estuaries, and coastal shelf waters. They often occur in large aggregations, making them more vulnerable to catastrophic events. Contaminants have been found in tissues of some sea duck species at concentrations known to affect survival and reproduction in other birds (SDJV). Their long life spans make them vulnerable to bioaccumulation of persistent pesticides and heavy metals. Direct mortality from lead poisoning has been documented on Alaskan breeding grounds. Offshore oil production, oil spills, and chronic exposure to low levels of petroleum contamination from bilge dumping are potential threats to the future well being of sea duck populations. In addition, they are exposed to loss of breeding habitat, and their wintering areas have been changed by urban and industrial development.

Commercial gillnet fisheries encountered along their migration routes and on their wintering grounds are an under-recognized threat to diving waterfowl and may be partly responsible for the unexplained declines in populations of scaup and other divers, including the sea ducks. A recent unpublished report by Doug Forsell (U.S. Fish and Wildlife Service, Annapolis) summarizes both published and antidotal information to determine the species affected by gillnetting in both fresh and salt water. The Forsell report and two recent reports by Price and Van Salisbury (2007) and Price (2007) indicate the following avian bycatch in commercial gillnet fisheries: brown pelican, canvasback, common loon, cormorant, diving ducks, double-crested cormorant, great black-backed gull, grebes, pied-billed grebe, red-breasted mergansers, red-throated loon, ruddy duck, ccaup, and surf scoter.

Snow geese, Canada geese, and mute and tundra swans, along with numerous species of dabbling ducks and bay ducks, make up the remaining component of the waterfowl of coastal waters in the Southeast. Based on Sibley (2003), ducks notable for occurrence in southeastern coastal waters are the mallard, gadwall, American wigeon, canvasback, greater and lesser scaup, redhead, bufflehead, and hooded, red-breasted, and common mergansers. The American black duck and Florida duck inhabit salt marshes. In the coastal environment, dabbling ducks and bay ducks feed on stems of aquatic vegetation and seeds of marsh grasses. Some species also feed on small crustaceans and mollusks. Sea ducks such as long-tailed ducks feed predominately on animals, including crustaceans and fish, but plant foods make up about 10% of their diet. Mollusks are more important than crustaceans in the diets of black scoter, which also consume plants—frequently eelgrass.

Almost all waterfowl species that use the Atlantic flyway have been affected by the loss of coastal wetland and changes in the flow of fresh water to the coast, brought about by dams, levees, canals, roads, and other structures. While changes in the timing, volume, or distribution of freshwater flow may not affect the birds directly, it affects their aquatic habitat and their food supply, made up of species of plants and animals that benefit from natural estuarine gradients of salinity and river-influenced estuarine circulation. The largest threats to diving ducks are changing habitats, over fishing, sand mining, loss of benthic reef habitats, sedimentation, disturbance, and many other anthropogenic effects of coastal development. Hunting is, of course, a major cause of mortality to those species sought after in this sport.

Estuarine and Coastal Wetland Species

Pelicans and cormorants, wading birds, certain raptors, shorebirds, and waterfowl are major avian groups inhabiting bays, lagoons, and wetlands. They feed on shallow mud flats and along tidal creeks and shorelines. Shorebirds and waterfowl have already been discussed in the previous section. The pelican group, wading birds, and marsh birds will be discussed in this section.

Pelicans and Their Relatives

Brown pelicans, double-crested cormorants, and magnificent frigate birds are characteristic species of coastal waters and estuaries, catching prey by various methods. They congregate around fishing boats and docks where they often find a free meal. Prey acquisition is facilitated by the expandable lower bill of these species, which belong to the taxonomic order Pelicaniformes, along with the boobies and gannets. The principal threats to populations of these species are loss or degradation of nesting or feeding habitat, blooms of toxic algae, and contaminants such as chlorinated hydrocarbons and heavy metals that accumulate in aquatic food chains. They are potentially vulnerable to inshore trawl, seine, gillnet fisheries, and hook and line fisheries. Entanglement in monofilament line is a common source of death or disablement of pelicans and cormorants. Bycatch of both brown pelicans and double-crested cormorants has been documented in North Carolina gillnet fisheries. Pound nets are a big attractant for cormorants and increasingly, pelicans, both for foraging and roosting, thus increasing conflicts with fishers (D. Forsell, pers. comm.).

The brown pelican, *Pelecanus occidentalis*, is confined to coastal regions of North and South America. Plunge diving is this bird's primary mode of fishing, although juveniles sometimes feed by dipping bills while floating on the water surface. Widespread use of DDT led to a serious decline of Brown Pelican populations, however population numbers stabilized and began increasing in the 1980s, and the range of this tropical to southern temperate species has been increasing northward (i.e., from North Carolina to Maryland). Surveys conducted in Atlantic states in the 1980s suggested the WNA population of Brown Pelicans was 18,000 pairs; but present numbers likely are considerably higher (Lee, in prep.). Kushlan et al. (2002) estimate there are 95,800-96,850 adult pairs in North America, not distinguishing Atlantic, Gulf of Mexico-Caribbean, and Pacific coasts.

The double-crested cormorant, *Phalacrocorax auritus*, is the most common and widespread WNA cormorant. Like the pelican and other cormorants, it resides in marine habitats only in coastal areas, feeding in bays and sounds and near inlets and nesting on cliffs, islands, and in trees. Only rarely is it seen at sea out of sight of land. This species occurs throughout much of North America, with northern freshwater populations migrating to ice-free coastal marine and estuarine habitats outside the breeding season. Cormorants often are seen in small groups and occasionally in flocks of thousands around inlets and other areas where fish concentrate. This cormorant forages by diving from the water surface and swimming underwater to catch prey, propelled by its webbed feet. There are three subspecies in the WNA; the most widespread Florida race (*P. a. floridanus*) nests from the Carolinas south into the Northern Bahamas and

Cuba. Lee (2007) provides a total WNA population estimate of about 55,000 pairs, based primarily on surveys from the 1980s, however the population has been growing. The Kushlan et al. (2002) estimate for North America is 370,000 breeder pairs.

The magnificent frigatebird, Fregata magnificens, is primarily a tropical species of both the Alantic and Pacific oceans. Nesting is mainly in the West Indies region, but also in the Marquesas and Dry Tortugas (off the Florida Keys), off Brazil, and in the Cape Verde Islands. Birds spend much of their time soaring over waters of the Caribbean and the Bahamas and off the southern and eastern coast of Florida, occasionally wandering north along the Atlantic coast to the Carolinas. This is a large, graceful, highly aerial seabird with long, forked tail streamers. It feeds in nearshore waters, snatching food from the water surface while in flight and pirating food from other seabirds. It can neither walk nor swim. Frigate birds cannot land on water and resume flight. Lee's (in prep.) population estimate for the North Atlantic region is 9,900-10,700 pairs.

Wading Birds

Wading birds form a major portion of the avifauna of coastal wetlands and estuaries, serving the important role of higher trophic level consumers. Wading birds are prominent members of estuarine ecosystems, notable for their graceful flight, beautiful plumage, stately appearance on the water, and interesting feeding behavior, which differs in detail from species to species. From the Outerbanks to Florida Bay and the Florida Keys, wading birds are characteristic wetland species. They form nesting colonies in both inland and coastal wetlands of the southeastern seaboard states and other places. The largest colonies may once have been in south Florida, but this has changed over time, following the drainage of large parts of the Everglades. Substantial population declines are thought to have occurred but are generally not well documented. Loss and degradation of wetland habitat are thought to be a major factor for declines.

Found coastally and in our region, there are many species of wading birds, which can be simply thought of as organized taxonomically into three main groups: the herons and egrets, the ibis and spoonbills, and the wood stork. Best-known species in this group that nest and/or forage in coastal wetlands are the great blue heron, great white Heron, common egret, snowy egret, little blue heron, white ibis, glossy ibis, roseate spoonbill, and wood stork. The great white heron occurs primarily in south Florida (i.e., mainly the southern Everglades, Florida Bay, and the Florida Keys), and not in the other southeastern states, but appears genetically to be a color morph of the great blue heron, whose range extends into Canada. . Most wading birds nest in colonies and forage within a multi-mile radius of their nesting sites. Some, such as the white ibis, feed in salt marshes but depend on freshwater wetlands for crustacean prey to raise young. Expanding and contracting water areas and consistent dry-downs to concentrate prey are important to the nesting success of some, especially the wood stork. Several wading birds are listed as of special conservation concern (Table 4.3-3). The wood stork is a Federally listed endangered species. Populations in south Florida have declined substantially since the 1960s, although new colonies have formed further north to other southeastern states. The new colonies all are small by comparison to the colonies that once existed in south Florida. Another species needing special mention is the reddish egret, which has recently raised concern because of limited known nesting sites and population numbers that are thought to be very low Great blue herons in the Chesapeake Bay utilize pound nets to forage for small fish. One study found half of the foraging flights from a colony were to pound nets.

Marsh Birds

Birds that live among the reed beds, lakes, ponds, and mudflats of the coastal wetlands form another group of Atlantic coast birds defined by habitat. In particular, these include, the American coot, the pied-billed grebe, the American woodcock, the limpkin, the Wilson's snipe, the purple gallinule, the American and least bitterns, several species of rails, and several species of sparrows—all listed in Table 4.3-3. Some, e.g., the limpkin, which feeds on apple snails, will be found primarily in freshwater areas of the coastal wetlands. Four sparrow species are listed as priority species for conservation by SAMBI, and three are of special concern in Georgia. South Carolina and Florida lists of species of conservation concern contain most of the other species. The limpkin is a species of special concern in Florida.

Abundance and status of stocks

(from Atlantic Croaker FMP Update 2005)

The population status and trend data on many species of seabirds are limited especially for small portions of the coast such as the mid-Atlantic. Of the species likely to interact with the croaker fishery the status of the red-throated loon is the least known, but it thought to be declining in the Pacific and probably on the East Coast. The common loon is listed by the Fish and Wildlife Service as a species of concern. Common loons breed on lakes where they face a number of hazards including mercury and lead poisoning, poaching, disturbance, loss of habitat and gillnet fishing. In their migration, molting, and wintering habitat along coastal Atlantic waters the major threat to both loons is from gillnets and oil spills. Northern gannets, brown pelicans, and double-crested cormorants have increasing populations. Of the ducks likely to interact with the fishery, the redbreasted merganser, bufflehead, common goldeneye, ruddy duck, and hooded merganser have populations that are increasing or stable, while the black, surf, and white winged scoters, long-tailed duck, and greater and lesser scaup have populations that are declining or thought to be declining.

4.3.4 Marine Fish

4.3.4.1 Smalltooth sawfish

Description and distribution

The smalltooth sawfish is a tropical marine and estuarine elasmobranch (sharks, skates, and rays) that have a circumtropical distribution. In the western Atlantic Ocean, the smalltooth sawfish has been reported from Brazil through the Caribbean Sea and, the Gulf of Mexico, and the Atlantic coast of the United States (Bigelow and Schroeder, 1953). Historic capture records within the U.S. range from Texas to New York. Water temperatures no lower than 16-18 °C and the availability of appropriate coastal habitat appear to serve as the major environmental constraints limiting the northern movements of smalltooth sawfish in the western North Atlantic Ocean. As a result, most records of this species from areas north of Florida occur during spring and summer periods (May to August) when inshore waters reach warmer temperatures. These larger individuals (> 3.0 m) captured along the Atlantic coast north of Florida represent seasonal migrants from a core population in southern states rather than being members of a continuous, uniform-density population (Bigelow and Schroeder, 1953). It is likely that these individuals migrated southward toward Florida as water temperatures declined in the fall, as there is only one winter record from the Atlantic coast north of Florida.

Reproduction

Fertilization in smalltooth sawfish is internal. Development in sawfish is believed to be ovoviviparous. The embryos of smalltooth sawfish, while still bearing the large yolk sac, already resemble adults relative to the position of their fins and absence of the lower caudal lobe. During embryonic development the rostral blade is soft and flexible. The rostral teeth are also encapsulated or enclosed in a sheath until birth. Shortly after birth, the teeth become exposed and attain their full size proportionate to the size of the saw. The size at birth is approximately 80 cm, with the smallest free-living specimens reported during field studies in Florida being 77 - 84 cm (Simpfendorfer, unpublished data). Bigelow and Schroeder (1953) reported gravid females carry 15-20 embryos. Simpfendorfer (2000) estimated age at maturity between 10 and 20 years. Studies of largetooth sawfish in Lake Nicaragua (Thorson 1976) report brood sizes of 1-13 individuals, with a mean of 7.3 individuals. The gestation period for largetooth sawfish is approximately 5 months and females likely produce litters every second year. Although there are no such studies on smalltooth sawfish, its similarity in size and habitat to the largetooth sawfish implies that their reproductive biology may be similar.

Development, growth and movement patterns

To date, no formal studies on the age and growth of wild smalltooth sawfish have been conducted. Individuals have been maintained in public aquaria for up to 20 years (Cerkleski, pers. comm., 2000) which can provide some information on growth. For example, Bohoroquez (2001) reported three specimens in Columbia grew at an average rate of 19.6 cm/year (one animal grew from 84 cm to 320 cm in 12 years). In a more comprehensive study, Clark et al. (2004) reported an average growth rate of 13.9 cm/year for16 captive smalltooth sawfish (size from 80 cm to 412 cm) in North American. Based on their growth parameters Clark et al. (2004) estimated an age at maturity of 19 yr for males and 33 yr for females while Simpfendorfer (2000) estimated age at maturity between 10 and 20 years, and a maximum age of 30 to 60 yr.

Sawfish in general inhabit the shallow coastal waters but recent data suggests adults can be found to much greater depths. Simpfendorfer and Wiley (2005) reported close associations between encounters and mangroves, seagrasses, and the shoreline than expected at random. Encounter data have also demonstrated that smaller smalltooth sawfish occur in shallower water and larger sawfish occur regularly at depths greater than 10 meters. Poulakis and Seitz (2004) reported that almost half of all sawfish < 3 meters in length were found in water less than 10 meters deep and 46% of encounters with adult sawfish (> 3 meters) in Florida bay and the Florida Keys occurred at depths between 70 to 122 meters. Simpfendorfer and Wiley (2005) also reported a substantial number of larger sawfish in depths greater than 10 meters. Encounter data bases have also identified river mouths as areas where many people observe sawfish. Seitz and Poulakis (2002) noted that many of the encounters occurred at or near river mouths in southwest Florida. Simpfendorfer and Wiley (2005) reported a similar pattern of distribution along the entire west coast of Florida. It is unclear whether this observation represents a preference for river mouths because of physical characteristics. Acoustic tracking results for very small smalltooth sawfish indicate depth and red mangrove root systems are potentially important in helping them avoid predators (Simpfendorfer 2003). Small juveniles have many of the same habitat use characteristics seen in the very small sawfish. However, their association with very shallow water (< 1 ft deep) is weaker, possibly because they are better suited to predator avoidance due to their larger size and greater experience. They do, however, still have a preference for shallow water, remaining in depths mostly less than three feet (90 cm). Information on the habitat use of adult smalltooth sawfish suggests that adult sawfish occur from shallow coastal waters to deeper shelf waters.

Abundance and status of stocks

There are few long-term abundance data sets that include smalltooth sawfish. Catch data from shrimp trawlers off Louisiana from the late 1940's to the 1970's suggests a rapid decline in the species from the period 1950-1964. However, this data set has not been validated nor subjected to statistical analysis to correct for factors unrelated to abundance. The Everglades National Park has established a fisheries monitoring program based on sport fisher dock-side interviews since 1972 (Schmidt et al. 2000). Analysis of these data using a lognormal generalized linear model to correct for factors unrelated to abundance (e.g., change in fishing practices) indicate a slight increasing trend in abundance for smalltooth sawfish in the park (Carlson et al. 2007). From 1989-2002, smalltooth sawfish relative abundance has increased by about 5% per year.

Using a demographic approach and life history data for smalltooth sawfish and similar species from the literature, Simpfendorfer (2000) estimated intrinsic rates of natural population increase as 8-13% per year and population doubling times from 5.4 years to 8.5 years. Musick (1999) and Musick et al. (2000) noted that intrinsic rates of increase less than ten percent were low, and are particularly vulnerable to excessive mortalities and rapid population declines, after which recovery may take decades. As such, smalltooth sawfish populations will recover slowly from depletion, confounding recovery efforts. Simpfendorfer (2000) concluded that recovery was likely to take decades or longer depending on how effectively sawfish could be protected.

Ecological relationships

Unknown.

Listing Designations

The National Marine Fisheries Service (NMFS) added the smalltooth sawfish to its list of candidate species in 1991 (56 FR 26797). Smalltooth sawfish were removed from the list in 1997 (62 FR 37561), but returned on a revised list published June 23, 1999 (64 FR 33466). On November 30, 1999, NMFS received a petition from the Center for Marine Conservation requesting listing of the North American population of smalltooth sawfish as endangered under the Endangered Species Act. Subsequently, NMFS announced the initiation of a smalltooth sawfish formal status review (65 FR 12959) and published a proposed rule (66 FR 19414) to list the U.S. population of smalltooth sawfish as endangered under the Endangered Species Act. On April 1, 2003, NMFS listed the U.S. population of smalltooth sawfish as an endangered species (50 CFR 224). A recent proposal by the United States of America to list all sawfish under Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora banning international trade was approved. The convention made an exception for one species of sawfish, listing them on Appendix II, allowing Australia to continue trade in live animals if it does not hinder the conservation of the species.

4.3.4.2 Shortnose sturgeon

Description and Distribution

The shortnose sturgeon (*Acipenser brevirostrum*) is a federally-listed endangered species, for which a Recovery Plan has been prepared (NMFS 1998). The species occurs in South Atlantic rivers, and on occasion in marine waters. There are apparently no documented records from the EEZ in the South Atlantic (Mark Collins, SC Department of Natural Resources, personal communication to R.W. Laney); however, the species is included here since the Council also must consider the impacts of its plans on federally listed protected species. It is an anadromous species which historically, with the Atlantic sturgeon, formed the basis for a valuable commercial fishery. Information in this account is taken largely from the December 1998 Final Recovery Plan for the species (NMFS 1998), with supplementation from other sources as cited.

The shortnose sturgeon occurs in large coastal rivers of eastern North America, historically from the St. John River in New Brunswick, Canada to the Indian River, Florida (NMFS 1998). NMFS currently recognizes 19 distinct population segments of shortnose sturgeon inhabiting 25 river systems ranging from the Saint John River in New Brunswick, Canada, to the St. Johns River, Florida. Genetic analysis of 11 of these population segments indicate most rivers and estuaries currently harboring shortnose sturgeon and identified as population segments in the NMFS 1998 Recovery Plan contain genetically distinct populations. Of the 11 population segments tested, at least 9 genetically distinct population segments of shortnose sturgeon were identified. Most comparisons among collections in the southeast showed significant genetic discontinuities between adjoining rivers, despite geographic proximity of their river mouths (20-100 km) (Wirgin et al. 2006).

Shortnose sturgeon historically occurred in most rivers of the four South Atlantic states from the Albemarle Sound system in NC through the Indian River system in FL. One relatively recent capture (1998) of a shortnose sturgeon in the Albemarle Sound system has been documented (Wayne Starnes, North Carolina Museum of Natural Sciences, personal communication). There have been no recent documented captures in the Pamlico Sound and its tributaries (Tar, Neuse Rivers). However, there are two recent reports of sturgeon from the Pamlico Sound identified by commercial fishery observers that were allegedly shortnose, but no photographs or tissue were taken for confirmation by professional fishery biologists or geneticists (Wilson Laney, USFWS, personal communication). There is currently a small population of shortnose in the Cape Fear River, North Carolina. At least one population presently exists in the Winyah Bay system (Waccamaw, Pee Dee and Black Rivers), as well as the Santee River, the Cooper River, the ACE Basin (Ashepoo, Combahee and Edisto Rivers) and the Savannah River. Georgia populations occur in the Savannah, Ogeechee, Altamaha, St. Marys and Satilla Rivers. Florida has shortnose presently only in the St. Johns River.

The shortnose is a small species of sturgeon, reaching maturity at fork lengths of 45-50 cm (18-20 in) and maximum size of approximately 120 cm (47 in) (Dadswell et al. 1984). It differs from juvenile Atlantic sturgeon in having a shorter nose, wider mouth, and no enlarged bony plates between the base of the anal fin and the lateral row of scutes (Gilbert 1989). Shortnose sturgeon are found in rivers, estuaries and the sea, but populations spend most of their time in their natal rivers and estuaries (NMFS 1998). In the southeast, the species is estuarine anadromous (i.e., spends most of the year in estuaries and ascends the freshwater portions of rivers to spawn in the spring). Adults in rivers in the south Atlantic forage at the interface of fresh tidal water and saline estuaries and migrate to the upper reaches of rivers to spawn during early spring (Savannah River: Hall et al. 1991; Altamaha River: Heidt and Gilbert 1979; Flouronoy et al. 1992, Rogers and Weber 1995a; Ogeechee River: Weber 1996).

Reproduction

Length and age at maturity

Length at maturity (45-55 cm FL) is similar throughout the shortnose sturgeon's range, but because fish in southern rivers grow faster than those in northern rivers, southern fish mature at younger ages. Males spawn first at 2-3 years in Georgia and 3-5 years in South Carolina, whereas females first spawn at 6 years or less in the Savannah River (Dadswell et al. 1984). Most shortnose sturgeon probably survive spawning, although there is some post-spawning mortality (B. Kynard, United States Geological Survey, personal observation).

Spawning periodicity

Spawning periodicity is poorly understood, but males seem to spawn more frequently than females. At least some males and females in the Savannah River may spawn in consecutive years, but most apparently do not (Collins and Smith 1993). Males may spawn every 1-2 years, but the minimum duration between spawning events for females is generally 3 years (Dadswell 1979, Cooke et al. 2002).

Fecundity and sex ratio

Gonadal maturity and fecundity of females were characterized by Dadswell (1979) for the Saint John River, Canada. Just prior to spawning, egg diameter was 3.1 mm and the ovaries composed 25 percent of the body weight. The number of eggs released ranged from 27,000 to 208,000 (11,568 eggs/kg body weight). Males were most abundant in the sex ratio estimate for the Savannah River (3.5:1, Collins and Smith 1997).

Spawning behavior

The shortnose sturgeon spawning period is estimated to last from a few days to multiple weeks. Sturgeon in the Savannah River remained on the spawning grounds for 2-3 weeks (Hall et al. 1991). Altamaha River fish remained on suspected spawning grounds for as long as nine weeks (Rogers and Weber 1995a). Cooper River fish residenced the spawning site for 89 days, longer than reports from other populations. It is hypothesized that these individuals were actively searching for an upstream route past Pinopolis Dam, but to no avail (Cooke and Leach, 2004a). Males fertilize the female's eggs as the eggs are released close to the substrate. In captivity, males nuzzle the anal and head areas of females, suggesting that females attract males with a chemical attractant (B. Kynard, personal observation).

Spawning habitat

In populations that have free access to the total length of a river, (e.g., no dam within the species' range in the river) spawning areas are located at the most upstream reach of the river used by sturgeon (Saint John, Kennebec, and Altamaha rivers: Dadswell et al. 1984, Rogers and Weber 1995a; Savannah River: Hall et al. 1991). Characteristic channel spawning habitats vary slightly among rivers: in curves with gravel/sand/log substrate in the Savannah River (Hall et al. 1991) and areas near limestone bluffs with gravel to boulder substrate in the Altamaha River (Rogers and Weber 1995a).

Timing of spawning and river conditions

Spawning begins in freshwater from late winter/early spring in southern rivers when water temperatures increase to 8-9°C. Spawning usually ceases when water temperatures reach 12-15° C (Dadswell et al. 1984; Buckley and Kynard 1985b; Hall et al. 1991; O'Herron et al 1993; Squiers et al. 1993; Kynard 1997). However, shortnose sturgeon may spawn at higher temperatures. For example, when high river flow conditions delayed spawning in the Connecticut River, shortnose sturgeon had the physiological flexibility to spawn successfully at 18° C (Kynard 1997). Spawning was detected from 11.5-19°C in the Cooper River, SC (Cooke and Leach, 2004a). In general, spawning occurs earlier in the year in southern rivers and at moderate river discharge levels (relative to northern rivers). For example, spawning occurs in early-February to mid-March in the Savannah River (Hall et al. 1991) and has been documented in late February to late March in the Cooper River (Cooke and Leach, 2004a). Shortnose spawning generally occurs earlier and at lower temperatures than Atlantic sturgeon. Dadswell et al. (1984) report that most shortnose spawn between 9 and 12°C.

Physical factors affecting spawning success

As observed in the Connecticut River, high river flows during the normal spawning period can cause unacceptably fast bottom water velocities and prevent females from spawning (Buckley and Kynard 1985b; Kynard 1997). Buckley and Kynard (1985b) speculated that the reproductive rhythm of females may be under endogenous control and suitable river conditions must be available or endogenous factors prevent females from spawning. Thus, reproductive success depends on suitable river conditions during the spawning season.

Development, growth and movement patterns

Habitat and Environmental Requirements

Shortnose sturgeon in the South Atlantic portion of the range require the use of large coastal rivers from the estuarine portions to upstream spawning areas. Habitat and environmental requirements of shortnose sturgeon are reviewed in Gilbert (1989). Shortnose require large rivers unobstructed by dams, or in which the dams are above their preferred spawning areas, or at which fish passage has been provided. Shortnose are apparently able to maintain completely freshwater populations, such as in the Santee-Cooper system (Collins et al. 2003). Preferred temperature ranges and upper and lower lethal temperatures for shortnose are not currently known. Shortnose sturgeon are seldom found in shallow water where water temperatures exceed 22°C; however, in the Altamaha they were found at temperatures as high as 34°C. Temperatures at wintering sites ranged from 5-10°C in Winyah Bay.

Shortnose sturgeon prefer waters of lower salinity than Atlantic sturgeon. The maximum salinity at which shortnose were found is 30-31 ppt, slightly less than sea water. In areas where shortnose sturgeon and Atlantic sturgeon co-occur, shortnose are typically found in waters less than 3 ppt. Adult sturgeon are typically found in areas with little or no current throughout their lives, especially when they are present in the lower portions of rivers and in the estuaries. Shortnose have been reported from shallower waters in the summer (2-10 m; 6.5-33 ft) and deeper water in the winter (10-30 m; 33-99 ft). They have been observed feeding in heavily vegetated, muddy backwater areas; however, in general submerged aquatic vegetation does not appear to be an important factor in their life history.

Early life stages

At hatching, shortnose sturgeon larvae are blackish-colored, 7-11 mm (0.3-0.4 in) long and resemble tadpoles (Dadswell et al. 1984). Larvae have a large yolk-sac, poorly developed eyes, mouth and fins, and are capable of only limited swimming. In laboratory experiments, 1 to 8-day–old shortnose sturgeon were photonegative, actively sought cover under any available material, and swam along the bottom until cover was found (Richmond and Kynard 1995). It is likely that they hide under available cover at spawning sites. The yolk-sac is absorbed in 9-12 days, and larvae resemble miniature adults by about 20 mm (0.8 in) in length. They likely begin swimming downstream at this size. Larvae collected in the wild were in the deepest waters of the channel. Laboratory studies suggest that there is a two-stage downstream migration: a 2-day migration by larvae, followed by a residency period of young-of-the-year fish, then a resumption of migration by yearlings the second summer of life.

Juveniles

Juveniles occur in or at the saltwater/freshwater interface in most rivers (Savannah: Hall et al. 1991; Altamaha: Flournoy et al. 1992; Ogeechee River: Weber 1996). Juveniles in the Ogeechee River moved into more saline areas (0-16 ppt) and were most active when water temperature dropped below 16°C (Weber 1996). In the Savannah River, juveniles use sand/mud substrate in depths of 10-14 m (33-46 ft) (Hall et al. 1991). Warm summer temperatures above 28 degrees F may severely limit available juvenile nursery habitat in some southern rivers. Summering habitat in the Altamaha River was limited mainly to one cool, deepwater refuge (Flournoy et al. 1992). Likewise, a similar distribution was observed in the Ogeechee River (Rogers and Weber 1994; Rogers and Weber 1995b, Weber 1996).

Adults

Adults that occur in freshwater or tidal fresh reaches of rivers in summer and winter often occupy only a few short reaches of the total river length (Savannah River: Hall et al. 1991; Altamaha River: Flouronoy et al. 1992). In the Connecticut and Merrimack Rivers, the “concentration areas” used by fish were reaches where natural or artificial features cause a decrease in river flow, possibly creating suitable substrate conditions for freshwater mussels (Keiffer and Kynard 1993), a major prey item for adult sturgeon (Dadswell et al. 1984). Summer concentration areas in southern rivers are cool, deep, thermal refugia, where adults and juveniles congregate (Flouronoy et al. 1992; Rogers and Weber 1994; Rogers and Weber 1995b; Weber 1996).

Growth

Growth of juvenile shortnose sturgeon is fast throughout the species’ range (Dadswell et al. 1984). YOY are 14-30 cm TL after the first year. Fish reach 50 cm after only 2-4 years in the southern part of the range. Fish grow faster in the South, but do not attain the large sizes of northern fish (Dadswell et al. 1984).

Survival and Recruitment

There is no information on survival of eggs or early life stages in the wild. Many eggs reared in captivity die of fungus infections (Dadswell et al. 1984). Richmond and Kynard (1995) maintain that the availability of spawning substrate with crevices is critical to survival of eggs and embryos. Year class strength of shortnose sturgeon populations is probably established early in life, perhaps in the initial few weeks. Although there is no commercial fishery for shortnose sturgeon (and thus, no fisheries recruitment information), some fisheries incidentally catch adult sturgeon and poaching impacts all populations to an unknown degree.

Incidental capture of shortnose sturgeon also occurs in gill net fisheries in the southern portion of the shortnose sturgeon's range. Gill net fisheries for American shad (Alosa sapidissima) and trawl fisheries for shrimp (Penaeus spp.) in Georgia and South Carolina captured about 2% of a tagged sample of shortnose sturgeon (Collins et al. 1996). The gill net fishery was responsible for 83% of the total shortnose sturgeon captures. Moser and Ross (1993) reported that 4 of 7 telemetered adult sturgeon in the Cape Fear River were captured in the gill net fishery for American shad or striped bass (Morone saxatilis). In addition, apprehension of poachers operating in South Carolina indicates that illegal directed take of shortnose sturgeon in southern rivers may be a significant source of mortality (D. Cooke, personal communication).

Natural mortality

Estimates of total instantaneous mortality rates (Z) are available for several river systems, albeit mainly northern populations. Total mortality for the Pee Dee-Winyah River in South Carolina was estimated at 0.08 to 0.12 (Dadswell et al. 1984). This estimate and the estimates for the other populations were based on catch curves which were adjusted for gill net selectivity and effort.

Annual egg production

Annual egg production is determined by the fecundity of females and the number of spawning females. Estimates of egg production from the Saint John River indicated mean fecundity per female was 94,000 eggs (Dadswell 1979). Monitoring of spawner abundance in the Connecticut River indicated that abundance varies greatly from year to year (Kieffer and Kynard unpublished data). Smith et al. (1992) also suggested that spawner abundance in the Savannah River can fluctuate greatly from year to year. This information indicates that the number of eggs spawned annually varies greatly (possibly by several magnitudes) over the species' range and complicates estimation of annual egg production.

Migration and Movements

Movement patterns in shortnose sturgeon vary with fish size and home river location. Juvenile shortnose sturgeon generally move upstream in spring and summer and move back downstream in fall and winter; however, these movements usually occur in the region above the saltwater/freshwater interface (Dadswell et al. 1984; Hall et al. 1991). Adult shortnose sturgeon are generally estuarine anadromous in southern rivers (Keiffer and Kynard 1993).

Spawning migrations are apparently triggered when water temperatures warm above 8°C (Dadswell et al. 1984). Consequently, spring spawning migrations occur earlier in southern systems than in northern ones: January-March (Altamaha River: Gilbert and Heidt 1979, Rogers and Weber 1995a; Savannah River: Hall et al. 1991; Pee-Dee/Waccamaw Rivers: Dadswell et al. 1984; Cape Fear River: Moser and Ross 1993). In the Altamaha River, Rogers and Weber (1995a) also documented upstream movement of most adults to suspected spawning grounds in autumn (late November-early December). A second spawning migration occurred in that system during mid-winter (late January-early February).

A shortnose sturgeon spawning migration is characterized by rapid, directed and often extensive upstream movement. Hall et al. (1991) tracked adults during pre-spawning upstream migrations of up to 200 km in the Savannah River and Dadswell et al. (1984) noted that a migration of 193 km occurred in the Altamaha River. Telemetry studies have documented maximum ground speeds of 20-33 km d-1, although mean ground speeds during riverine spawning migrations were around 16 km d-1 (Buckley and Kynard 1985a; Hall et al. 1991; Moser and Ross 1993). Both Hall et al. (1991) and Moser and Ross (1993) observed that spawning migrations are easily interrupted by capture and handling or by dams. Non-spawning movements include rapid, directed post-spawning movements to downstream feeding areas in spring and localized, wandering movements in summer and winter (Dadswell et al. 1984; Buckley and Kynard 1985a; O'Herron et al. 1993). Shortnose sturgeon usually leave the spawning grounds soon after spawning. Keiffer and Kynard (1993) reported that post-spawning migrations were correlated with increasing spring water temperature and river discharge. Post-spawning migration rates range from 3.5-36 km d-1 (Buckley and Kynard 1985a; Hall et al. 1991; Kieffer and Kynard 1993). During these movements shortnose sturgeon apparently move singly and "home" to very specific sites (Dadswell et al. 1984; Kieffer and Kynard 1993; Savoy and Shake 1992).

Continuous tracking of shortnose sturgeon provides detailed information on their migratory behavior. Moser and Ross (1994) demonstrated that, in the Cape Fear River estuary, upstream spawning migration in saltwater was slower (10 km d-1) than migration in freshwater (15 km d-1). This was due to the saltatory nature of movement in the estuary and faster swimming (0.8 body lengths (BL) s-1) in freshwater than in the estuary (0.6 BL s-1). Estimated swimming speed during summer, 0.07-0.37 BL s-1, is considerably slower than during spawning migrations (McCleave et al. 1977), while shortnose sturgeon are even less active in winter (Seibel 1993). Moser and Ross (1994) and McCleave et al. (1977) estimated swimming speed to be greatest when sturgeon oriented against rapid ebbing currents. Moser and Ross (1994) and McCleave et al. (1977) reported that shortnose sturgeon do not display any diel activity pattern, traveled in the upper part of the water column (within 2 m of the surface), and that their movement was apparently unaffected by temperature and salinity.

Abundance and status of stocks

As stated earlier, shortnose sturgeon historically occurred in most rivers of the four South Atlantic states from the Albemarle Sound system in NC through the Indian River system in FL. One relatively recent capture (1998) of a shortnose sturgeon in the Albemarle Sound system has been documented (Wayne Starnes, North Carolina Museum of Natural Sciences, personal communication). There have been no recent documented captures in the Pamlico Sound and its tributaries (Tar, Neuse Rivers). However, there are two recent reports of sturgeon from the Pamlico Sound identified by commercial fishery observers that were allegedly shortnose, but no photographs or tissue were taken for confirmation by professional fishery biologists or geneticists (Wilson Laney, USFWS, personal communication). There is currently a small population of shortnose in the Cape Fear River, North Carolina. At least one population presently exists in the Winyah Bay system (Waccamaw, Pee Dee and Black Rivers), as well as the Santee River, the Cooper River, the ACE Basin (Ashepoo, Combahee and Edisto Rivers) and the Savannah River. Georgia populations occur in the Savannah, Ogeechee, Altamaha, St. Marys and Satilla Rivers. Within the State of Florida, shortnose sturgeon are known only in the St. Johns River.

Total population estimates are not available for the Cape Fear, Winyah Bay, Santee, Cooper, ACE Basin, Savannah, Satilla, St. Marys and St. Johns Rivers. For the Ogeechee River, the total population estimate using Modified Schnabel methodology was 361 (95% CI= 326-400) in 1993 and 147 (95% CI= 104-249) in 2000 (Rogers and Weber 1994; Fleming et al. 2003). For the Altamaha River, the total population estimate using Modified Schnabel methodology was 2,862 (95% CI= 1,069-4,226) in 1988, 798 (95% CI= 645-1,045) in 1990, and 468 (95% CI= 316-903) in 1993 (Rogers unpublished data). A more recent study conducted in the Altamaha system from 2004-2006 resulted in a Schnabel population estimate of 6048 (95% CI= 4526-9110) (Peterson unpublished data).

Analysis of data for 1996, 1997, and 1998 resulted in estimates of 87 (95% CL 56-170), 193 (95% CL 123-319), and 301 (95% CL 150-659) adult fish, respectively residing in the Pinopolis Dam tailrace area during the spawning season (Cooke and Leach, 2004c). The population in the Cape Fear River is thought to be less than 50 fish (Moser and Ross 1995). Some of these population estimates should be viewed with caution as sampling biases may have violated the assumptions of the abundance models, effort may be limited therefore biasing data, or sampling periodicity may have been inadequate (NMFS 1998).

Albemarle Sound/Roanoke and Chowan Rivers

A historic record of a shortnose sturgeon in this area, confirmed by a museum specimen, was from Salmon Creek in the lower Chowan River, April, 1881 (USNM 64330, Vladykov and Greeley, 1963). More recently, an individual was caught in the north Batchelor Bay portion of Albemarle Sound (i.e., ca. mouth of Roanoke River) on 18 April 1998. It died in a net, was brought to the North Carolina Museum of Natural Sciences by Jim Armstrong of United States Fish and Wildlife Service, and is vouchered at the museum (NCSM 27062, Wayne Starnes, North Carolina Museum of Natural Sciences, personal communication). Additionally, an unconfirmed record from Oregon Inlet (Holland and Yelverton 1973) was also reported in Gruchy and Parker (1980), Dadswell et al. (1984), and Gilbert (1989).

Pamlico Sound/Pamlico and Neuse River

Yarrow (1877) reported that shortnose sturgeon were abundant in the North, New, and Neuse Rivers, but these records are doubtful due to their apparent basis in hearsay (Ross et al. 1988). Shortnose sturgeon were also reported from the Beaufort (Jordan 1886) and Neuse Rivers by Fowler (1945). Nearshore records of shortnose sturgeon in this area (Holland and Yelverton 1973) may be misidentifications (Ross et al. 1988). There are two recent reports of sturgeon from the Pamlico Sound identified by commercial fishery observers that were allegedly shortnose, but no photographs or tissue were taken for confirmation by professional fishery biologists or geneticists (Wilson Laney, USFWS, personal communication).

Cape Fear River

Since the first confirmed capture of shortnose sturgeon in the Cape Fear River (January 1987, Ross et al. 1988), an extensive sampling program has produced eight additional specimens (Moser and Ross 1993). All nine specimens captured were adults; no juveniles were collected. The river is dammed in the coastal plain, a short distance upstream of Wilmington, North Carolina. The river channel near the coast is channelized and heavy industries exist near the port. At least two additional records have been reported from fishermen (Fritz Rohde, North Carolina Division of Marine Fisheries, personal communication).

Winyah Bay Drainages

Shortnose sturgeon were documented in the Winyah Bay system during the late 1970's and early 1980's (Dadswell et al. 1984). Fed by the Waccamaw, Pee Dee, and Black Rivers, this coastal plain watershed produced over 100 collections of juveniles and adults during the study period. Within North Carolina, a vouchered specimen was collected from the North Carolina portion of the Pee Dee River in 1984 (Wayne Starnes, North Carolina Museum of Natural Sciences, personal communication), most likely the same individual that was collected below Blewett Falls Dam (Mark Collins, SCDNR-MRD, personal communication). In South Carolina, shortnose sturgeon have been located in the Waccamaw River, although it is possible that they were seasonal migrants from the Pee Dee River. Shortnose sturgeon from the Winyah Bay/Pee Dee River population are able to migrate upstream to the base of Lake Waccamaw (within North Carolina) if so inclined; however, there are currently no evidence/data to support the existence of a separate Waccamaw River shortnose sturgeon population. Shortnose sturgeon spawning has been verified in the Pee Dee River, South Carolina via egg collection (Mark Collins, SCDNR-MRD, personal communication).

Santee River

Seven shortnose sturgeon were recorded from the Santee River drainage in 1978, and one fish was captured in a gillnet in 1992 (Collins and Smith 1997). In addition, 20 specimens were recovered from a fishkill in the Lower Rediversion Canal, St. Stephen Dam tailrace that occurred during a low dissolved oxygen event below the dam. During the period from 1979-1991, shortnose sturgeon were also recorded from Lake Marion, and in the Congaree and Wateree rivers above the dam (Collins and Smith 1997). These fish may represent an essentially landlocked population (Collins et al. 2003). However, during a very high water year, 15 of 16 (94%) Cooper River adult transmittered shortnose sturgeon that were released in Lake Moultrie were able to exit the Santee-Cooper Lakes (Lakes) (1 possible mortality within the Lakes), primarily to the Santee River, although one individual appears to have exited through the lock at Pinopolis Dam on the Cooper River. At least 14 of the 15 (93%) shortnose sturgeon that exited the Lakes are thought to have survived downstream passage (Cooke and Leach 2004b, Cooke and Leach 2004d). Of the 13 shortnose sturgeon that successfully survived downstream passage specifically into the Santee River, all appear to have exited the Santee River system. Eight were relocated in the Winyah Bay system, two in the Cooper River, two in the Intracoastal Waterway, and one disappeared altogether. This behavior appears to be similar to four shortnose sturgeon that were implanted with transmitters in the Santee River. Albeit a small sample size, one was relocated in the Savannah River, the other seemed to disappear from the Santee River only to reappear approximately a year and a half later, and two disappeared altogether (Cooke and Leach 2004d).

Cooper River

Shortnose sturgeon were documented in what is now the metro Charleston area during the late 1800's (Jordan and Evermann 1896). Shortnose sturgeon were collected in this heavily altered (dammed and urbanized) drainage in the 1980's during research on the American shad (*Alosa sapidissima*) fishery. A functionally landlocked segment may exist in Lake Marion (Collins et al. 2003) above the dam that blocks the system in the lower coastal plain (Pinopolis Dam). However, during a very high water year, 15 of 16 (94%) Cooper River adult transmittered shortnose sturgeon that were released in Lake Moultrie were able to exit the Santee-Cooper Lakes (1 possible mortality within the Lakes), primarily to the Santee River, although one individual appears to have exited through the lock at Pinopolis Dam on the Cooper River. At least 14 of the 15 (93%) shortnose sturgeon that exited the Lakes are thought to have survived downstream passage (Cooke and Leach 2004b, Cooke and Leach 2004d). 14 of 15 (93%) Cooper River adult transmittered shortnose sturgeon that were placed in Pinopolis Lock did not pass upstream into the Santee-Cooper Lakes (Lakes), indicating that upstream passage in the Cooper River into the Lakes is extremely limited (Cooke and Leach 2004b). Below Pinopolis Dam, the lowermost dam on the Cooper River, eleven sturgeon were taken in gillnets in the tailrace in February 1995 (Collins et al. 1996). Cooke and Leach (1999) found that shortnose sturgeon congregate and spawn below Pinopolis Dam. Successful egg fertilization and development is occurring, but only one newly hatched yolk sac larva and no juveniles have been documented (Duncan et al. 2004).). Analysis of data for 1996, 1997, and 1998 resulted in estimates of 87 (95% CL 56-170), 193 (95% CL 123-319), and 301 (95% CL 150-659) adult fish, respectively residing in the Pinopolis Dam tailrace area during the spawning season (Cooke and Leach 2004c). Limited gillnet sampling in 2003 in the spawning area resulted in 8 of the 12 adults (67%) as recaptured fish from previous years (Cooke and Leach 2004a).

Ashepoo, Combahee and Edisto Rivers (The "ACE" Basin)

The Ashepoo, Combahee, and Edisto drainages form one of the most pristine coastal plain watersheds in the southeastern United States. Shortnose sturgeon were incidentally collected during American shad studies in the Ashepoo and Edisto Rivers in the 1970's and early 1980's (Collins and Smith 1997). Ripe adults, as well as YOY/age-1 fish, have been more recently collected by the South Carolina Department of Natural Resources-Marine Resources Division (SCDNR-MRD) from the Edisto River. It is possible that these are actually Savannah River fish that were stocked into the Savannah River and then strayed to colonize the Edisto River (Mark Collins, SCDNR-MRD, personal communication).

Savannah River

The Savannah River is a heavily industrialized and channelized drainage that forms the South Carolina/Georgia border. The river is dammed, but not below the fall line. Shortnose sturgeon were first documented in the system in the mid-1970's (Dadswell et al. 1984). During 1984-1992, over 600 adults were collected by shad fishermen and researchers using gillnets and trammel nets (Collins and Smith 1993). The ratio of adults to juveniles in this study was very high, indicating that recruitment is low in this river (Smith et al. 1992). Adult population estimates were calculated using Jolly Seber (96-1075) and Schnabel (1676) techniques, but were deemed unreliable as not all basic assumptions were met (M. Collins, South Carolina Department of Natural Resources, personal communication). During 1984-1992, approximately 97,000 shortnose sturgeon (19% tagged) of various sizes were stocked in the Savannah River to evaluate the potential for shortnose sturgeon stock enhancement (Smith and Jenkins 1991). Subsequent investigation showed that stocked fish were at large for an average of 416 days and comprised 41% of all juvenile sturgeon collected (Smith et al. 1995). It is thought that the Savannah River population and the Altamaha River population are the two largest populations in the Southeast (Wirgin et al. 2006).

Ogeechee River

The Ogeechee is primarily a coastal plain drainage with 5% of its watershed in the piedmont. The river is undammed, but water quality has changed (eutrophied) during the last 30 years (Weber 1996). Shortnose sturgeon were first documented in the system during the early 1970's (Dadswell et al. 1984). A survey of shortnose sturgeon occurrence, distribution, and abundance, including a 1994-1995 mark/recapture experiment, was conducted from 1993 to 1995 and then from 1999 to 2004 in the tidal portion of the drainage (Rogers and Weber 1994; Weber 1996). The size distribution of shortnose sturgeon sampled indicated that, as in the Cape Fear and Savannah Rivers, the Ogeechee population is dominated by adults. Mark/recapture analysis indicated that abundance is low and possibly declining in the Ogeechee system; the highest point estimate yielded less than 400 individuals from all age classes in 1993 (Weber 1996) and less than 200 individuals from all age classes in 2000 (Fleming et al. 2003). Size frequency, abundance, and catch rate data indicate that natural recruitment does occur in the Ogeechee River system but shortnose sturgeon may be experiencing higher juvenile mortality rates in this system than in the Altamaha (below), with evidence of total recruitment failure in some years. A portion of the shortnose sturgeon that were stocked in the Savannah system have migrated to the Ogeechee River and have contributed substantially to some year-classes in this system (Fleming et al. 2003). Coalescence-based migration estimates suggest that populations south of the Pee Dee River exchange between 1-9.8 individuals per generation, with the highest rate occurring between the Ogeechee and the Altamaha Rivers (Wirgin et al. 2005).

Altamaha River

The Altamaha River system drains the largest watershed east of the Mississippi River and comprises the confluence of the Ocmulgee and Oconee Rivers plus additional, smaller piedmont and coastal plain drainages. The system is moderately industrialized including two kraft process paper mills and a nuclear generating plant. The watershed landscape has been heavily altered by urbanization, suburban development, agriculture, and silviculture. The system is also dammed, but not below the fall line. Shortnose sturgeon were first documented in the Altamaha in the early 1970's (Dadswell et al. 1984), and, later, in a cursory study of spawning movements conducted in the late 1970's (Heidt and Gilbert 1979).

A two-year study of population structure and dynamics was conducted during the early 1990's (Flournoy et al. 1992), building on three additional years of survey data from the late 1980's (B. T-A.Woodward, Georgia Department of Natural Resources, unpublished data). Over 650 individuals were collected during the five years of study, with samples heavily dominated by juveniles (90%). Subsequent analysis of tag/recapture data indicated that, during the two-year study period in the 1990's, abundance did not exceed 6,055 individuals for all size and age classes. However, under the more rigorous constraints imposed by the assumptions of the recapture model and (probably) met under the conditions experienced during the summer of 1990, the point estimate is 798 individuals with a 95% confidence interval (CI) of 645-1,045 fish. The next time that those conditions were met (during the late summer of 1993), a similar 95% CI of 316-903 individuals was generated with a point estimate of 468 fish. An estimate generated from 1988 data, which met the same criteria, yielded 2,862 fish (95% CI 1,069-4,226). A more recent study conducted in the Altamaha system from 2004-2006 resulted in a Schnabel population estimate of 6048 (95% CI=4526-9110) (Peterson unpublished data). Based on these data, the Altamaha population segment is likely the largest and most viable one south of Cape Hatteras, NC (Joel Fleming, GDNR, personal communication). Similarly, Wirgin et al. (2006) suggested that the Savannah River population and the Altamaha River population are the two largest populations in the Southeast (Wirgin et al. 2006).

Satilla and St. Marys

The Satilla and St. Marys Rivers are relatively small coastal plain drainages emptying into the Atlantic Ocean between the Altamaha River, GA and St. Johns River, FL. There are no dams and few human impacts beyond agriculture and timber management along the Satilla system. The St. Marys system (draining the eastern portion of the Okefenokee Swamp and forming a portion of the GA/FL border) is likewise undammed, but is heavily channelized in its estuary to support a small port and military installation. The estuary also receives effluents from three major forest product plants. Collections of shortnose sturgeon were made in the estuaries of both systems during the late 1980's and early 1990's during crustacean monitoring (G. Rogers, Georgia Department of Natural Resources, personal communication). Surveys for sturgeon in the St. Marys (1994 and 1995, 117 net hours) and in the Satilla (1995, 74 net hours) failed to yield any shortnose sturgeon (Rogers and Weber 1995b).

St. Johns River

The St. Johns River in FL is a heavily altered system flowing northward from the east-central portion of the state and emptying into the Atlantic Ocean near Jacksonville, FL. The system is dammed by Rodman Dam in the headwaters (although currently scheduled for removal), heavily industrialized and channelized near the sea, and affected by urbanization, suburban development, agriculture, and silviculture throughout portions of the basin. Shortnose sturgeon have been reported from the system since 1949 (Kilby et al. 1959). Five shortnose sturgeon were collected in the St. Johns in the late 1970's (Dadswell et al. 1984) and, in 1981, three sturgeon were collected and released by the Florida Game and Freshwater Fish Commission. A shortnose sturgeon tagged in Georgia by Georgia Department of Natural Resources near St. Simons Island in March 1996 was captured from the St. Johns River in August 2000 (Jay Holder, FLFWC, personal communication).

Most recently, a shortnose sturgeon was collected by Florida Fish and Wildlife Commission personnel in 2002 on the south side of Federal Point near Palatka, Florida during a 2002-2003 study to determine presence/absence of shortnose sturgeon in the St. Johns River. This single shortnose sturgeon was collected in 4,493 hours of 100-m gillnet sets. Preliminary analysis by Joe Quattro at the University of South Carolina indicated that the sample was genetically similar to other shortnose sturgeon populations found in the southern United States (FLFWC 2005). Historically, few shortnose sturgeon in the St. John's River have been positively identified by biologists and commercial landings were relatively low compared to other southern states. However, there have been several verified incidental captures off the coast of Daytona Beach (Allan Brown, United States Fish and Wildlife Service, personal communication). No sturgeon reproduction has ever been documented in the St. Johns River and the spawning habitat that is currently accessible seems to be marginal (FLFWC 2005).

Ecological relationships

Feeding

Shortnose sturgeon are benthic omnivores but have also been observed feeding off plant surfaces (Dadswell et al. 1984). Based on the high incidence of non-food items in juvenile shortnose sturgeon, Dadswell et al. (1984) concluded that juveniles randomly vacuum the bottom while adults are more selective feeders. Dadswell (1979) determined that adult shortnose sturgeon in the Saint John River, Canada are not opportunists and only switch to other prey when preferred food are unavailable. The presence of food in the gut during all times of day indicated that shortnose sturgeon are continuous feeders (Dadswell 1979).

Shortnose sturgeon feed on crustaceans, insect larvae, worms, and mollusks; however, they apparently undergo ontogenetic shifts in preferred foods. Insect larvae (*Hexagenia* sp., *Chaoborus* sp., *Chironomous* sp.) and small crustaceans (*Gammarus* sp., *Asellus* sp., *Cyathura polita*) predominate in the diet of juveniles (Dadswell et al. 1984; Carlson and Simpson 1987) while adults feed primarily on small mollusks (Dadswell 1984; Hastings 1983). Molluscs ingested by adults captured in freshwater include *Physa* sp., *Heliosoma* sp., *Corbicula manilensis*, *Amnicola limnosa*, *Valvata* sp., *Pisidium* sp., and small *Elliptio complanata* (Dadswell et al. 1984). In saline areas molluscan prey include small *Mya arenaria*, and *Macoma balthica* (Dadswell 1979).

Probable foraging activity in southern rivers has been described at the saltwater/freshwater interface during fall and winter in the Pee Dee and Savannah rivers (Dadswell et al. 1984; Hall et al. 1991) and just downstream of the saltwater/freshwater interface in the Altamaha and Ogeechee rivers (Rogers and Weber 1995a; Weber 1996). During summer, shortnose sturgeon in these southern systems appear to reduce activity, fast, and lose weight (Dadswell et al. 1984; Rogers et al. 1994).

Predators, Parasites, and Diseases

There is very little documentation of predation on any life stage of shortnose sturgeon. Young-of-the-year shortnose sturgeon (approximately 5 cm FL) were found in the stomachs of yellow perch (*Perca flavescens*) in the Androscoggin River, Maine (Dadswell et al. 1984). It is likely that sharks and seals may occasionally prey on shortnose sturgeon based on the occasional specimen lacking a tail (Dadswell et al. 1984).

Parasites recorded from shortnose sturgeon (all data from northern populations) include Coelenterata (*Polypodium* sp.), Platyhelminthes (*Diclybothrium armatum*, *Spirochis* sp., *Nitzschia sturionis*), Nematoda (*Capillospirura pseudoargumentosus*), Acanthocephala (*Fessesentis friedi*, *Echinorhynchus attenuatus*), Hirudinea (*Calliobdella vivida*, *Piscicola milneri*, *Piscicola punctata*), Arthropoda (*Argulus alosa*), and Pisces (*Petromyzon marinus*). The degree of infestation has been reported as being quite low with the exception of

Capillospirura sp. (Dadswell et al. 1984). Sturgeon do not appear to be harmed by these parasites. There have been no reported incidences of disease for shortnose sturgeon in the wild, although an epizootic of *Columnaris* sp. occurred at the FWS' Orangeburg Hatchery in South Carolina (Willie Booker, FWS, South Carolina, personal communication).

Listing designations

4.3.5 Marine Plants

(material from the 2002 Recovery Team Status Review)

Description and distribution

Description

After many years of confusion over identification, Johnson's seagrass (*Halophila johnsonii*) was formally proposed as a separate species by Eiseman and McMillan (1980). *Halophila johnsonii* was previously referred to either as *H. decipiens* or *H. baillonis* Ascherson, but it most closely resembles *H. ovalis* (R. Brown) Hooker f., an Indo-Pacific species, both morphologically and genetically (McMillan and Williams 1980). Plant classification schemes based on anatomical (den Hartog 1970) and molecular phylogenetic (Les et al. 1997) methods both place the seagrass genus *Halophila* in the angiosperm family Hydrocharitaceae, along with two other seagrass genera, *Thalassia* and *Enhalus*. Morphologically, Johnson's seagrass is recognized by the presence of pairs of linearly shaped foliage leaves, each with a petiole formed on the node of a horizontally creeping rhizome (Figure 4.3-2)(NMFS 2001).

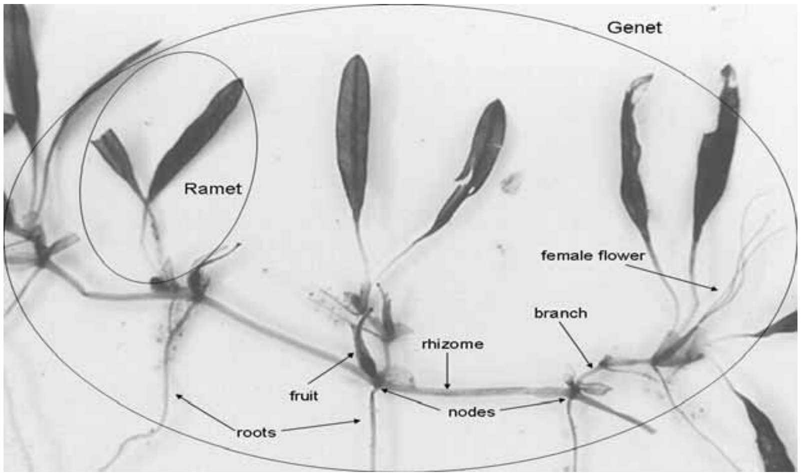
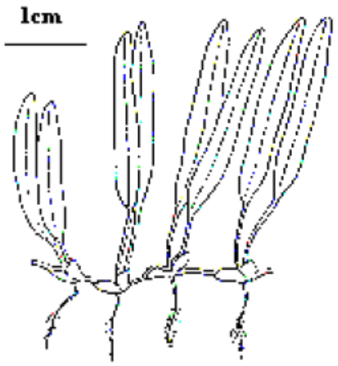
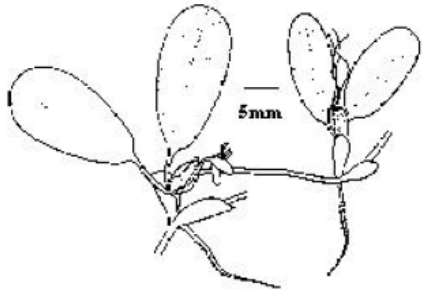


Figure 4.3-2. Photograph of *Halophila johnsonii* showing the genet and individual ramets, the rhizome, a female flower, fruit, nodes, and lateral branching of rhizome

The rhizome is located at or just below the sediment surface and is anchored to unconsolidated substrate by unbranched roots. The leaves are generally 2-5 cm long (including the petioles), and the rhizome internodes rarely exceed 3-5 cm in length, making this species appear diminutive relative to the larger seagrasses. *Halophila johnsonii* differs from *H. decipiens* in a number of morphological, reproductive, and genetic characteristics (Table 4.3-5). The diagnostic characteristics of *H. johnsonii* remain relatively unchanged when plants are cultured in artificial conditions; thus, differences between the two species are not due to phenoplasticity (NMFS 2001).

Table 4.3-5. Morphological, reproductive, and genetic characteristics of *H. johnsonii* and *H. decipiens*. Illustrations adapted from Phillips and Menez, 1988.

H. johnsonii	***H. decipiens***
Linear leaves with entire (smooth) margins.	Oblong-elliptical leaves with serrate margins.
No hairs on blade surface.	Unicellular prickle hairs on both surfaces (unique to *H. decipiens*).
Leaf cross veins diverge at ca. 45° angles.	Leaf cross veins at ca. 60° angles.
Only pistillate (female) flowers are known so it is possibly dioecious (male and female plants) or apomictic (produces seeds without pollination or meiosis so seeds are clones of female parent).	Monoecious (both sexes on one plant).
Populations of *H. johnsonii* collected in the Indian River Lagoon (IRL) differed from *H. decipiens* in five isozymes of the seven isozyme systems tested, with major differences in three of the enzymes (Jewett-Smith et al. 1997).	See box at left.
	

Distribution

Johnson's seagrass is found only in southeastern Florida from near Sebastian Inlet (27.85°, -80.45°) to Virginia Key (27.74°, -80.14°) (Figure 4.3-3). Recently, however, the St. Johns River Water Management District (SJRWMD) observed *H. johnsonii* 3 km north of the Sebastian River mouth on the western shore of the lagoon (27.88°, -80.50°) – a discovery that slightly extends the species known northern range. Where it does occur, its distribution is patchy, both spatially and temporally (Virnstein and Morris 2007).

Halophila johnsonii is a perennial species showing no consistent seasonal or year-to-year pattern in surveys of the Indian River Lagoon (IRL). Although perennial, it exhibited some winter decline. However, during exceptionally mild winters, as in the winter of 2004, *H. johnsonii* can maintain or even increase its abundance from summer to winter (Virnstein et al. 1997, Virnstein and Morris 2007).

Depth of occurrence ranged from 0.03 to 2.5 m within transects monitored in the IRL (Virnstein et al. 1997, Virnstein and Morris 2007). When data from all transects were combined, there was no correlation of *H. johnsonii* abundance with depth. However, the deep edge at some transects was only 0.1 m; at other transects, it was 2.5 m. When all depths of occurrence were standardized (as percent of maximum depth of a transect), *H. johnsonii* was more abundant in the deeper parts of the transects. Most (78% or 574 out of 733) occurrences of *H. johnsonii* were at >70% of maximum transect depth; half were at >90% of maximum depth (Virnstein et al. 1997, Virnstein and Morris 2007).

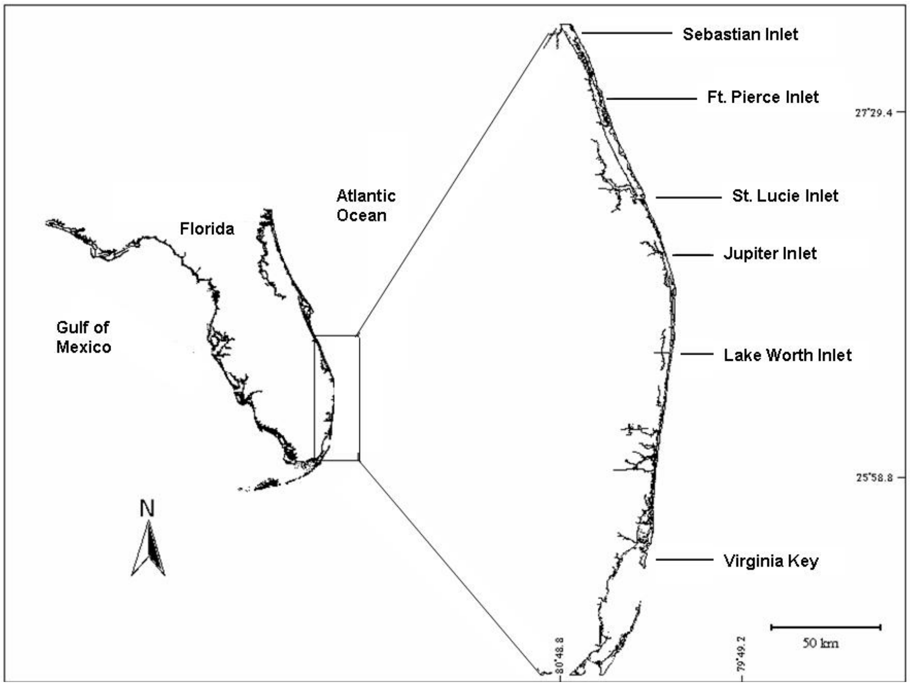


Figure 4.3-3. Geographic range of *Halophila johnsonii*: Sebastian Inlet to northern Virginia Key (Kenworthy 1997).

Observations of its distribution and the results of limited experimental work suggest that *H. johnsonii* has a wider tolerance range for salinity, temperature, and optical water quality conditions than *H. decipiens* (Dawes et al. 1989, Gallegos and Kenworthy 1996, Durako et al. 2003, Kunzelman et al. 2005, Torquemada et al. 2005). *Halophila johnsonii* has been observed growing perennially near the mouths of freshwater discharge canals (Gallegos and Kenworthy 1996), in deeper turbid waters of the interior portion of the Indian River Lagoon (Kenworthy

2000, Virnstein and Morris 2007), and in clear water associated with the high energy environments and flood deltas inside ocean inlets (Kenworthy 1993, 1997; Virnstein et al. 1997, Heidelbaugh et al. 2000, Virnstein and Morris 2007).

While *H. johnsonii* is negatively affected by both extreme hypo- and hyper-salinity conditions, it does tolerate hypersaline conditions better than hyposaline conditions. Most other seagrasses, conversely, are thought to be more sensitive to increased salinity (Ogata and Matsui 1965, Biebl and McRoy 1971, Zieman 1975, Adams and Bate 1994, Doering and Chamberlain 1998). Torquemada et al. (2005) and Dawes et al. (1989) concluded that *H. johnsonii* could be seriously affected by salinity variations produced by human activities, such as freshwater discharges through water management practices or brine discharges from seawater desalination plants. Interestingly, salinity changes do not seem to alter the tolerance of this species to other environmental factors, such as temperature or pH (Torquemada et al. 2005).

Reproduction

Like all other seagrasses, *H. johnsonii* is clonal, which refers to plants that have many semi-independent units (ramets) acting together as a single organism (Cook 1983). Reproduction is achieved primarily by asexual means. While all other species of seagrass reproduce sexually, there is still no evidence of sexual reproduction in *H. johnsonii*. All attempts to find seeds and seedlings have failed to detect any evidence of their occurrence (Jewitt-Smith et al. 1997, Hammerstom and Kenworthy 2003). Likewise, despite widespread sampling and surveys throughout the entire range of the species, no male flowers have ever been reported and confirmed. Female flowers, however, have been documented in both culture and nature (Eiseman and McMillan 1980, Heidelbaugh et al. 2000). They are common and often very abundant (Heidelbaugh et al. 2000). They have been observed throughout the entire range of the species during all times of the year, but no consistent patterns of spatial or temporal distribution have been observed or reported.

Although male flowers have never been observed, it is not possible to completely rule out their existence and the potential for sexual reproduction. They may occur cryptically in isolation or in the vicinity of females. They may be extremely rare, or they may express themselves only at night, as was the case in a related species, *Halophila hawaiiana* (Herbert 1986).

While sexual reproduction of *H. johnsonii* remains somewhat of a mystery, reproduction by asexual means and clonal growth is well understood. Asexual reproduction occurs when rhizome apical meristems divide and form new leaf pairs, flowers, or rhizome apices (Posluszny and Tomlinson 1990) (Figure 4.3-2). The divisions and subsequent differentiation of meristems (meristem dependence) into the various attributes of the ramets are the foundation of growth and productivity in all seagrasses (Tomlinson 1974). *Halophila johnsonii* grows by division of apical meristems on horizontal rhizomes which branch, forming leaf pairs, female flowers and new lateral branches (Figure 4.3-4). On average, new meristems are formed on rhizomes every 2 to 4 days (Kenworthy 1997, Bolen 1997) and meristem densities can reach hundreds to thousands per square meter (Kenworthy 1997, Heidelbaugh et al. 2000).

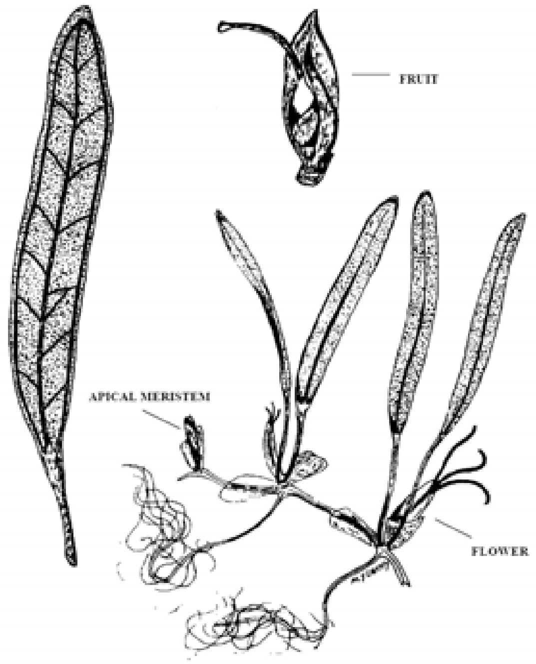


Figure 4.3-4. Johnson's seagrass, *Halophila johnsonii*. Leaves are generally 2-5 cm long. Adapted from Eiseman and McMillan (1980).

Development and growth

The species spreads as clones expand in local space by rhizome extension and leaf pair formation, eventually forming high density "patches." Rhizomes can elongate at rates approaching 0.5 cm per day (Bolen 1997, Kenworthy 1997), and when combined with prolific branching, individual patches (clones) can expand at extraordinary rates, ranging from 0.3 to 1.0 m-^{2} per month (Kenworthy 1997, 2003; Greening and Holland 2003). This expansion can lead to coalescence of adjacent patches and the formation of larger meadows. Widely spaced patches, usually on the order of 1-20 square meters in size, are the most commonly encountered feature of *H. johnsonii* meadows (Virnstein et al. 1997, Kenworthy 1997, 2000; Virnstein and Morris 2007; Kenworthy 2003). Although it is more commonly found in monotypic patches, *H. johnsonii* can also grow among low to moderate densities of *Halodule wrightii* and *Syringodium filiforme*, and in deeper water mixed with *H. decipiens* (Kenworthy 1993, 1997, 2000; Virnstein et al. 1997, Virnstein and Morris 2007).

Patches can also disappear rapidly. Sometimes they will disappear for several years and then re-establish: a process referred to as "pulsating patches" (Heidelbaugh et al. 2000, Virnstein and Morris 2007). Mortality, or the disappearance of patches, can be caused by a number of processes, including burial from bioturbation and sediment deposition, erosion, herbivory, desiccation, and turbidity. *Halophila johnsonii*'s canopy is only 2-5 cm tall and may be easily covered by sediments transported during storms or redistributed by macrofaunal bioturbation during the feeding activities of benthic organisms (Heidelbaugh et al. 2000).

In the absence of sexual reproduction, one possible explanation for the pulsating patches is dispersal and re-establishment of vegetative fragments, a process which commonly occurs in aquatic plants and has been demonstrated in other seagrasses (DiCarlo et al., 2005). While *H. johnsonii* is vulnerable to uprooting by wind waves, storm events, tidal currents, bioturbation, and motor vessels, these are also mechanisms capable of disturbing patches and creating clonal fragments for dispersal. Hall et al. (2006) showed that drifting fragments of *H. johnsonii* can remain viable for 4 to 8 days, after which time they can settle, root, and grow.

Ecological relationships

Seagrasses have recently received increasing attention from scientists and managers because of the valuable functional roles they play in coastal ecosystems (Costanza et al. 1997, Larkum et al. 2006). Seagrass beds are one of the primary nursery habitats because of their abundance of prey items as well as the protection they provide from predators (Zieman and Zieman 1989, Heck et al. 2003). Other functions associated with seagrasses include nutrient recycling, detrital production and export, and sediment stabilization. Very little work has been done on the functional value of *H. johnsonii*, therefore, the functional roles of its closest relative, *H. ovalis*, and other *Halophila* spp. are used a proxy in this discussion.

The most well-known function of seagrasses is their role as habitat for numerous fishes and invertebrates. Some species spend their entire lives within seagrass beds and others utilize it only during certain stages of their life cycle (usually the postlarval and juvenile stages). Heidelbaugh (1999) conducted one of the only studies that examined benthic fauna associated with *H. johnsonii*. In this study, differences in benthic fauna among *H. johnsonii*, *H. wrightii*, and bare sand were compared on the flood tidal delta just inside Sebastian Inlet, Fl. *Halophila johnsonii* beds yielded a total of 126 species (69 epifauna and 57 infauna), while 117 species were collected from *H. wrightii* beds and 99 species from bare sand. The most abundant infaunal organisms belonged to Nematoda while the most abundant epifaunal species were amphipods and tanaids. The majority of macrofaunal organisms consisted of decapod crustaceans (*Callinectes sapidus*), fishes (*Eucinostomus* sp.), and some gastropods (especially *Bursatella leachii*). Three hundred and twenty macrofaunal organisms were collected from *H. johnsonii* beds compared to 690 from *H. wrightii* beds and 78 from bare sand.

Rapid growth, high turnover rates, and labile tissues make *Halophila* spp. a good source of nutrition for several marine herbivores (Kenworthy et al. 1989, Lanyon 1991, Preen 1995, Bolen 1997). The Florida manatee (*Trichechus manatus latirostris*) has been observed grazing on *H. johnsonii* near a power plant in Palm Beach, Florida (J. Reid, Sirennia Project, U.S.G.S., Gainesville, FL, personal observation). Green turtles (*Chelonia mydas*) are known to eat several species of *Halophila* (Hasbun et al. 2000, Kannan and Rajagopalan 2004, Russell et al. 2003, Whiting and Miller 1998). *Halophila* species also provides nutrition for herbivorous fish. Through consumption, the stareye parrotfish (*Calotomus carolinus*) has the ability to control the abundance and distribution of short lived seagrass species such as *H. stipulacea* in Kenya (Mariani and Alcoverro 1999). Even invertebrates such as the queen conch (*Strombus gigas*) (Thayer et al. 1984) and various species of harpacticoid copepods (Shimode and Shirayama 2006) have been observed feeding on *Halophila* species.

Seagrasses play an important role in nutrient cycling within systems and can act as both a source and sink for nutrients. Processes that lead to a loss of nutrients from the system include: exudation/leaching from living and dead plant material, export of sloughed leaves and leaf fragments, nutrient transfer by foraging animals, denitrification, and diffusion from sediment. Processes that result in an increase of nutrients include: nitrogen-fixation, sedimentation, and nutrient uptake by leaves. It is the fluctuation of these processes that leads to interannual variations in net losses or net gains of nutrients, and therefore, fluctuations in the productivity of seagrass meadows (Hemminga et al., 1991).

Bacteria mediate the recycling of nutrients and may be important in regulating the flow of energy from seagrass detritus to consumer organisms (Robertson et al. 1982). Studies in the Salt River Submarine Canyon at St. Croix, US Virgin Islands show that *H. decipiens* is an important source of organic matter and detritus for the Canyon (Josselyn et al. 1983, Josselyn et al. 1986, Kenworthy et al. 1989). Despite its production being less than other seagrasses, *H. decipiens* has a fast turnover time and is a major source of primary production on the floor of the Canyon (Kenworthy et al. 1989). Disturbance and burial of plant material are important mechanisms influencing the disposition of organic matter (Williams et al. 1985, Josselyn et al. 1986). Burial of *H. decipiens* through wave action and animal activities increases the rate of detrital input and retains the detritus within the Canyon (Kenworthy et al. 1989).

Seagrasses have long been recognized for their ability to stabilize sediments. It was once assumed, however, that due to its small size and sparse biomass, *Halophila* spp. were not capable of stabilization (den Hartog 1970). Fonseca (1989) proved this assumption incorrect using a surface-supplied, inverted seawater flume. He found the cumulative effect of *H. decipiens* in reducing sediment erosion was significantly greater than adjacent, unvegetated sand.

Abundance and status

Johnson's seagrass has only relatively recently been identified as a distinct species (Eiseman and McMillan 1980) and no historical information on the species' distribution is available. However, since 1994, the St. Johns River Water Management District has monitored 73 permanent transects in the Indian River Lagoon (IRL) in both summer (June-July) and winter (January-February) (Virnstein et al. 1997, Virnstein and Morris 2007). Despite extensive ground-truthing since 1986 and monitoring all 73 transects throughout the IRL beginning in the summer of 1994 (a total of about 25,000 quadrats), *H. johnsonii* has never been found more than 3 km north of the Sebastian Inlet area. Where it does occur, its distribution is patchy, both spatially and temporally.

Halophila jonsonii is a perennial plant with no strong seasonal pattern, although it generally exhibits some winter decline. Monitoring in the IRL indicates that there is spatial and temporal variation in the abundance of *H. johnsonii* patches (Virnstein et al. 1997). Although the monitoring data are limited, no large distributional gaps have been detected in the IRL, and there has been no overall increase or decrease in abundance or geographic range over the period from summer 1994 to summer 1999.

Halophila. johnsonii was listed as threatened under the Endangered Species Act on September 14, 1998 (63 FR 49035). NMFS concluded that Johnson's seagrass is rare, has a limited reproductive capacity, and is vulnerable to a number of anthropogenic and natural disturbances. It also exhibits the most limited geographic distribution of any seagrass. Within its small geographic range (lagoons on the east coast of Florida from Sebastian Inlet to central Biscayne

Bay), it is one of the least abundant species. Because of its limited reproductive capacity and energy storage capacity, it is less likely to survive environmental perturbations and to be able to repopulate an area when lost. Finally, environmental degradation and habitat loss have continued despite existing federal and state conservation efforts. Completion of a report reviewing the current status of *H. johnsonii* is anticipated in the fall of 2007.

Critical Habitat

Ten areas in the geographic range of Johnson's seagrass were designated as critical habitat on April 5, 2000 (65 FR 17768). These areas and their approximate acreage include: a portion of the Indian River Lagoon, north of the Sebastian Inlet Channel (5.7); a portion of the Indian River Lagoon, south of the Sebastian Inlet Channel (2.0); a portion of the Indian River Lagoon near the Fort Pierce Inlet (4.3); a portion of the Indian River Lagoon, north of the St. Lucie Inlet (2770); a portion of Hobe Sound (900); a site on the south side of Jupiter Inlet (4.3); a site in central Lake Worth Lagoon (15.0); a site in Lake Worth Lagoon, Boynton Beach (95.5); a site in Lake Wyman, Boca Raton (20.0); and a portion of Biscayne Bay (18,757). This designated area accounts for approximately 22,574 acres or 9,139 hectares.

4.3.6 Marine Invertebrates

(all information below from *Acropora* Status review)

Description

All Atlantic *Acropora* spp. are considered to be environmentally sensitive, requiring relatively clear, well-circulated water (Jaap et al. 1989). Atlantic *Acropora* spp. are almost entirely dependent upon sunlight for nourishment compared to massive, boulder-shaped species in the region (Porter 1976; Lewis 1977), with these latter types of corals more dependent on zooplankton. Thus, Atlantic *Acropora* spp. are much more susceptible to increases in water turbidity than some other coral species. Dredging or pollution activities that reduce long-term water clarity can also reduce the coral photosynthetic to respiration ratio (P/R ratio) below unity. Therefore, *Acropora* spp. may not be able to compensate with an alternate food source, such as zooplankton and suspended particulate matter, like other corals.

Optimal water temperatures for *A. palmata* range from 25 to 29°C, although colonies in the U.S.V.I. have been known to tolerate short-term temperatures around 30°C without obvious bleaching (loss of zooxanthellae). Jaap (1979) and Roberts et al. (1982) note an upper temperature tolerance of 35.8°C for *A. palmata*. All Atlantic acroporids are susceptible to bleaching due to adverse environmental conditions (Ghiold and Smith 1990; Williams and Bunkley-Williams 1990). Major mortality of *A. palmata* and *A. cervicornis* occurred in the Dry Tortugas, Florida, in 1977 due to a winter cold front that depressed surface water temperatures to 14 to 16°C. Some reduction in growth rates of *A. cervicornis* was reported in Florida when temperatures dropped to less than 26°C (Shinn 1966). All *Acropora* spp. require near oceanic salinities (34 to 37 ppt).

Staghorn Coral

Historically, *A. cervicornis* (Figure 4.3-5) was reported from depths ranging from <1 to 60 m (Goreau and Goreau 1973). It is believed that 60 m is an extreme situation and that the coral is relatively rare below 20 m depth. The common depth range is currently observed at 5 to 15 m.

In southeastern Florida, this species historically occurred on the outer reef platform (16 to 20 m) (Goldberg 1973), on spur and groove bank reefs and transitional reefs (Jaap 1984; Wheaton and Jaap 1988), and on octocoral-dominated hardbottom (Davis 1982). In the Florida Keys *A. cervicornis* can occur from 1 to 34 m depths (Wells 1933; Davis 1982; Jaap 1984; Jaap and Wheaton 1988; Jaap et al. 1989). Colonies may also be common in back- and patch-reef habitats (Gilmore and Hall 1976; Cairns 1982).

Although *A. cervicornis* colonies are sometimes found interspersed among colonies of *A. palmata*, they are generally in more protected, deeper water or seaward of the *A. palmata* zone and hence, protected from waves. Historically, *A. cervicornis* was the primary constructor of mid-depth (10 to 15 m) reef terraces in the western Caribbean, including Jamaica, the Cayman Islands, Belize, and some reefs along the eastern Yucatan peninsula (Adey 1978).

Figure 4.3-5a. Staghorn coral, *Acropora cervicornis* (Source: Walt Jaap).

As depth increases, *A. cervicornis* colonies tend to be less compacted, have longer branches, and branching tends to be at greater intervals. Gladfelter (1982) demonstrated that infilling occurs as the branch elongates. Thus, at the tip, the porosity of the axial calyx is >90% and the wall is 60%, while at 60 cm from the tip, the porosity of the axial calyx is dead and the porosity of the wall is about 20%. This strengthens the branch as it elongates and the momentum of the branch increases. At depths of 20 to 40 m, where currents and wave force are minimal, branch diameter is thinner, being approximately half the diameter of a colony in the shallow surge zone. The porosity of the skeletons of *A. cervicornis* ranges from 35 to 65% by volume, with the mechanical strength of the skeleton proportional to the porosity (Schumacher and Plewka 1981). Because the skeleton is quite porous, it breaks readily in strong wave forces.

Elkhorn Coral

The maximum range in depth reported for *A. palmata* Figure 4.3-5b is <1 m to 30 m, but the optimal depth range for this coral is considered to be 1 to 5 m depth (Goreau and Wells 1967).

Figure 4.3-5b. Elkhorn coral, *Acropora palmata* (Source: W. Jaap).

Currently, the deepest known colonies of *A. palmata* occur at 21 m in the Flower Garden Banks National Marine Sanctuary (Hickerson, pers. comm.) and at Navassa National Wildlife Refuge (Miller, pers. comm.). The preferred habitat of *A. palmata* is the seaward face of a reef (turbulent shallow water), including the reef crest, and shallow spur and groove zone (Shinn 1963; Cairns 1982; Rogers et al. 1982). At low tide, colonies are sometimes exposed. Colonies of *A. palmata* often grow in nearly mono-specific, dense stands and form interlocking framework known as thickets in fringing and barrier reefs (Jaap 1984; Tomascik and Sander 1987; Wheaton and Jaap 1988). Storm-generated fragments are often found occupying back reef areas immediately landward of the reef flat/reef crest, while colonies are rare on lagoonal patch reefs (Dunne 1979). *Acropora palmata* formed extensive barrier-reef structures in Belize (Cairns 1982), the greater and lesser Corn Islands, Nicaragua (Gladfelter 1982; Lighty et al. 1982), and Roatan, Honduras, and built extensive fringing reef structures throughout much of the Caribbean (Adey 1978). Colonies generally do not form a thicket below 5 m depth, with maximum water depths of framework construction ranging from 3 m to 12 m (see Table 1 in Lighty et al. 1982).

Distribution and Abundance

When discussing historic distribution and abundance, it is important to briefly mention the environmental setting of the wider Caribbean region (tropical western Atlantic, Caribbean-Atlantic province), insofar as environmental differences across the region influence the extent to which *Acropora* spp. have been able to build extensive reef structures. Specifically, although both *A. cervicornis* and *A. palmtata* are found throughout the Caribbean Sea, their historical abundance patterns are not necessarily similar and there is ample evidence to suggest that many reef systems were constructed without significant contributions by acroporids. Early reviews of western Atlantic reefs and coral species, as well as discussions of reef geomorphology in the western Atlantic, are provided elsewhere (e.g., Glynn 1973, Milliman 1973, Adey 1977; 1978), but provide context to the historical patterns of these corals.

The entire Caribbean-Atlantic province is characterized as microtidal and is impacted by largely unidirectional trade winds and waves subject, in part, to strong ocean flows. The most northern reefs in the province (i.e. Florida, northwestern Bahamas, and Bermuda) are cyclically stressed by the occasional effect of polar air during winter months and thus have limited reef development by *Acropora* spp. or lack these species altogether (Bermuda). Throughout the Caribbean, wave energy influences the degree to which crustose coralline algae and *Acropora* spp. dominate as reef-building elements (Adey 1977; Geister 1977). For example, large swells from the Atlantic Ocean limit acroporid reef development in the Windward Islands (eastern Caribbean) and the eastern flanks of the Bahamas (Roberts et al. 1992). In the Lesser Antilles, neither *A. cervicornis* nor *A. palmata* are significant agents of reef framework construction, due principally to higher wind strength, easterly consistencies, and longer fetch; this area is also subjected to longperiod swells or rollers during the winter months that further limits shallow and middepth reef construction (Adey 1977). In the southwestern Caribbean (e.g., Panama), reef terraces are present that are potentially conducive to acroporid-reef development, but seasonally rough seas batter the area resulting in wave-swept pavements (Glynn 1973).

In contrast, the northwestern Caribbean (e.g. Cuba, Cayman Islands, Jamaica, eastern Yucatan, Belize) is characterized by relatively low winds of medium to high easterly consistencies, that allows extensive acroporid growth at shallow and mid-depth (10 to 25 m). For example, the Belize Barrier Reef, the largest barrier reef in the province, appears to be based upon an *A. cervicornis* framework (Adey 1977).

The current range for both *A. cervicornis* and *A. palmata* remains unchanged from the historical (Figure 4.3-6) as far as data are available; there is a paucity of quantitative data for many locations throughout the wider Caribbean. Historically most data collected has been from a few specific reef sites that may or may not represent the regional condition of the acroporids or coral reefs in general. In contrast, there are many qualitative data/observations indicating drastic declines in abundance of both *A. palmata* and *A. cervicornis* throughout their geographic range (e.g., Aronson and Precht 2001a).

Figure 4.3-6. Approximate range of *Acropora* spp. (highlighted), including the Gulf of Mexico, Atlantic Ocean and Caribbean Sea. The highlighted areas are not specific locations of the corals, rather reflect general distribution.

Recently, there have been two publications that have summarized status (abundance and distribution) of *A. cervicornis* and *A. palmata*. The Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program (Lang 2003) provides results (1997–2004) of a regional systematic survey of corals, including *Acropora* spp., from many locations throughout the Caribbean. While data from this survey represent a snapshot in time of the reef, the geographic scope of the survey is great; targeted areas are visited by data collectors of varying expertise, and data represent a single survey. AGRRA data (1997-2004) indicate that the historic range of both species remains intact, that *A. cervicornis* is rarely found throughout the range (including areas of previously known occurrence) and a moderate occurrence of *A. palmata*.

An AGRRA bio-area index for *A. palmata* was recently developed to summarize data for nearly 300 sites throughout the wider Caribbean (Garza-Perez and Ginsburg pers. comm.). This bio-area index utilizes maximum diameter and partial mortality values of *A. palmata* colonies per site (total area of living tissue/10 transects) and is presented in Figures 4.3-7a and 4.3-7b. Results from the spatial analysis are as follows:

1. most (n=61) bio-areas (Figure 4.3-7a) ranked as moderate to high (100 to 500 m^2/10 transects) are concentrated in Andros Barrier Reef (Bahamas) and the northern Caribbean (Cuba and Belize);
2. 195 sites (Figure 4.3-7b) distributed throughout the geographic area were ranked as low bio-areas (from 0.01 to 100 m^2/10 transects)

3. standing dead colonies of *A. palmata* were found throughout the geographic range (Figure 4.3-7b).

It is important to note that the data for the Andros Barrier Reef AGRRA surveys were conducted prior to the Caribbean-wide 1998 coral die-off and the site has not been resurveyed since 1997. Furthermore, status of *A. palmata* has not been updated following the 2004 hurricane season where Hurricanes Charley passed over Cuba, and Hurricanes Frances and Jeanne passed over the Bahamas.

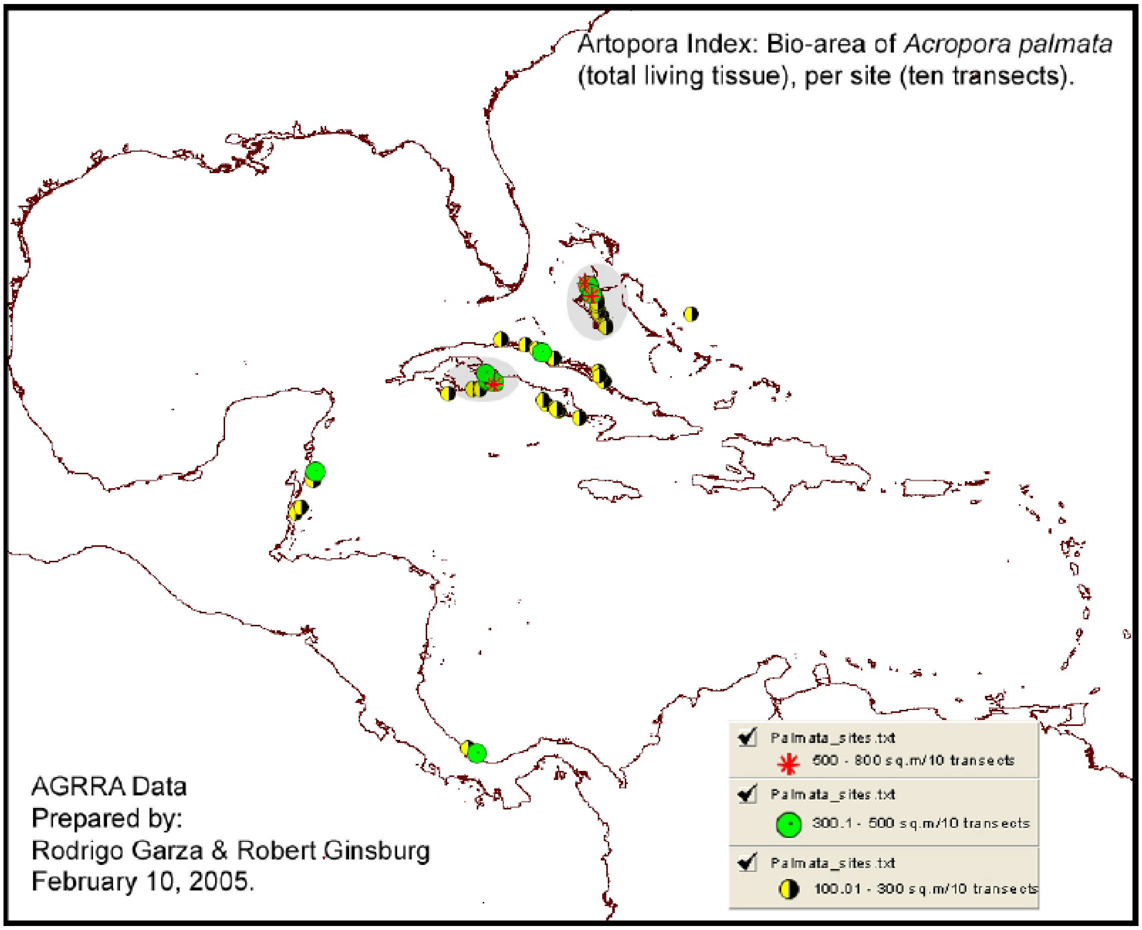


Figure 4.3-7a. Locations of reefs indexed with moderate or high (circles) *Acropora palmata* bio-area as reported from 1997- 2004 AGRRA surveys. Map provided courtesy Garza-Perez and Ginsburg.

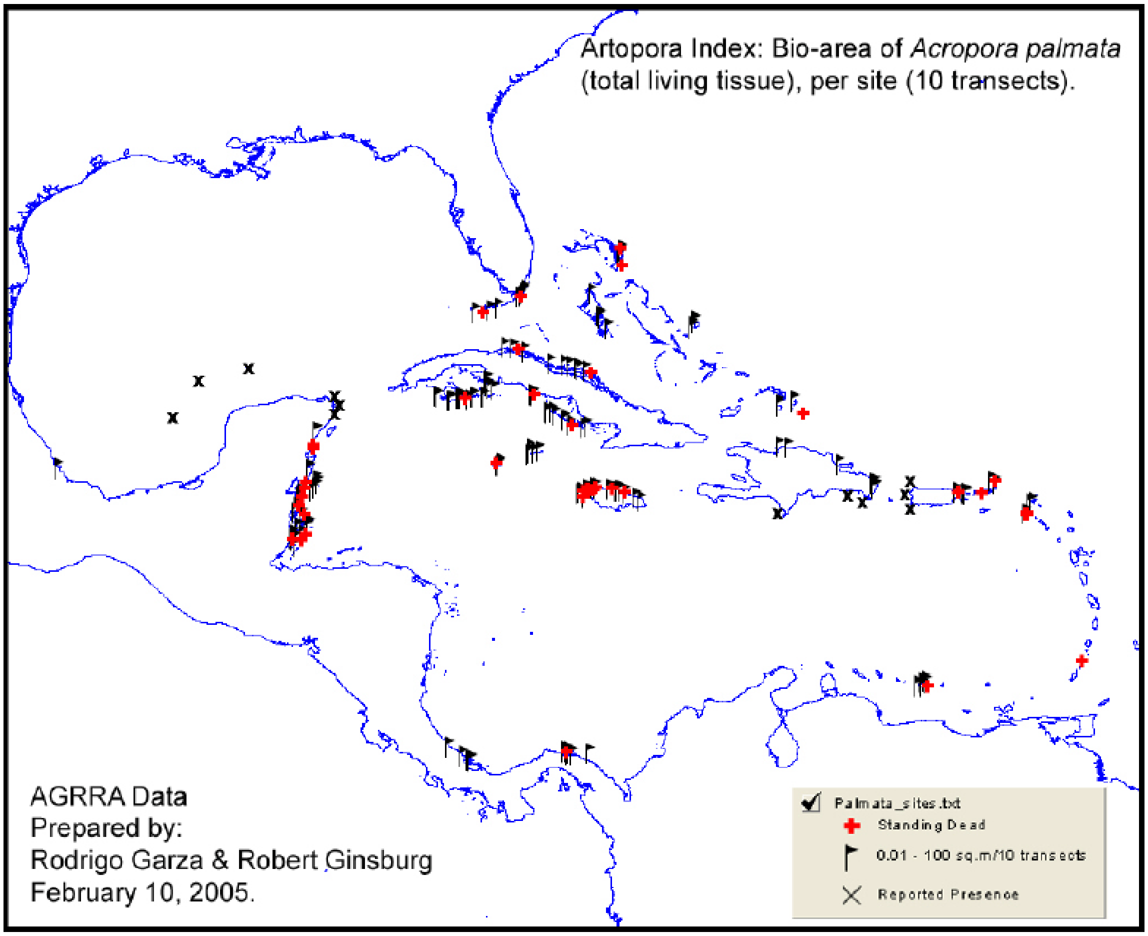


Figure 4.3-7b. Locations of reefs indexed with low (flag) *Acropora palmata* bio-areas as reported from 1997-2004 AGRRA surveys. Locations of standing-dead *A. palmata* colonies are indicated by a cross. Map provided courtesy Garza-Perez and Ginsburg.

Prior to the AGRRA summary, Bruckner (2002) provided a comprehensive summary of the best-known quantitative and qualitative data on the status of the Atlantic acroporids resulting from a NOAA-sponsored workshop wherein participants compiled data and summarized conditions throughout the range. Much of the data from the Bruckner (2002) report are summarized below, and some are updated and included in the case studies at the end of this section.

Abundance and distribution (historic and current) of *Acropora cervicornis*

Historically, *A. cervicornis* so dominated the reef within the 7 to 15 m depth that the area became known as the staghorn zone (Figure 4.3-8) throughout much of the Caribeean. In many other reef systems in the wider Caribbean, most notably the western Caribbean areas of Jamaica, Cayman Islands, Belize and eastern Yucatan (Adey 1977), *A. cervicornis* was a major mid-depth (10 to 25 m) reef-builder. Principally due to wind conditions and rough seas, *A. cervicornis* has not been known to build extensive reef structures in the Lesser Antilles and southwestern Caribbean.

Acropora cervicornis has also been documented in deeper water (16 to 30 m) (Goldberg 1973) and as far north as Palm Beach, Florida (26° 3'N). It is also distributed further south and west throughout the coral and hardbottom habitats of the Florida Keys (Antonius et al. 1978; Burns 1985; Dustan 1988; Dustan and Halas 1987; Glynn et al. 1989; Jaap 1984; Jaap and Wheaton 1975; Jaap et al. 1988; Wheaton and Jaap 1988), and Dry Tortugas (Vaughan 1915; Davis 1982; Dustan 1985, 1988; Jaap et al. 1989). In Biscayne National Park (upper Florida Keys), *A. cervicornis* was more abundant on reefs further from tidal passes (e.g., Ajax and Long Reefs) than those nearby, with historical coverage ranging from 0.1% to 2.7% in the 1980s (Burns 1985).

Because Florida is one of the few areas where multi-year quantitative data are available for *A. cervicornis* at more than a single location (Carysfort Reef; Dustan and Halas 1987, Looe Key Reef; Wheaton and Jaap 1988, Dry Tortugas; Davis 1982 and Porter et al. 1982) (Figure 4.3-9), those data are further analyzed and presented as a case study in section 4.5.3 of the *Acropora* Status Review document.

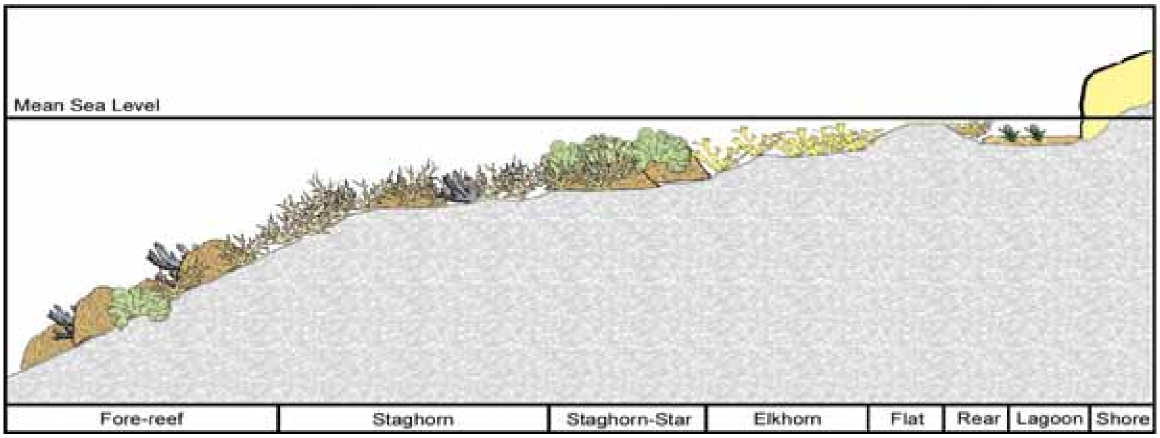


Figure 4.3-8. Reef zonation schematic example modified from several reef zonation-descriptive studies (Goreau 1959; Kinzie 1973; Bak 1977).

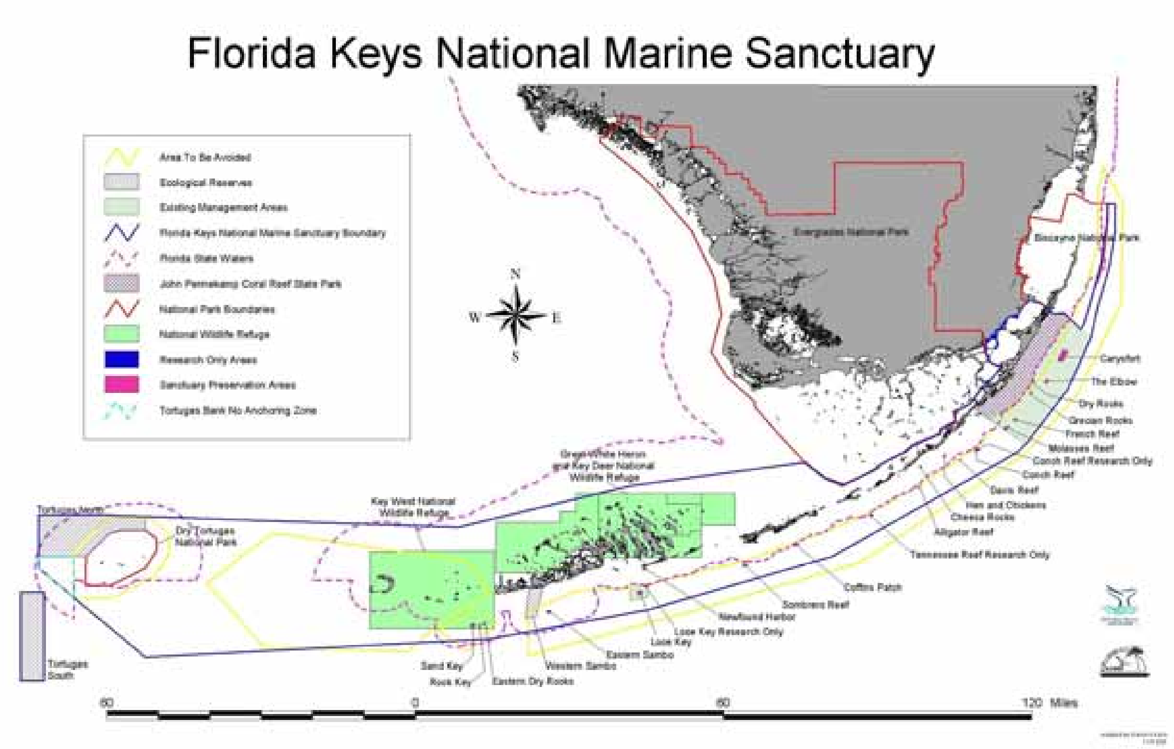


Figure 4.3-9. Map of the Florida Keys National Marine Sanctuary and reefs of the Florida Keys.

Historical and current distribution and abundance of *Acropora palmata*

Throughout much of the Caribbean, *A. palmata* historically occupied the 1 to 8 m depth range (reef flat, wave zone, reef crest) known as the 'elkhorn zone' (Figure 4.3-8). *Acropora palmata* occupied this zone in Jamaica (Goreau 1959), Alacran Reef, Yucatan peninsula (Kornicker and Boyd 1962), Abaco Island, Bahamas (Storr 1964), the southwestern Gulf of Mexico, Bonaire (Scatterday 1974), and the Florida Keys (Jaap 1984; Dustan and Halas 1987).

The predominance of *A. palmata* in shallow reef zones is related to the degree of wave energy. In areas with strong wave energy conditions only isolated colonies may occur, while thickets may develop in areas of intermediate wave energy (Geister 1977). Although considered a turbulent water species, *A. palmata* is sensitive to breakage by wave action, and is often replaced by coralline algae in heavy surf zones throughout the province (Adey 1977).

While *A. cervicornis* has been documented further north along the Florida east coast, the northern extension of *A. palmata* is at Fowey Rocks offshore the Miami area (25° 37' N) (Porter 1987). This area technically begins the Florida Reef Tract where all of the major reef-building corals appear in shallow water in the southeastern U.S. (Burns 1985).

Surveys in the early 1970s north of Miami (e.g., Palm Beach) did not note the occurrence of *A. palmata* (Goldberg 1973). Between Fowey Rocks and Carysfort Reef, *A. palmata* has been historically rare as the significant reef development or framework construction by *A. palmata* begins further south at Carysfort Reef (25° 20'N), extending discontinuously southwestward to the Dry Tortugas (Jaap 1984). Notably, recent surveys have reported a few colonies of *A.*

palmata off Pompano Beach, Broward County, FL (Figure 4.3-10). The status of these few northern-most colonies presently is unknown.

Figure 4.3-10. *Acropora palmata* off of Pompano Beach, Broward County, Florida, in 2003; (Photo credit: J. Sprung).

Distribution records of *A. palmata* for the southeast Florida coast include: upper Florida Keys (Burns 1985; Dustan 1985, 1988; Dustan and Halas 1987; Jaap et al. 1988), lower Florida Keys (Jaap and Wheaton 1975; Antonius et al. 1978; Jaap 1979; Wheaton and Jaap 1988), and Dry Tortugas (Davis 1982; Jaap et al. 1989). Offshore reefs built primarily by *A. palmata* are situated along the outer margin of an arc-shaped limestone plateau (south Florida shelf). "Flourishing" *A. palmata* reefs (i.e., those with a shallow or emergent reef flat) are limited to the northern seaward half of Key Largo where an *Acropora* zone (reef flat/reef crest) was present. At Molasses Reef (see Figure 4.3-9) living *A. palmata* was almost absent in 1959-60 (Shinn 1963) and it was later suggested that conditions necessary for the growth of this coral changed since the coralline spurs were originally accreted (Shinn et al. 1981).

Numerous other studies describing *A. palmata* abundance and distribution in the Florida Keys are available. When possible, data (e.g., Chiappone and Sullivan 1997) were further analyzed and presented as a case study in section 4.5.3 of the *Acropora* Status Review document. Other data from short-term projects throughout the Florida Keys are summarized below:

- From 1984 to 1991, a decline in *A. palmata* abundance at shallow depths (4 to 6 m) but not deeper were noted in coral communities on six reefs (including sites in both the upper Keys and lower Keys) (Porter and Meier 1992). These changes were attributed to disease and the demise of the long-spined sea urchin (*Diadema antillarum*).
- Living and dead assemblages of corals on two offshore sites and two patch reefs were compared and significant differences in taxonomic composition between live and dead

coral assemblages were found between reef types (Greenstein and Pandolfi 1997). While both the patch and offshore reefs historically had more *A. cervicornis* and *A. palmata*, they were now dominated by other corals (*Porites astreoides* and *Siderastrea siderea*). Interestingly, massive growth forms were under-represented in the dead assemblage, while branching growth forms (*Acropora* spp.) were underrepresented in the live coral assemblage.

Reproduction

The distribution and abundance of Atlantic *Acropora* spp., like other coral species, reflects patterns of larval recruitment, asexual reproduction via fragmentation, mortality, regenerative capabilities, and aggressive interactions (Richmond and Hunter 1990). Interspecific differences in the mechanisms of recruitment, dispersal, and mortality are likely important in determining the species composition of reef corals in different environments. These differences reflect the differential allocation of energy to the basic life history functions of growth (rate and rigidity of the skeleton), reproduction (fecundity, mode of larval dispersal, recruitment success), and colony maintenance (intra- and interspecific interactions, competitive ability, regeneration) (Connell 1973; Lang 1973; Bak and Engel 1979; Szmant 1986). Populations of Atlantic *Acropora* spp. are dependent upon sexual recruits for recovery after catastrophic disturbance, but can locally dominate hardbottom and coral reef habitats when colonies fragment and propagate across the bottom.

Extensive research has been conducted on the diverse reproductive strategies employed by scleractinian corals (Fadlallah 1983; Szmant 1986; Richmond and Hunter 1990). Atlantic *Acropora* spp., like many stony coral species, employ both sexual and asexual reproductive propagation. Sexual reproduction in corals includes gametogenesis (i.e., development of gametes) within the polyps near the base of the mesenteries. Some coral species have separate sexes, while others such as the Atlantic *Acropora* spp., are hermaphroditic. *Acropora cervicornis* and *A. palmata* in particular do not differ substantially in their sexual reproductive biology. Both species are spawners, meaning that coral larvae develop externally to the parental colonies (Szmant 1986) and both species are simultaneous hermaphrodites, meaning that a given colony will contain both female and male reproductive parts during the spawning season. Gametes (eggs and sperm) are located in different mesenteries of the same polyp (Soong 1991). The development period is longer for eggs than sperm, lasting approximately 10 months (Szmant 1986).

The spawning season for *A. cervicornis* and *A. palmata* is relatively short; with gametes released only a few nights during July, August, and/or September. In some populations, spawning is synchronous after the full moon during any of these three months. Annual egg production in *A. cervicornis* and *A. palmata* populations studied in Puerto Rico was estimated to be 600 to 800 eggs per cm^2 of living coral tissue (Szmant 1986). Eggs from both corals are ~300 µm in diameter. Colonies of *A. cervicornis* studied on the Caribbean coast of Panama during 1987-88 produced eggs 0.3 to 1.0 mm in length along the long axis that were elliptical in shape (Soong 1991). Spermaries were present during July and August and not during other times of the year. In the same study, *A. palmata* eggs were 0.2 to 1.0 mm in length along the long axis and shaped as irregular ellipses.

Spermaries were present during July, August, and September. In a subsequent study, Soong and Lang (1992) observed that large axial polyps and basal tissues (1.0 to 4.5 cm from the colony base) in *A. cervicornis* were infertile, whereas gonads located within 2 to 6 cm of the branch tips always had smaller eggs than those in the mid-region of the branches. In *A. palmata*, small eggs were found in the whole colony, while infertile areas were observed in the encrusting base and along the growing edges of branches (Soong and Lang 1992). Upper surfaces of *A. palmata* colonies had significantly greater fecundity (more fertile polyps per unit surface area) and larger numbers of eggs within fertile polyps.

Colonies of *A. cervicornis* and *A. palmata* studied on the Caribbean coast of Panama indicated that larger colonies of both species (as measured by surface area of the live colony) have higher fertility rates (Soong and Lang 1992). For *A. palmata*, no colonies with a surface area between 4 and 15 cm^2 (n=4) or between 15 to 60 cm^2 (n=9) were fertile, while 7% of those 60 to 250 cm^2 in tissue surface area were fertile (n=14). Over 30% of the colonies between 250 and 1000 cm^2 in tissue surface area were fertile (n=16), 43% of colonies between 1000 and 4000 cm^2 (n=7), and 88% of colonies larger than 4000 cm^2 (n=33). In the same study, only colonies of *A. cervicornis* with a branch length larger than 9 cm were fertile, with 38% fertility for those 9 to 13 cm in branch length (n=13), 59% for 13 to 17 cm (n=17), and 89% for colonies with branches longer than 17 cm (n=18). Estimated size at puberty for *A. palmata* was 1600 cm^2 (n=84 colonies sampled) and for *A. cervicornis* was 17 cm in branch length (n=52 colonies sampled). The smallest reproductive colony of *A. palmata* was 16 x 8 cm^2 and for *A. cervicornis* was 9 cm in branch length (Soong and Lang 1992).

In corals, fertilization can occur internally or externally, but in Atlantic *Acropora* spp., fertilization and development are exclusively external. Embryonic development culminates with the development of planktonic larvae called planulae. Little is known concerning the settlement patterns of planula larvae of Atlantic *Acropora* spp. (Bak et al. 1977 ; Sammarco 1980 ; Rylaarsdam 1983). In general, upon proper stimulation, coral larvae, whether released from parental colonies or developed in the water column external to the parental colonies, settle and metamorphose on appropriate substrates. Unlike most other coral larvae, *A. palmata* planulae appear to prefer to settle on upper, exposed surfaces, rather than in dark or cryptic ones (Szmant and Miller, accepted), at least in a laboratory setting. Initial calcification ensues with the forming of the basal plate and the initial protosepta, followed by the theca or polyp wall and axial skeletal members. Buds that form on the initial corallite develop into daughter corallites. Both externally and internally produced coral planula larvae presumably experience considerable mortality (up to 90% or more) from predation or other factors prior to settlement and metamorphosis (Goreau et al. 1981). Once larvae are able to settle onto appropriate hard substrates, metabolic energy is diverted to colony growth and maintenance. Because newly settled corals barely protrude above the substrate, juveniles need to reach a certain size to reduce damage or mortality from impacts such as grazing, sediment burial, and algal overgrowth (Bak and Elgershuizen 1976; Birkeland 1977; Sammarco 1985). Recent studies examining early survivorship of lab cultured *A. palmata* settled onto experimental limestone plates and placed in the field indicate that survivorship is substantially higher than for *Montastraea faveolata*, another spawner, and similar to brooding species over the first nine months after settlement (Szmant and Miller, accepted).

This pattern corresponds to the size of planulae; *A. palmata* eggs and larvae are much larger than those of *Montastraea* spp. Overall, older recruits (i.e., after they have survived to a size they are visible to the human eye, probably 1 to 2 yrs after settlement (Figure 4.3-11) appear to have similar growth and post-settlement mortality rates across species (Van Moorsel 1988).

Figure 4.3-11. *Acropora palmata* sexual recruit, St. John, U.S.V.I. Photo credit: C. Rogers.

Spatial and temporal patterns of coral recruitment have been intensively studied on Caribbean reefs (Birkeland 1977; Bak and Engel 1979; Rogers et al. 1984; Baggett and Bright 1985; Chiappone and Sullivan 1996). Biological and physical factors that have been shown to affect spatial and temporal patterns of coral recruitment include substrate availability and community structure (Birkeland 1977), grazing pressure (Rogers et al. 1984; Sammarco 1985), fecundity, mode and timing of reproduction (Harriot 1985; Richmond and Hunter 1990), behavior of larvae (Lewis 1974; Goreau et al. 1981), hurricane disturbance (Hughes and Jackson 1985), physical oceanography (Baggett and Bright 1985; Fisk and Harriot 1990), the structure of established coral assemblages (Lewis 1974; Harriot 1985), and chemical cues (Morse et al. 1988).

Relatively few studies, however, have examined variation in Caribbean coral recruitment over larger spatial scales (10 to 100 km) or among different structural types of reefs (Wallace and Bull 1981; Harriot and Fisk 1987; Fisk and Harriot 1990). Many studies of Caribbean reefs have used the quantification of juvenile coral densities as a proxy to measure recruitment success, with juvenile corals defined as metamorphosed corals visible underwater to the unaided eye ranging up to 4 cm in maximum diameter (Bak and Engel 1979). Newly settled corals are visible in the field at approximately 5 to 10 mm in diameter, and colonies approaching 4 cm in diameter are approximately 1 to 3 years old (Van Moorsel 1988).

Studies of *Acropora* spp. from across the Caribbean confirm two overall patterns of sexual recruitment: (1) Low juvenile densities relative to other coral species and (2) low juvenile densities relative to the commonness of adults (Porter 1987). This pattern suggests that the composition of the adult population is dependent upon variable recruitment. It also likely reflects the dominance of asexual reproduction by fragmentation for these species (for example, surviving fragments are usually larger than 4 cm and thus never undergo a "juvenile" stage by this definition). In both Curaçao and Bonaire in the 1970s, densities of juvenile *A. palmata* reached 0.13 per m^2, while no *A. cervicornis* juveniles were found (Bak and Engel 1979). On the north coast of Jamaica, juvenile *A. cervicornis* densities were as high as 4.3 per m^2 at 11 m depth on barren substrate (Rylaarsdam 1983). However, phototransects revealed no *Acropora* spp. recruitment in 1976 or 1980 at <20 m depth, with smaller colonies presumably originated from the larger colonies via fragmentation (Porter et al. 1981). In Salt River, St. Croix, *A. palmata* juveniles occurred at densities of 0.1 to 0.3 per m^2 at 3 to 9 m depth, while densities of juvenile *A. cervicornis* ranged from 0.01 to 0.30 per m^2 at 9 m depth (Rogers et al. 1984). Similar results were obtained in the Florida Keys (Dustan 1977; Porter and Meier 1992; Chiappone and Sullivan 1996). Surveys of nine sites representing three different offshore reef types from 3 to 15 m depth yielded no juveniles of *Acropora* spp. from 450, 1-m^2 quadrats (Chiappone and Sullivan 1996). To date, however, the settlement rates (number of larvae settling per unit area) of Atlantic *Acropora* spp. have still not been quantified; the juvenile density measurements cited above represent larvae that have not only settled, but metamorphosed (i.e., excreted a calcium carbonate skeleton) and survived to a specific size visible to surveyors underwater. Anecdotal evidence and observations in the Caribbean indicate that both *A. cervicornis* and *A. palmata* sexually recruit onto reefs, and in several instances, populations that have experienced major declines (>90%) are showing signs of recovery in terms of newly settled sexual recruits (Bruckner 2002).

Besides sexual reproduction, most coral species, including Atlantic acroporids, also reproduce asexually. Asexual reproduction involves fragmentation, wherein colony pieces or fragments are dislodged from larger colonies to form new colonies (Highsmith 1982). The budding of new polyps within a colony can also be considered asexual reproduction. Fragmentation can occur during storms (Porter et al. 1981; Tunnicliffe 1981; Highsmith 1982), with susceptibility to mechanical breakage of colony branches influenced by the boring activities of sponges and lithophagus bivalves. Fragmentation is a common means of propagation in many species of branching corals and historically has been considered to be the most common means of forming new colonies in Atlantic *Acropora* spp. (Gilmore and Hall 1976; Davis 1977; Tunnicliffe 1981; Bak and Criens 1982; Hughes 1985). The perception of the dominance of fragmentation as a reproductive mode for *A. palmata* and *A. cervicornis* implies that colonies derived from fragmentation can be distinguished from those derived from larvae. However, this may not always be the case. Recently developed genetic tools can detect colonies with the same genotype (implying one was fragmented from the other). Application of these tools in the field to a population of *A. palmata* (where individual small colonies were scored by field experts as larval or asexual recruits) indicated very poor correlation (Miller et al. in review). It appears that the reliability of assessing the contribution of sexual versus asexual reproduction in *Acropora* populations by field survey is limited, but is an area of study that warrants further investigation.

Asexual reproduction can play a major role in maintaining local populations when sexual recruitment is very limited. Fragmentation, followed by stabilization, survivorship, and growth can provide a mechanism for maintaining and expanding Atlantic *Acropora* spp. populations. However, region-wide declines have increased the reliance of *Acropora* spp. on sexual recruitment as a means of establishing and sustaining populations (Bruckner 2002). Atlantic *Acropora* spp. may require a certain storm frequency to maintain and expand populations through asexual reproduction, principally by fragmentation, when sexual recruitment is limited (Bruckner 2002). Frequent occurrence of storms or a single intense storm, however, may negatively impact colony survival, since a fragment may become abraded during the storm or may not encounter suitable substrate to reattach after the storm passes.

Development and growth

Staghorn Coral

The growth rate for *A. cervicornis* has been reported to range from 3 to 11.5 cm/yr (Table 4.3-6). This growth rate is relatively fast in comparison to that of other corals and historically enabled the species to construct significant bioherms (reef structures) in several locations throughout the Caribbean (Adey 1978).

Table 4.3-6. The annual growth rate for *Acropora cervicornis* as reported from several sources.

Growth rate (cm/yr)	Location	Record
4	Dry Tortugas	Vaughan (1915)
10.9	Key Largo, Florida	Shinn (1966)
11.5	Eastern Sambo, Florida	Jaap (1974)
10	Key Largo, Florida	Shinn (1976)
7.1	U.S. Virgin Islands	Gladfelter et al. (1978)
3 to 4	Exuma, Bahamas	Becker and Muller (2001)

Gladfelter (1982, 1983a) used a scanning electron microscope to describe the growth process in *A. cervicornis*. She reported that crystals are initially deposited randomly on the distal margin of the axial corallite. Subsequently, needle-like crystals attach and grow outward from the surface of the crystals. The needle-like crystals in contact with the calicoblastic epithelial cells grow and fuse together generating the skeletal foundation or septotheca. During daylight, calcium carbonate accretion occurs on all of the skeletal elements; at night the activity is limited to fusiform crystal formation. Gladfelter (1983b) reported daily tissue growth of 300 μm in the region of the axial polyp. "*A. cervicornis* exhibits a daily rhythm in calcification capacity, with daily maxima at sunrise and sunset. Daily minima occur shortly after sunrise and sunset" (Chalker 1977; Chalker and Taylor 1978; Gladfelter 1983b). Contrasting growth of in situ and laboratory-reared specimens revealed differences in the basal extension; however, other measurements (e.g., $CaCO_3$ accretion and vertical extension) were equivalent (Becker and Mueller 2001).

Growth in *A. cervicornis* is also expressed in expansion, occurring as a result of fragmenting and forming new centers of growth (Bak and Criens 1982; Tunnicliffe 1981). A broken off branch may be carried by waves and currents to a distant location or may land in close proximity to the original colony. If the location is favorable, branches grow into a new colony, expanding and occupying additional area. Fragmenting and expansion, coupled with a relatively fast growth rate, facilitates potential spatial competitive superiority for *A. cervicornis* relative to other corals and other benthic organisms (Shinn 1976; Neigel and Advise 1983; Jaap et al. 1989). Fragments that contained the axial corallite were found to have lower mortality than fragments that came from the inner portions of a colony and did not have axial corallites (Bowden-Kerby 2001a). There was up to a six-fold difference in growth rate over 12 months based on the fragment's origin (Bowden-Kerby 2001b).

Elkhorn Coral

The growth rate of *A. palmata*, expressed as the linear extension of branches, is reported to range from 4 to 11 cm annually (Table 4.3-7) (Vaughan 1915, Jaap 1974). The 4-cm annual growth rate cited by Vaughan (1915) undoubtedly underestimates growth. Annual linear extension was estimated to be 8.8 cm; basal extension was 2.3 mm/month, and tissue growth was 200 cm^2 per month at Quintana Roo, Puerto Morelos, Mexico (Padilla and Lara 1996). A colony two meters in height could theoretically be 20 to 29 years old based on a 7- to 10-cm annual growth rate. The theoretical age of a much larger colony (4 m) is 40 to 57 years old. Linear extension and tissue growth were dependent on the size of the colony; however, basal extension was independent of colony size (Padilla and Lara 1996). Colonies of *A. palmata* in the field had a greater calcification rate and rate of extension relative to specimens grown in an experimental tank (Becker and Mueller 2001). Wells (1933) reported from observations in 1932 that colonies of *A. palmata* were eight feet high (2.4 m) and 15 feet (4.5 m) in diameter at Bird Key Reef, Dry Tortugas; this is probably the maximum size that this species can attain.

Settled larvae typically create a small crust or patch with tubular corallites oriented at approximately 90 degrees from the plane of attachment. One or more protuberances develop and grow outward to form proto-branches.

Table 4.3-7. *Acropora palmata* growth rates reported from several sources.

Growth rate (cm/yr)	Location	Record
4	Dry Tortugas, Florida	Vaughan (1915)
10	Florida Keys	Jaap (1974)
4.7 to 9.9	U.S. Virgin Islands	Gladfelter, et al. (1978)
5.2	Colombia	Garcia et al. (1996)
2 to 11	Exuma, Bahamas	Becker and Mueller (2001)

The range of growth forms in *A. palmata* includes the iconic broad frond, with symmetrical colonies that are two or more meters across. Branches are up to 50 cm across and range in thickness from 4 to 5 cm, tapering toward the branch terminal; these colonies are most typical of the spur and groove formations where water circulation is omni-directional. In areas where wind and waves are predominantly from a single direction, the branches tend to grow in to the direction of the waves. The series of branches look like a medieval fortification (palisade); this growth form is typical of the barrier reef habitat. As depth increases, the branches are oriented in a more vertical orientation (Wainwright 1976; Graus et al. 1977). This compensates for hydraulic bending forces, but the thickening of the base also helps to counteract the hydrodynamic forces (Schumacher and Plewka 1981). *Acropora palmata* porosity ranges from approximately 35 to 45% by volume (Schumacher and Plewka 1981).

Acropora palmata can rapidly monopolize large areas by fragment propagation. A branch of *A. palmata* may be carried by waves and currents away from the mother colony to distances that range from 0.1 to 100 m, but usually less than 30 m (Baums et al., unpublished data). Fragments cleaved from the colony may grow into new colonies (Highsmith et al. 1980; Bak and Criens 1982; Highsmith 1982; Rogers et al. 1982).

Fragmentation during storm events is a significant means of generating new colonies, as documented during several storms: Hurricanes Hattie (Stoddart 1962, 1969), Edith (Glynn et al. 1964), Gerta (Highsmith et al. 1980), Allen (Woodley et al. 1981), David and Frederic (Rogers et al. 1982), Hugo (Bythell et al. 1991), Joan (Geister 1992, Zea et al. 1998), Gilbert (Kobluk and Lysenko 1992; Jordan-Dahlgren and Rodriguez-Martinez 1998), Andrew (Lirman and Fong 1996, 1997, Jaap pers. observ.), Georges and Charley (2004) (Jaap pers. observ.), as well as after Storms Bret (Van Veghel and Hoetjes 1995) and Gordon (Lirman and Fong 1997). Lirman and Fong (1997) reported that *A. palmata* fragment wounds healed rapidly (1.59 cm of linear growth/month). Nine months after Tropical Storm Gordon, 157 of 218 fragments had fused to the sea floor, and protobranches on the fragments grew rapidly.

Population dynamics

Atlantic *Acropora* spp. are generally considered intermediate along the continuum from r-selected (rapid colonizers, fast growth, early maturation, but small maximum size and thus limited contribution to reef growth; generally brooding corals) to k-selected (slow growing, generally spawning, but attaining large colony size via indeterminate growth) life history strategies. *Acropora palmata* and *A. cervicornis* tend to be fast growing, have rapid wound healing, high rates of survival of asexually produced fragments, and the ability of broken branches to grow into new colonies (Gladfelter et al. 1978; Bak and Criens 1982; Highsmith 1982). Their level of aggression (i.e., ability to extend their mesenterial digestive filaments onto neighboring species and digest away living tissue) is relatively low compared to many other Caribbean corals (Lang 1973). However, Atlantic *Acropora* spp. have superior overgrowth capabilities. These life history characteristics, supported by documentation of recent trends in populations across the Caribbean, illustrate that once *Acropora* spp. experience local (reef-scale) reductions in colony numbers and size, recovery may not occur for decades.

There are several implications of the current low population sizes of *Acropora* spp. throughout much of the Caribbean. First, the number of sexual recruits to a population will be most influenced by larval availability, recruitment, and early juvenile mortality. Because corals cannot move and are dependent upon external fertilization in order to produce larvae, fertilization success declines greatly as adult density declines; this is termed an Allee effect (Levitan 1991). To compound the impact, *Acropora* spp., although hermaphroditic, do not effectively self-fertilize; gametes must be outcrossed with a different genotype to form viable offspring. Thus, in populations where fragmentation is prevalent, the effective density (of genetically distinct adults) will be even lower than colony density. It is highly likely that this type of recruitment limitation

(Allee effect) is occurring in some local *A. palmata* and *A. cervicornis* populations, given their state of drastically reduced abundance/density. Simultaneously, when adult abundances of *A. palmata* and *A. cervicornis* are reduced, the source for fragments (to provide for asexual recruitment) is also compromised. These conditions imply that once a threshold level of population decline has been reached (i.e., a density where fertilization success becomes negligible) the chances for recovery are low.

Population Genetics

Understanding the population structure of *A. cervicornis* and *A. palmata* is complicated by the fact that both corals undergo both sexual and asexual (clonal) reproduction (see Reproduction section above) and the relative contribution of each is not readily discernable in the field (Miller et al. in review). Two aspects of population structure are of critical importance in assessing extinction risk in widespread clonal species: (1) The degree of genotypic diversity (within populations and overall); and (2) the degree of genetic exchange between populations. The levels of genotypic diversity in *A. palmata* and *A. cervicornis* are of particular concern given their presumed dominant asexual reproductive mode (Highsmith 1982) and rapid range-wide decline (see Description and Distribution section above). That is, while quantitative field surveys may provide abundance estimates based on number of colonies or percent cover, it is conceivable that the genotypic diversity in either species might be drastically lower. The degree of genetic connectivity among populations is important in understanding the potential adaptation of local populations to specific environmental conditions and the potential for re-colonization from neighboring or distant reefs in areas of extirpation.

Immunological self-recognition (fusion versus rejection response when two individuals are placed in contact) was used in an early study to investigate clonal structure in *A. cervicornis* (Neigel and Avise 1983). This approach indicated that ramets of individual genets occurred at up to 20 m distance and individual genets occupied up to 10 m^2 in Jamaica and St. Croix, U.S.V.I. (Neigel and Avise 1983). However, there has been subsequent questioning of the genetic basis of the self-recognition response, as electrophoretically distinct individuals have been shown to fuse (e.g., Heyward and Stoddart 1985). Molecular genetic analysis seems to be necessary to reliably evaluate clonal structure.

Common molecular approaches to study genetic population structure such as mitochondrial DNA markers have yielded low levels of intraspecific variation in anthozoans in general and corals in particular and, hence, are of limited use in coral population genetic studies (Shearer et al. 2002). The presence of intracellular symbionts in coral tissue greatly complicates the application of highly polymorphic, anonymous DNA markers since it is difficult to distinguish between coral and symbiont DNA.

Previous efforts at developing coral-specific microsatellite markers for *Acropora* spp. also met with little success (Marquez et al. 2000). Nonetheless, molecular genetic tools have recently become available to address questions of population genetic structure and gene flow in *A. cervicornis* (Vollmer and Palumbi in prep) and *A. palmata* (Baums et al. in press a). These tools are summarized below, based upon manuscripts in development or under scientific review.

A recent study examined genetic exchange and clonal population structure in *A. palmata* by sampling and genotyping colonies from eleven locations throughout its geographic range using microsatellite markers (Baums et al. in press a). Results (Baums et al. in press b) indicate that populations in the eastern Caribbean (St. Vincent and the Grenadines, U.S.V.I., Curaçao, and Bonaire) have experienced little or no genetic exchange with populations in the western Caribbean (Bahamas, Florida, Mexico, Panama, Navassa, and Mona Island). Puerto Rico is an area of mixing where populations show genetic contribution from both regions, though it is more closely connected with the western Caribbean. Within these regions, the degree of larval exchange appears to be asymmetrical with some locations being entirely self-recruiting and some receiving immigrants from other locations within their region (Baums et al. in press b).

The clonal structure of individual *A. palmata* populations was found to be highly variable, ranging from completely sexual where each colony represents a different genet to completely asexual, where all colonies comprise a single genet (Baums et al. in prep). The overall range-wide average, expressed as Ng/N (the number of genotypes found divided by the total number of colonies sampled) was about 0.5. Interestingly, clonal structure appeared to vary between the eastern and western Caribbean, with eastern populations being denser and more genotypically diverse (i.e., greater contribution by sexual recruitment) than western populations (Baums et al. in prep). In fact, four out of five populations sampled in the Florida Keys were monoclonal, indicating they were derived from fragmentation of a single larval recruit (Baums et al. in press (a) and unpublished data). This lack of genotypic diversity in several *A. palmata* populations implies that sexual reproduction may be completely lost and is thus a basis for concern for the long-term persistence of this species. Measures of genetic diversity such as heterozygosity are unknown for either species and are not likely to be revealed from the current genetic approaches.

Vollmer and Palumbi (in prep.) used DNA sequences of specific nuclear and mitochondrial genes, to analyze connectivity of *A. cervicornis* populations on a Caribbean-wide scale. Their results indicate a much finer scale of geographic differentiation (i.e., less connectivity across large areas) than the microsatellite results for *A. palmata* (Baums et al. in press b). They report that larval exchange between *A. cervicornis* populations as close as 2 to 15 km is extremely limited, implying that larval sources need to be conserved on a very small spatial scale. Little is known regarding clonal structure of *A. cervicornis* populations throughout their geographic range, although Vollmer and Palumbi (in prep.) indicate that approximately 60% of the colonies they sampled (purposely sampling colonies distant from each other) from areas throughout the Caribbean represented distinct genotypes. As in *A. palmata*, populations of *A. cervicornis* in southeast Florida (Broward County, probably the most abundant extant stands anywhere) appear to have low genotypic diversity as each of the large thickets sampled to date is monoclonal (Baums and Vargas unpubl. data).

Ecological relationships

Coral reefs serve a number of functional roles in subtropical and tropical environments of the Caribbean, including, but not limited to primary production, recycling of nutrients in relatively oligotrophic seas, calcium carbonate deposition yielding reef construction, refuge and foraging base for other organisms, and modification of near-field or local water circulation patterns (De Freese 1991). Coral reefs also protect shorelines, serving to buffer inshore subtidal (e.g., seagrass) and intertidal (e.g., mangroves) communities from otherwise high wave energy conditions in certain localities. Coral reefs are host to a multitude of species of algae, invertebrates, and fishes. Reef environments are characterized by an incredible diversity of species packed into a relatively small spatial dimension (m^2 to km^2) defined by high benthic diversity (Connell 1978; Richards and Lindeman 1987). Organisms essential in the construction of tropical reefs are hermatypic (reef-building) corals and coralline algae. Through reef construction, these organisms provide habitat for sedentary and mobile species (Lewis 1981).

The functional roles discussed below are presented for *Acropora* spp. where information specific to acroporids are available, and otherwise for coral reefs in general. This generalization to function in coral reef systems as a whole is appropriate in evaluating the role of *Acropora* spp. given their status as constructional or "foundation" species in Caribbean coral reef ecosystems as described below.

Acropora **spp. were important shallow and mid-depth reef builders in the wider Caribbean**

Acropora palmata and *A. cervicornis* are two of the major reef-building corals in the wider Caribbean. Historically, both of these species formed dense thickets at shallow (<5 m) and intermediate (10 to 15 m) depths in many reef systems, including some locations in the Florida Keys, western Caribbean (e.g., Jamaica, Cayman Islands, Caribbean Mexico, Belize), and eastern Caribbean. In the Florida Keys, for example, *A. palmata* was the primary builder of constructional spur and groove reefs along much of the Florida reef tract, with coralline spurs up to several meters in height and up to 15 m in length (Shinn 1963; Shinn et al. 1981). Early descriptions of Florida Keys reefs referred to reef zones, of which the elkhorn (*A. palmata*) zone was described for many shallow-water reefs (Figure 4.3-8) (Jaap 1984; Dustan 1985; Dustan and Halas 1987).

Interestingly, Shinn et al. (1977) noted that in southeastern Florida, some reefs were able to form and keep pace with sea level rise without the "help" of reef construction of *A. palmata*. As summarized in Bruckner (2002), however, the structural and ecological roles of Atlantic *Acropora* spp. in the Caribbean are unique and cannot be filled by other reef-building corals in terms of accretion rates and the formation of structurally complex reefs.

Coral reefs influence water circulation patterns

An important characteristic of coral reefs is their ability to modify the surrounding physicalchemical environment (Ginsburg and Lowenstam 1958). The reef framework controls the accumulation of sediments on and adjacent to the reef, as well as local circulation patterns (Jaap 1984). Barrier reefs are the best example of the ability of organic communities to affect circulation patterns that in turn influence benthic community distribution and sedimentation. Barrier reefs provide shelter for the back reef lagoon, allowing for benthic communities adapted to low-wave energy conditions, such as seagrass beds, to persist and flourish. Several studies have noted the differences in sediment and habitat characteristics between inshore and offshore environments (Enos 1977; Szmant and Forrester 1996) and associated differences in sediment nutrient characteristics. Sediments in the back reef (inner shelf margin) consist of finer grain particles with greater nutrient pools relative to sediments directly associated with reefs, such as large skeletal fragments. Benthic community distribution also differs considerably between nearshore and offshore. Seagrasses and other soft-sediment communities dominate the inner shelf margin, while reefs and bare sand slope areas dominate the outer shelf margin.

Coral reefs serve important refuge and foraging functions

Coral reefs, including hard substrate and associated sediments, afford organisms an incredible array of refuges (Jaap 1984). Epifauna are organisms living on the reef surface, and include mobile epifauna (crustaceans, echinoderms, mollusks, and fishes) and sessile epifauna (e.g., sponges, corals, gorgonians, and bryozoans). Infauna are those animals which burrow into hard substrate, such as polychaete and sipunculid worms, sponges, and mollusks, while minute meiofauna are associated with reef sediments. Holes and crevices in the reef structure provide shelter for echinoderms, mollusks, polychaetes, crustaceans, other invertebrate groups, and fishes. In a single coral colony, for example, Grassle (1973) counted 1,441 polychaetes representing 103 species. In several coral colonies, McClosky (1970) counted 1,517 individuals representing 37 different invertebrate species. Gastropods, crustaceans, echinoderms, and fishes consume benthic algae associated with the reef structure (i.e., coral-produced substrate); these herbivores, in turn, fuel the production of higher trophic levels such as invertivores and carnivores.

While no comprehensive quantitative inventories have been made of all of the flora and fauna associated with coral reefs (Lewis 1981), probably the best information illustrating the diversity associated with these structures is for fishes. In western Atlantic reef environments, the number of fish species directly or indirectly associated with the reef system can exceed 400 species (Starck and Davis 1967; Jones and Thompson 1978; Bohnsack et al. 1987). The high taxonomic diversity of reef fishes indicates that many species are highly evolved, with several families entirely restricted to the reef environment, among them: Chaetodontidae (butterflyfishes), Scaridae (parrotfishes), Acanthuridae (surgeonfishes), Labridae (wrasses), Holocentridae (squirrelfishes), Balistidae (triggerfishes), and Pomacentridae (damselfishes) (Sale 1977; Longhurst and Pauly 1987). Many reef fishes are highly sedentary, with some species (e.g., damselfishes) actively defending territories. Even the spatial distribution of larger predatory species tends to be very reef-specific, with individuals rarely traveling more than 5 km from a home site after post-settlement, except for spawning purposes (Longhurst and Pauly 1987).

In addition to the important functions of reef building and reef maintenance provided by Atlantic *Acropora* spp., these species serve as fish habitat (Ogden and Ehrlich 1977; Appeldoorn et al. 1996), including essential fish habitat (CFMC 1998), for species of economic and ecologic importance. Loss of *Acropora* spp. from the Caribbean would have substantial impacts on many coral reef species and by extension on the composition of reef communities.

Assessments of reef fish abundances and diversity have been conducted in the Caribbean and the Florida Keys over the last four to five decades. Invariably, these studies have quantified fish populations relative to geomorphic strata or reef zonation (Ehrlich 1975; Sale 1980; McGehee 1994; Lindeman 1997; Kendall at al. 2003), or relative to substrate characteristics such as rugosity (Luckhurst and Luckhurst 1978), complexity (Nunez Lara and Arias Gonzalez 1998), or refuge (hole) size (Hixon and Beets 1989, 1993). A number of long-term sampling efforts may have data that can be used to infer habitat use or value, but these analyses have either not been published or are limited in spatial scope.

However in St. Croix, U.S.V.I., heterotypic schools of juvenile French and white grunts (*Haemulon flavolineatum* and *H. plumieri*) were found to transfer substantial amounts of nitrogen and phosphorous in the nutrient-poor waters of a coral reef; water nearby *A. palmata* with grunts had ammonia (NH^{4+}) concentrations up to 0.7 µM (micromolar) greater compared to a nearby colony without fish (Meyer et al. 1983). While direct connections between reef fishes and Atlantic *Acropora* spp. have not been well reported (with the exceptions below), several studies have found a positive relationship between substrate complexity and fish densities and diversity. Unfortunately, few of these studies provide data on the use of certain coral species or growth forms by particular fish species.

One exception to this pattern is the study by Lirman (1999) who reported significantly higher abundances of grunts (Haemulidae), snappers (Lutjanidae), and sweepers (Pempheridae) in high-topography areas with coverage by *A. palmata* compared to lower topography or lower coral cover sites. Comparisons between sites where *A. palmata* was absent and present suggested that fish schools, comprised primarily of grunts and snappers, use *A. palmata* colonies preferentially.

Settlement habitats of the white grunt, *Haemulon plumieri*, in another study were examined in southwest Puerto Rico in a *Thalassia-Acropora cervicornis* back-reef lagoon (Hill 2001). Although this site might nominally be classed as a seagrass bed, *A. cervicornis* was the primary focus of newly settling grunts. Neither the *Thalassia* (seagrass) nor other available coral sites (boulder or brain corals, gorgonians, algal covered corals) attracted or maintained significant numbers of juveniles during the study.

Hill (2001) indicated that *A. cervicornis* thickets were the preferred settlement habitat for grunts that became saturated during high recruitment seasons, yielding greater usage of supposed sub-optimal habitats nearby (e.g., seagrass or gorgonians). Numerous reef studies have described the relationship between increased habitat complexity, and increased species richness, abundance and diversity of fishes. Habitat selection is viewed as a trade-off between refuge from predation and access to feeding resources (Werner and Gillliam 1984). Settlement and juvenile habitats typically are thought to reduce exposure to predators (Shulman 1984). Hixon and Beets (1989, 1993) showed that appropriately sized refuges could moderate predation effects and thus alter reef fish distribution patterns. At a larger scale, complete absence of particular habitats has been shown to affect fish assemblage composition if species are not able to use alternate habitats (Nagelkerken et al. 2000). Loss of the complex habitats provided by *A. cervicornis* and *A. palmata* could result in increased rates of predation on juvenile snappers and grunts, with likely reductions of habitat-specifics like *H. plumieri*. It is important to note that *A. palmata* and *A. cervicornis* are the only large, branching coral species in Caribbean reef systems capable of creating large amounts of complex reef habitat. Though "standing dead" coral skeletons (especially *A. palmata*, as *A. cervicornis* tends to crumble into rubble) can still serve as habitat for fishes, subsequent storms and bioerosion will eventually destroy this habitat if none is being constructed to replace it.

In the current situation, with low abundance of *Acropora* spp. on most Caribbean reefs, very little new complex reef habitat is being created and, hence, its availability to ecologically and economically important reef fishes is likely to continue to decline in the coming years.

Competition

Coral reefs are described as space-limited systems and thus it is believed that competition for space is an important structuring factor. Because of their fast growth rates and canopy-forming morphology, *A. palmata* and *A. cervicornis* are known to be competitive dominants within coral communities, in terms of their ability to overgrow other stony and soft corals. However, other types of reef benthic organisms (i.e., algae) have higher growth rates and, hence, expected greater competitive ability than *Acropora* spp. Since the 1980s, many Caribbean reef areas have undergone a shift in benthic community structure involving reduced cover by stony corals and increased coverage by macroalgae. This shift is generally attributed to the greater persistence of macroalgae under reduced grazing regimes due to human overexploitation of herbivorous fishes (Hughes 1994) and the regional mass mortality of the long-spined sea urchin in 1983-84. Impacts to water quality (principally nutrient input) are also believed to enhance macroalgal productivity.

Aronson and Precht (2001) emphasize, however, that these Caribbean-wide changes in benthic assemblages were precipitated by massive coral mortality events (namely the loss of *Acropora* spp. from White Band Disease) as macroalgae are generally unable to actively overgrow and kill live corals. In other words, the coral-dominated Caribbean reef system was resistant to reduced herbivory regimes for a period of time as long as corals maintained their occupation of space. However, when coral mortality occurred, macroalgae were able to pre-empt that space (especially following the loss of grazing by *Diadema*) and were subsequently resistant to coral re-colonization (Hughes and Connell 1999). Thus the described shifts have been persistent on a decadal scale. The noted exception is in areas where the grazing sea urchins (*Diadema antillarum*) have recently recovered and removed the macroalgal dominants, thereby clearing space to allow enhanced coral recruitment (Edmunds and Carpenter 2001).

In summary, macroalgae are now the major space-occupiers on many Caribbean reefs. Their dominant occupation of reef surfaces impedes the recruitment of new corals (McCook et al. 2001) and hence, recovery by sexual recruits of *Acropora* spp. It is unlikely, however, that macroalgae have major impacts as direct competitors with healthy adult colonies. Other encrusting invertebrates may also pose a direct overgrowth threat to small colonies or bases of *Acropora* spp., but the extent of such interactions is not well documented.

Predation

Acropora spp. are subject to invertebrate (e.g., polychaete, mollusk, echinoderm) and vertebrate (fish) predation, but "plagues" of coral predators such as the Indo-Pacific crown-of-thorns outbreaks (*Acanthaster planci*) have not been described in the Atlantic.
Predation may directly cause mortality or injuries that lead to invasion of other biota (e.g., algae, boring sponges).

The most important predators on Atlantic *Acropora* spp. are the fireworm, *Hermodice carunculata*, and the muricid snail, *Coralliophila abbreviata*. Both these predators will feed on a wide range of cnidarian prey, but may prefer *Acropora* spp. *Hermodice* are commonly found enveloping the long branch tips of *A. cervicornis* that are subsequently left devoid of tissue (Marsden 1962; Lizama and Blanquet 1975; Dustan 1977). *Hermodice* also feeds on branch tips or protuberances of *A. palmata*, where the predation scars appear as white patches (Porter 1987). Vargas-Angel et al. (2003) report a density between 86 and ~618 *Hermodice* ha^{-1} in *A. cervicornis* thickets in southeast Florida with predation scars affecting <0.2% of the *A. cervicornis* cover. There are few other data on the prevalence or impact of *Hermodice* on *Acropora* spp. populations.

Although these predators rarely kill entire colonies, there are several possible mechanisms of indirect impact. Because they prey on the growing tips (including the apical polyps), especially of *A. cervicornis*, growth of the colony may be arrested for prolonged periods of time. Additionally, *Hermodice carunculata* from the Mediterranean Sea has been shown to serve as a vector for a bacterial bleaching pathogen in laboratory experiments (Sussman et al. 2003).

The other important predator of Atlantic *Acropora* spp. is the gastropod, *Coralliophila abbreviata*. This predator also feeds on a wide range of corals, but seems to be particularly damaging to *Acropora* spp. (Baums et al. 2003b). Prevalence data from throughout the Caribbean indicates that approximately 10% to 20% of *Acropora* spp. colonies harbor snails (Baums et al. 2003a). The rate of consumption by *Coralliophila* is highly variable, but may reach 6.5 cm^2 of coral tissue per snail per day (Bruckner et al. 1997) and probably averages ~1.5 cm^2 of coral tissue per snail per day (Baums et al. 2003b). Given that the mean snail density on infested *A. palmata* colonies is reported at over three snails per colony (Bruckner et al. 1997; Baums et al. 2003a) with a maximum of at least 23 snails per colony (Baums et al. 2003a), snail predation clearly represents a significant potential source of tissue loss. There is evidence that these predators concentrate on remnant *Acropora* populations following host coral decline (Knowlton et al. 1990; Baums et al. 2003a). For example, after Hurricane Allen struck the north coast of Jamaica in 1980 and greatly reduced the acroporid population, *C. abbreviata* continued to feed on remnant *A. cervicornis* colonies, reducing the population further (Knowlton et al. 1981). It should be noted, however, that *Coralliophila* seem to be extremely rare or absent on *Acropora* spp. in certain areas (e.g., Bocas del Toro, Panama, Baums pers. comm.; Dry Tortugas, Miller pers. observ.).

The three-spot damselfish (*Pomacentrus planifrons*) and other species in the genus establish algal nursery gardens within branching *Acropora* spp. when available and on other coral species when acroporids are rare (Thresher 1976; Brawley and Adey 1977; Kaufman 1977; Itzkowitz 1978; Williams 1978; Sammarco and Carleton 1982). Although not predators in the strict sense, the damselfishes nip off living coral tissue, thus denuding the skeleton to make a place for their algal gardens. Again, it is likely that *P. planifrons* impacts are proportionally greater when the abundance of *Acropora* is reduced. Observations in several areas (e.g., Dry Tortugas, Navassa) suggest that isolated small colonies, particularly of *A. cervicornis*, have a very high prevalence of damselfish occupation.

Other predators also consume *Acropora* tissue to a lesser degree. Although not widely documented, the Caribbean long-spined sea urchin (*Diadema antillarum*) is known to feed upon live *Acropora* coral tissue (Bak and van Eys 1975, Sammarco 1980). Laboratory experiments confirmed that this sea urchin will feed on coral tissue when starved, but may also do so when feeding on turf algae when sea urchin population numbers are relatively high (e.g., >4 individuals/m^2) (Porter 1987). More recent studies indicate that besides damselfishes, parrotfishes, such as the stoplight parrotfish (*Sparisoma viride*), may also incidentally feed upon *Acropora* tissue. Very little is known concerning the extent of parrotfish grazing on Atlantic *Acropora* spp., but monitoring in the Florida Keys indicates that these scars usually heal in a matter of weeks to months (Williams pers. comm.).

Overall, predators can have important direct and indirect impacts on *A. palmata* and *A. cervicornis*. Predation impacts are greater in the current scenario of low coral abundance as coral predators have not been subject to the same degrees of disturbance mortality and their broad diet breadth has allowed them to persist at high levels despite decreases in acroporid prey. However, predation impacts on *Acropora* spp. appear to be much lower in certain geographic areas.

4.4 State Comprehensive Wildlife Conservation Stategies

(excerpted from the State Wildlife Action Plans Summary Report (August 2006): http://www.teaming.com/pdf/StateWildlifeActionPlansReportwithStateSummaries.pdf)

The wildlife action plans represent a collective vision for the future of conservation. For the first time, states have had the opportunity to assess the full range of challenges and actions that are vital to keeping wildlife from becoming endangered.

The impetus for the historic planning effort comes from the Teaming with Wildlife coalition, representing more than 3,500 agencies, conservation groups, and businesses who for more than a decade have tirelessly championed the cause for funding to keep wildlife from becoming endangered. The coalition's work led to passage of the Wildlife Conservation and Restoration Program and the State Wildlife Grants Program in 2000. As a requirement of these programs, Congress asked each state wildlife agency to develop a "comprehensive wildlife conservation strategy"—a wildlife action plan—that evaluates wildlife conservation needs and outlines the necessary action steps.

While the wildlife action plans share a common framework of the eight required elements, they are tailored to reflect each state's unique wildlife, habitat, and conservation needs. States worked closely through the Association of Fish and Wildlife Agencies and the U.S. Fish and Wildlife Service on the development of the wildlife action plans. By combining the best scientific information available with extensive public participation, states developed effective action plans that will work for wildlife and for people.

The wildlife action plans focus on practical, proactive measures to conserve and restore important lands and waters, curb establishment of invasive species and address other pressing conservation needs. The tools for conservation employed in the action plans emphasize incentives, partnerships and collaborative management, rather than top-down regulations. The action plans also stress the importance of gaining the knowledge necessary to effectively conserve a broad range of wildlife species. In addition, every state wildlife action plan incorporates continued monitoring and evaluation in order to measure the success of the proposed actions in conserving wildlife.

Taken as a whole, the wildlife action plans present a national action agenda for the conservation of wildlife species that is focused on those that have not benefited from conservation attention due to lack of dedicated funding. The results are already apparent in improved relationships at all levels—across public and private ownerships, across state boundaries, and in the growing list of new groups and individuals working together for wildlife. Taking the timely next steps to adequately fund these wildlife action plans is crucial in order to achieve the goal of preventing wildlife from becoming endangered.

Below are the Executive Summaries for each of the South Atlantic states' Comprehensive Widlife Conservation Strategies. For detailed information contained in each Plan, please refer to each document. The documents can be downloaded in pdf format at http://www.teaming.com/state_pages.htm).

North Carolina

For more than fifty years, state fish and wildlife agencies have benefited from funds accumulated through the Federal Aid in Wildlife Restoration Act (Pittman-Robertson), the Federal Aid in Sport Fisheries Restoration Act (Dingell-Johnson), and the Aquatic Resources Trust Fund (Wallop- Breaux), to support the conservation and management of game fish and wildlife species. These funds have been critical to the establishment of long-term state agency planning related to game species. Yet conservation efforts for the majority of fish and wildlife species, those that are not hunted or fished, have in large part been opportunistic and crisis-driven, limited by the availability of funding, and by a lack of strategic approaches to species and habitat conservation. With more than 1,000 species now listed on the Federal Endangered and Threatened species list, the need has never been greater for funding and planning to support the conservation, protection, and restoration of the full array of wildlife species, especially those not covered under traditional funding sources.

In 2001 Congress, recognizing this need, began providing annual funding allocations to supplement existing state fish and wildlife conservation programs. Along with this new funding came the responsibility of each state and territory to develop a Wildlife Action Plan. The North Carolina Wildlife Action Plan was submitted to meet that obligation, and in the process, provide a conservation blueprint for agencies, organizations, industries, and academics across the state to advance the sound management of our fish and wildlife resources into the future. Within the document, we identify critical fish and wildlife resources and priority conservation needs associated with those resources. Our Plan is strengthened by all of the local, state, and regional conservation planning efforts that have preceded it; these efforts provided us a foundation upon which to build.

Our Plan promotes proactive conservation measures to ensure cost-effective solutions ("keeping common species common") instead of reactive measures enacted in the face of imminent losses.

Five goals form the core of the Plan: 1) to improve understanding of the species diversity in North Carolina and enhance our ability to make conservation or management decisions for all species, 2) to conserve and enhance habitats and the communities they support, 3) to foster partnerships and cooperative efforts among natural resource agencies, organizations, academia and private industry, 4) to support educational efforts to improve understanding of wildlife resources among the general public and conservation stakeholders, and 5) to support and improve existing regulations and programs aimed at conserving habitats and communities.

In order to meet these goals, we engaged hundreds of people across a broad spectrum of agencies and organizations. We continue to seek the feedback and input of conservation stakeholders.

Key themes that are perpetuated through the document include:

- The need to strengthen partnerships among natural resource agencies, organizations, academics, and individuals in order to meet shared goals and visions,
- The need to impact the landscape in a large-scale fashion, and to consider all components of a sustainable community of plants and animals,
- The need to gather additional information and fill knowledge gaps in order to advance our understanding of species and their habitats,
- The need to work cooperatively with private landowners to influence the conservation of natural resources across the majority of the state, and
- The need to educate and engage local governments, planning commissions, and urban public about the importance of fish and wildlife conservation as a key component of successful land use planning.

The sections of the Plan build on one another in similar fashion to its development. Within the **Approach** section are summaries of key processes and exercises that were carried out in order to develop the Plan, including organizational frameworks, partnerships and stakeholder involvement, and the species prioritization process. Next, in the **State of the State** we provide an overview of the condition of the state's natural resources, threats affecting species and habitats in the state, key conservation partners, and challenges faced in program administration and efficacy. In **Statewide Conservation Strategies** we address four broad-scale conservation issues, including strategies on urban wildlife issues, private lands wildlife management, land conservation priorities, and education and outreach. Following is the most detailed chapter of the report, entitled **Species and Habitat Assessments & Conservation Strategies**. In this chapter, we feature the conservation needs of terrestrial resources within habitats across the three ecoregions of the state (the Southern Blue Ridge, Piedmont, and Mid-Atlantic Coastal Plain), aquatic resources within the 17 river basins in the state, and marine resources at our coast (this section is largely based on the North Carolina Division of Marine Fisheries Coastal Habitat Protection Plan). Next, we address cross-cutting conservation needs among habitats and basins within **Synthesis of Conservation Priorities**. In **Status and Trends Monitoring** we discuss species and habitat monitoring needs. We outline ways to monitor the implementation of conservation activities, adapt to new information, and revise future iterations of the Plan in our final chapter, **Implementation Monitoring, Adaptive Management, & Review and Revision Procedures**. Last, we present **Acknowledgements**, a comprehensive **Glossary**, a **Key to Abbreviations and Acronyms**, and multiple **Appendices**.

This document was developed at the strategic level, meaning that the implementation of activities identified in the Plan must go one step farther to consider the operational details of involving partners, setting explicit objectives and targets, detailing monitoring protocols, etc. We have organized the format and content of the Plan to provide maximum utility as a resource to set conservation priorities. The Plan is designed to flow from beginning to end, but individual chapters and sections can also be used independently, as stand-alone documents. For example, users may turn to a particular habitat or basin section to review priority needs and recommendations pertaining specifically to their region or expertise area (e.g., the Catawba River basin, maritime forest habitat).

We hope that the information provided within each chapter and section translates into clear and objective conservation planning at that level.

Our Plan has been nearly three years in development. The development process was strengthened by the input, feedback, and participation of hundreds of stakeholders across the state (stakeholder representation extended across more than 15 state and federal agencies, 12 non-governmental organizations, five universities, and four private companies). But the completion of this first edition is just the beginning. The Plan is a work in progress, and will continue to evolve during implementation and through future revisions. Though the funding that initiated development of the state Plan continues to be allocated on an annual basis (making long-term planning difficult), there is hope across the nation that our state Strategies will clearly demonstrate to Congress the need for increased and permanent Federal fish and wildlife conservation funding in the future. Regardless of funding sources, the partnerships and collaborative efforts that this Plan fosters should lead to significant accomplishments in the conservation of North Carolina's wildlife resources.

South Carolina

In May of 2002, the South Carolina Department of Natural Resources (SCDNR) began a process to develop the Comprehensive Wildlife Conservation Strategy (CWCS) that was funded through the State Wildlife Grants (SWG) program. The SCDNR committed to developing the Strategy and begin implementing the conservation actions by October 1, 2005. The goal of the Strategy is to emphasize a cooperative, proactive approach to conservation while working with federal, state and local governments; local businesses; and conservation-minded individuals to join in the effort of maintaining the fish and wildlife resources of South Carolina.

In order to sustain South Carolina's diverse wildlife resources in the future, the following actions are critical: (1) increase baseline biological inventories with emphasis on natural history, distribution and status of native species; (2) increase commitment by natural resource agencies, conservation organizations and academia toward establishing effective conservation strategies; (3) increase financial support and technological resources for planning and implementation of these strategies; and (4) create public-private partnerships and educational outreach programs for broad-scale conservation efforts. South Carolina's CWCS is a first step toward instituting these actions.

The diversity of animals in South Carolina is vast. Habitats in this state range from the mountains to the ocean and include many different taxonomic animal groups. SCDNR wanted to address as many of those groups as possible for inclusion in the list of priority species for the CWCS; as such, twelve taxonomic groups are included in the Strategy: mammals, birds, reptiles, amphibians, freshwater fishes, diadromous fishes, marine fishes, marine invertebrates, crayfish, freshwater mussels, freshwater snails, and insects (both freshwater and terrestrial).

The SCDNR identified 1,240 species to include on the state's Priority Species List. Reports were prepared for each species, guild or indicator; in these reports, authors described the species, their status, population and abundance, habitat needs, challenges, conservation accomplishments and conservation actions. This approach allows for identification of both general conservation strategies for wildlife and habitats in South Carolina, as well as development of species-based conservation strategies. The latter allows for management of particular species within a given habitat. A separate volume, **Supplemental Volume: Species and Habitat Accounts**, contains these reports in their entirety. The SCDNR also identified habitats critical for the priority species considered in the CWCS. Both terrestrial and aquatic habitats were considered and reports were prepared for 38 habitats (terrestrial and marine) organized within five ecoregions, as well as 13 ecobasins, which characterize the freshwater aquatic habitats of the state. These reports are also presented in the Supplemental Volume.

As conservation strategies were developed for each species, it became evident that they could be separated into eight categories, which we have designated as Conservation Action Areas (CAAs). These eight CAAs are: Education and Outreach; Habitat Protection; Invasive and Nonnative Species; Private Land Cooperation; Public Land Management; Regulatory Actions; Survey and Research Needs; and Urban and Developing Lands. Within each CAA, conservation actions were condensed from the recommendations prepared for each animal on South Carolina's Priority Species List. Some of the actions identified will affect all species included in the CWCS; others may affect only a few species. Each of these actions was prioritized and measures that indicate success of implementing the action were identified.

It is also critical that we monitor priority species, their habitats and the effectiveness of the actions that are implemented to conserve them. With the information gathered in this program, project leaders will be required to produce annual progress reports for review by a steering committee and the CWCS coordination team. These reports will be evaluated for insight into adaptive management needs and reassessments of the CWCS.

From the beginning of the CWCS effort, SCDNR and the planning team sought to realize successful partnerships and public involvement in the development of the strategy. It is understood that successful conservation is furthered by the existence of a strong collaborative involvement between all resource stakeholders, private or public, governmental or nongovernmental. Task forces were convened to assist in determining important natural resource issues in South Carolina. Taxa teams were assembled to determine challenges to species and conservation actions to address those challenges. Public meetings were held to gather input from the citizens of the state. Prior to submission of the CWCS, the SCDNR began creating Conservation Action Committees around the CAAs identified above; two of these committees have convened and have begun working toward identifying statewide strategies for species and habitat conservation. Partnerships will continue to be critical in implementing the actions identified in South Carolina's CWCS.

Georgia

In December 2002 the Wildlife Resources Division (WRD) of the Georgia Department of Natural Resources (DNR) began a process to develop a comprehensive wildlife conservation strategy. Through the Wildlife Conservation and Reinvestment Program, WRD made a commitment to develop and begin implementation of this comprehensive wildlife conservation strategy (CWCS) by October 1, 2005. Funding for this planning effort came from a federal grant to WRD through the State Wildlife Grant program; matching funds were provided through Georgia's Nongame Wildlife Conservation Fund.

The goal of the strategy is to conserve Georgia's animals, plants, and natural habitats through proactive measures emphasizing voluntary and incentive-based programs on private lands, habitat restoration and management by public agencies and private conservation organizations, rare species survey and recovery efforts, and environmental education and public outreach activities.

The best available wildlife data were used to develop this CWCS. The strategy included an assessment of habitats required by these species, as well as problems affecting these habitats. Further, this strategy addressed research and survey needs, habitat restoration needs, and monitoring needs. It also included an evaluation of existing programs and policies for wildlife conservation in Georgia and recommendations for improvements in these areas. Coordination with other organizations that manage land or administer conservation programs in Georgia was a key component of this effort.

The planning process involved staff within DNR, representatives of private and public conservation organizations and land managers and owners in Georgia. A Steering Committee composed of representatives of various agencies, organizations, and land management groups provided project oversight. Technical teams addressed specific components of the conservation strategy; these teams included WRD staff and representatives of other agencies and organizations. Input from the Steering Committee, stakeholders, representatives of other conservation organizations, consulting biologists, academic researchers, and the public was used in the development of the conservation strategy. Educational materials were developed to inform the public about the project's goals and milestones; these materials were posted on a website developed specifically for this project and distributed at public meetings.

Components of this planning effort included: 1) development of databases on rare species and natural communities; 2) identification of high priority species and habitats; 3) identification of high priority research and biological inventory needs; 4) surveys for rare species on public and private lands; 5) development of databases of conservation lands and high priority watersheds and landscapes; 6) prioritization of conservation, education, and habitat protection needs; 7) collaboration with state and federal agencies on habitat protection/restoration plans; 8) technical assistance to private conservation organizations and local governments; 9) review of existing conservation laws, rules, and policies; and 10) public input and educational outreach.

Three technical teams focused on biodiversity database development and use, GIS/mapping support and land cover assessments, and environmental education, respectively. The GIS support team developed and distributed a survey to WRD staff to determine priority needs for geographically based dataset needs. Team members also reviewed the land cover database produced by the Georgia Gap Analysis Program, continued development of a statewide conservation lands database, and produced land cover and vegetation maps. The database support/enhancements team discussed uses of biological diversity data. This team developed specific recommendations for exchange and application of biodiversity information, including improved Web-based access to rare species/natural community information, region-specific rare species datasets for WRD law enforcement personnel, and watershed-based datasets. The environmental education team developed recommendations for improvements in wildlife-related education programs, and was assisted by the Environmental Education Alliance of Georgia.

Six technical teams focused on the following groups of species: birds, amphibians and reptiles, mammals, fishes and aquatic invertebrates, terrestrial invertebrates, and plants.
Although conservation efforts for plants could not be addressed under this grant, a parallel conservation planning process was undertaken, funded in part through a federal grant to the Wildlife Resources Division, with matching funds provided from the Nongame Wildlife Conservation Fund. These technical teams consulted numerous data sources and used a variety of criteria to identify high priority species for Georgia; these included critically imperiled species, habitat indicator species known to be in decline, species endemic to Georgia, and rare or uncommon species in need of further research to determine conservation objectives.

Results of the various biological and ecological assessments undertaken in this planning effort are presented in this document. Many of the details of these analyses can be found in the appendices that follow the main report. Ranges of distribution, habitat associations, conservation needs, and research priorities for 296 species of high priority animals and 323 species of high priority plants are outlined in Section IV and in appendices A and B. Similarly, high priority habitats are defined for each ecoregion and management needs for these habitats are discussed in Section IV and Appendix C.

In this document, conservation goals are defined broadly, while discussions of strategies and partnerships more specifically address the objectives that must be met to achieve these goals. Conservation goals, strategies and partnerships are identified for each of the five ecological regions of the state in Section IV of this report. In addition, statewide wildlife conservation themes and strategies are addressed in Section V. Lists of specific high priority conservation actions were also developed. These conservation actions were first identified by the technical teams, Steering Committee, and other stakeholders and included specific programs for improvements in habitat protection, conservation of high priority habitats and species, research and surveys, and environmental education and public outreach. These identified conservation actions were then evaluated by the Steering Committee using a set of seven ranking criteria. The complete set of 78 prioritized conservation actions can be found in Appendix L of this report. Summaries of existing programs and resources for habitat protection and recommendations to increase capacity for wildlife conservation in Georgia are provided in Section V of this document.

The following goals represent important conservation themes in this document:

- Maintain known viable populations of all high-priority species and functional examples of all high priority habitats through voluntary land protection and incentive-based habitat management programs on private lands and habitat restoration and management on public lands.

- Increase public awareness of high priority species and habitats by developing educational messages and lesson plans for use in environmental education facilities, local schools, and other facilities.
- Facilitate restoration of important wildlife habitats through reintroduction of prescribed fire, hydrologic enhancements, and vegetation restoration.
- Conduct statewide assessments of rare natural communities and habitats that support species of conservation concern.
- Improve efforts to protect vulnerable and ecologically important habitats such as isolated wetlands, headwater streams, and caves.
- Combat the spread of invasive/noxious species in high priority natural habitats by identifying problem areas, providing technical and financial assistance, developing specific educational messages, and managing exotic species populations on public lands.
- Minimize impacts from development and other activities on high-priority species and habitats by improving environmental review procedures and facilitating training for and compliance with best management practices.
- Update the state protected species list and work with conservation partners to improve management of these species and their habitats.
- Conduct targeted field inventories of neglected taxonomic groups, including invertebrates and nonvascular plants.
- Continue efforts to recover federally listed species through implementation of recovery plans, and restore populations of other high priority species.
- Establish a consistent source of state funding for land protection to support wildlife conservation, and increase availability and use of federal funds for land acquisition and management.
- Continue efforts to monitor land use changes statewide and in each ecoregion, and use predictive models to assess impacts to high priority species and habitats.

Monitoring needs for species, habitats, and conservation programs are also addressed in Sections IV and V of this document. Monitoring programs are acknowledged as critical components of adaptive management efforts in wildlife conservation, and specific recommendations are provided to improve existing monitoring programs. In addition, partnerships with other organizations involved in monitoring efforts are recommended.
Specific high priority monitoring projects are mentioned in the body of the report and in Appendix L. The approach taken in this planning effort was to identify the types of data to be collected and relevant performance indicators for every high priority conservation action as a first step to development of monitoring programs.

Several projects undertaken as components of this planning project represent efforts to develop new analytical tools and methods that can inform future conservation plans at various geographic scales. A pilot project to develop historic vegetation maps was completed by researchers at the University of Georgia. Using land lot survey data from the 1800s, researchers developed historic vegetation maps for three state-owned wildlife management areas. This pilot project produced analytical tools and data that will facilitate development of habitat management plans for public lands. A second pilot project utilized land cover data from the Georgia Gap Analysis Program and occurrence data for rare and declining species to identify regions of the state that may represent important areas for conservation work in the future. These two projects are described in appendices J and K, respectively.

Project staff began development of a new natural community classification system that will serve as a standard for habitat mapping on public lands. The new classification system is based on ecosystems and vegetation alliances described by NatureServe and the Natural Heritage Network. WRD staff also collaborated with a group of volunteers working on a detailed guide to Georgia's natural environments. This document will be based on the NatureServe ecosystem classification and written for a broad audience including teachers, science students, and practicing biologists. Development of this document will facilitate mapping and tracking of natural communities consistently across the state and increase public awareness of Georgia's ecosystems.

Public involvement in the development, review and revision of this document was facilitated by a series of fourteen public meetings undertaken over the project period.
These included regional stakeholder meetings as well as traditional public meetings. In addition, public input was solicited through materials posted on the CWCS website, news releases, brochures, fact sheets, and presentations given to various groups and organizations around the state. These public outreach efforts will continue as we begin to implement the conservation strategy.

The CWCS reflects an assessment of wildlife conservation needs and programs to address those needs based on data available in 2003-2005. Our understanding of the conservation needs of Georgia's species and habitats is likely to change based on the result of additional surveys, results of monitoring efforts associated with management efforts, or new trends in land uses. In addition, the development of new analytical techniques, funding programs, or legislative mandates may result in a need to reassess some of the conservation priorities described in this document.

The intent of the Wildlife Resources Division is to begin a formal process of reviewing the current wildlife conservation strategy within the next five years and to adopt revisions to the strategy as deemed necessary based on this review. In order to do this, we propose to reconvene the technical teams and Steering Committee and hold public meetings to assess and address changing conservation needs for species and habitats in Georgia. The proposed procedure for this review is outlined in Section VI of this document.

The first piece of legislation to be approved by the 2005 session of Georgia General Assembly was the Georgia Land Conservation Act and on April 14, 2005, Governor Perdue signed into law this important piece of legislation. The bill enjoyed overwhelming public and legislative support and was generally lauded throughout the state. The intent of the Act is to provide funding options and a flexible administrative framework to conserve land resources, recognize the values of the State's natural and cultural resources, and promote land conservation partnerships.

The Wildlife Resources Division of the Georgia Department of Natural Resources views this new state land conservation program as an important and timely component of the

Comprehensive Wildlife Conservation Strategy that will aid significantly in its implementation. This Act directs some $100 million for land conservation efforts in the state of Georgia and makes available $45 million in state and private funding that can and will be used to match and leverage various federal wildlife conservation grants consistent with the strategies and priorities included in this document.

The changes that are occurring in the Georgia landscape as a result of population growth and increasing development pressures present daunting challenges to those involved in wildlife conservation. The trend of increasing fragmentation and degradation of natural habitats is likely to continue in the coming decades, driven by local, national, and global economic and demographic factors. Many scientists believe that the next fifty years will be a critical period in the struggle to protect our remaining biological resources.

The following elements are critical for conservation of Georgia's natural heritage: (1) increased emphasis on field research focused on the identification and assessment of species, biotic communities, and ecosystems; (2) greater commitment of resources to identify and protect those habitats that contribute most significantly to biodiversity; (3) further development and funding of conservation programs that emphasize public-private partnerships for broad-scale conservation of "working landscapes"; (4) greater emphasis on land use planning to minimize impacts of future developments on natural habitats; and (5) increased collaboration between researchers and educators to heighten public awareness of the magnitude and significance of biodiversity decline in the state. The Department of Natural Resources will continue to work with a wide array of public agencies, private conservation organizations, research institutions, sportsmen's groups, educators, local governments, and landowners in the coming years to address these critical elements of wildlife conservation.

Florida

The primary support and focus for wildlife conservation and management within the United States historically has come from state hunting and fishing interests and Federal Assistance programs for game species under the Pittman–Robertson, Dingle–Johnson, and Wallop–Breaux Acts. Additionally, the Endangered Species Act has provided support to recover federally threatened and endangered species. Although these programs have been successful, the majority of wildlife species have unmet conservation needs and many are at risk of becoming imperiled.

Waiting until a species is on the verge of extinction and then trying to recover it is costly and results in the inevitable loss of some species. To encourage a new conservation paradigm and work towards managing species before they become imperiled, the U. S. Congress created the State Wildlife Grants Program. This program is dedicated to a holistic approach that includes all species, but is centered on conservation of species that have not fallen under historical efforts. As a requirement of participating in the State Wildlife Grants Program, the Florida Fish and Wildlife Conservation Commission (FWC) has joined the other 55 states, territories, and district by committing to develop a Comprehensive Wildlife Conservation Strategy (Strategy) for the state.

To meet the intent of the State Wildlife Grants Program, the FWC has created Florida's Wildlife Legacy Initiative (Initiative). The goal of the Initiative is to develop a strategic vision for conserving all of Florida's wildlife. The three main objectives of the Initiative are: (1) to create partnerships for wildlife conservation across the State of Florida; (2) to support partnership building and use of the Strategy by making funding available through Florida's State Wildlife Grants Program; and (3) to develop and implement Florida's Strategy. Thousands of experts and stakeholders have participated and provided input to meet these objectives. These partners, including representatives from other state and federal agencies, organizations, businesses, and individuals, have been integral throughout the Strategy development process.

As discussions and work have progressed on planning, development, and implementation of Florida's Wildlife Legacy Initiative, several major premises have been employed and incorporated throughout the Strategy:

- The goal of Florida's Strategy is to build a blueprint and action plan for conserving the vast array of wildlife that makes Florida such a unique place to live and visit. This blueprint should be compatible with human needs and not preclude recreational or other use of wildlife resources and landscapes.
- Florida already has developed and implemented significant wildlife resource management tools and programs. The Strategy has been designed to build upon these efforts in a cumulative manner, identify gaps and further needs, and create a comprehensive vision for coordinating efforts across the state.
- Florida's Strategy uses a habitat category approach to arrange wildlife species and habitats, and the conservation threats and actions needed to conserve them, into meaningful and manageable categories. By taking actions that sustain the health and integrity of the habitat categories, the broad array of wildlife that lives within each will be conserved and maintained.
- The Strategy encompasses the entire state and therefore is too broad for any one individual, group, or agency to develop and implement. Coordination and cooperation among federal and state agencies, local governments, Native American tribes, non-governmental organizations, private entities, and individuals is essential.
- A non-regulatory approach is paramount to create partnerships for implementation of actions needed to conserve wildlife. The Strategy focuses on voluntary and cooperative efforts providing a starting point to develop non-regulatory mechanisms. The Strategy is not regulatory in nature and is not intended to be used in a regulatory manner.
- Meeting the needs of wildlife will mean a healthier environment for future generations of Floridians. Florida faces a huge challenge to meet the needs of an expanding human population while conserving wildlife resources.
- Education has played a vital role in conservation of Florida's wildlife and other natural resources. Support for conservation education is needed to promote awareness, responsible action and behavior.
- The Strategy should clearly meet or exceed the eight elements required under the State Wildlife Grants Program and federal guidance.

The Strategy is organized in chapters, which follow a progression of thought and content development. The **Introduction**, **Approach**, and **State of the State** form the beginning section of the Strategy. The **Introduction** briefly outlines what the effort is and provides context for how it has been undertaken in Florida. The **Approach** summarizes the processes that were carried out in order to develop the Strategy, including organizational structure and methods specific to each Strategy requirement. The **State of the State** provides a discussion of Florida's natural resources, including economics, wildlife species, and conservation resources.

Florida's Strategic Vision forms the central section of the Strategy and synthesizes a strategic view for wildlife conservation at the statewide-level. Priority conservation issues are addressed in this chapter, including species, habitats, threats, actions, data gaps, monitoring tools, and conservation challenges. Species form the basis for Florida's entire endeavor and focus should continually be placed back upon them as the Strategy is implemented and reviewed. Several habitats have been highlighted for their importance and generally were associated with coastal, wetland, upland pine, reef, and submerged aquatic vegetation areas. Major statewide threats identified include: habitat loss and fragmentation, degradation of water resources, incompatible fire management, invasive plants and animals, and management of the physical environment (e.g., dams, shoreline hardening, dredging, etc.). Major statewide actions developed to abate these threats include: development of incentive-based programs for conservation, acquisition of important lands and waters, coordination of conservation efforts, public education, and development of a cooperative conservation effort. Priority data gaps to be filled focus on improved habitat mapping capability, filling species information needs, improving understanding and methodology for marine systems, and initiation of more efforts related to genetic diversity issues. Monitoring and adaptive management are focused on species, habitat, threat, and overall Strategy levels and will be critical to documenting success and refining efforts. Lastly, key conservation challenges such as partnership development, information management, and public awareness must be met and overcome for efforts to be successful.

The chapters on **Species of Greatest Conservation Need** (SGCN), **Habitats**, and **Multiple Habitat Threats and Conservation Actions** form the final and most extensive section of the Strategy. The SGCN chapter identifies 974 species of interest and lists their status and trends. The Habitats chapter describes 45 terrestrial, freshwater, and marine habitat categories that comprise the state of Florida. These habitat category descriptions include information on their status and trends, associated SGCN, related threats, and conservation measures needed. Additionally, the chapter **Multiple Habitat Threats and Conservation Actions** lists threats that apply to greater than five habitats and the suite of actions to abate each threat. Last, the Strategy contains **Acknowledgements**, **References/Literature Cited**, a **Glossary of Acronyms**, a **Glossary of Terms**, and four **Appendices**.

Florida's Strategy is a strategic vision of the integrated conservation efforts needed to sustain the broad array of wildlife in the state. More detailed operation-level plans will be needed to complete many of the actions identified in the Strategy. Such plans should be developed by the appropriate entities whose interest, authority, or responsibility encompass each action. Although the Strategy is not intended to be a work or management plan for the FWC or any other organization, support provided by the State Wildlife Grants Program will enable coordination and implementation of many projects through Florida's Wildlife Legacy Initiative. The Strategy is a work in progress that will continually be updated, revised, and improved based on the input and deliberations of all those interested in wildlife conservation. Working together, Floridians can shape a future that is filled with the wonderful wildlife resources that define this great state and provide for the enjoyment, recreation, sustenance, and livelihood of its citizens and visitors.