SAFMC Fishery Ecosystem Plan II: South Atlantic Food Webs and Connectivity Section

1. Introduction

A key tenet of ecosystem-based fisheries management (EBFM) is the explicit consideration of indirect effects of fisheries, such as through food web processes, when developing harvest strategies and management plans. This is crucial because of the high likelihood that fishing leads to unintended and unforeseen consequences on the ecosystem. These indirect effects of fishing can arise through "top-down" (predator dominated) or "bottom-up" (nutrient driven) disruptions to the food web, or both. For example, over exploitation of predators can cause an increase in abundance of their prey and a decline of organisms two trophic levels below them, a phenomenon known as a trophic cascade (Carpenter et al. 1985). Fishing on lower trophic level species, planktivorous "forage" fishes for example, can also have effects on other components of the system (e.g. Okey et al. 2014). When the net productivity of a prey species is diverted to harvest, predator populations will ultimately decline (Walters and Martell 2004). Interspecific competition for food occurs when there are two or more species that overlap in time and space and utilize the same limited resource. Competition within a food web also has implications for management, for example when simultaneously rebuilding two competing species or when a non-native species becomes established. Changes in primary production can have noticeable effects on the food web. These "bottom-up" processes are largely driven by changes in climate or physical oceanography, particularly those that drive patterns of precipitation or upwelling and therefore nutrient input. While dynamics of lower trophic level species are more strongly tied to environmental forcing, for most species it's the combination of both fishing and environmental forcing that drive changes in population size (Chagaris and Mahmoudi 2009; Mackinson et al. 2009).

Food webs also serve to connect different components of the larger ecosystem. Seasonal and ontogenetic migrations by some species out of estuaries to coastal areas where they become prey is one mechanism that transfers energy from the inshore to offshore environments. Latitudinal (north-south) migrations provide a means to transfer energy from seasonally productive regions where prey is abundant to less productive regions at other times. Connectivity between the benthic and pelagic food webs is also important for transfer of pelagic and midwater production to seafloor communities and *vice versa*. For example, food web linkages connect pelagic forage fishes and their piscivorous predators to demersal carnivores. This connectivity between food webs over space, time, and depth creates multiple energy pathways that enhance ecosystem stability and resilience.

One way to incorporate food web processes into management is through models. Mathematical trophic-dynamic models are particularly useful because they can assist in determining the tradeoffs associated with harvesting fish from different parts of the food web while also allowing for examination of impacts resulting from changes in primary production and other bottom-up processes. Food web models are increasingly being utilized by fisheries managers as ecological prediction tools because they provide the capability to simulate the entire ecosystem from primary producers to top predators and fisheries. Such models can be used to screen policy options for unintended consequences on the system and evaluate their effectiveness in an ever changing environment. Additionally, food web models can serve to inform single species assessment and management and are capable of generating reference points (Walters et al. 2005) and ecosystem-level indicators (Coll et al. 2006; Fulton et al. 2005).

The overall objective of this chapter is to provide background, contextual information about food webs that should be considered by the SAFMC when developing single species and fisheries ecosystem plans in the South Atlantic. When possible we provided case studies and examples that are specific to South Atlantic species and ecosystems, however we also recognize that many of the principles discussed in this chapter have not been studied in the region. This chapter begins with a brief overview of estuarine, nearshore, and offshore food webs of the South Atlantic Ecosystem. Next we discuss energy flow through food webs and provide contextual information on basal energy sources, the processes regulating energy flow, dominant energy pathways, and how these attributes are related to ecosystem stability and resilience. We then describe how various sub food webs are linked through inshore-offshore, benthic-pelagic, and seasonal connections. The fourth section describes important fishery and non-fishery related threats to food webs. The fifth section gives an overview food web models and is followed by a brief description of food web indicators. Lastly, we end with a discussion of how these principles and topics can be applied in a fisheries management context and provide summary recommendations for improving our understanding of food webs.

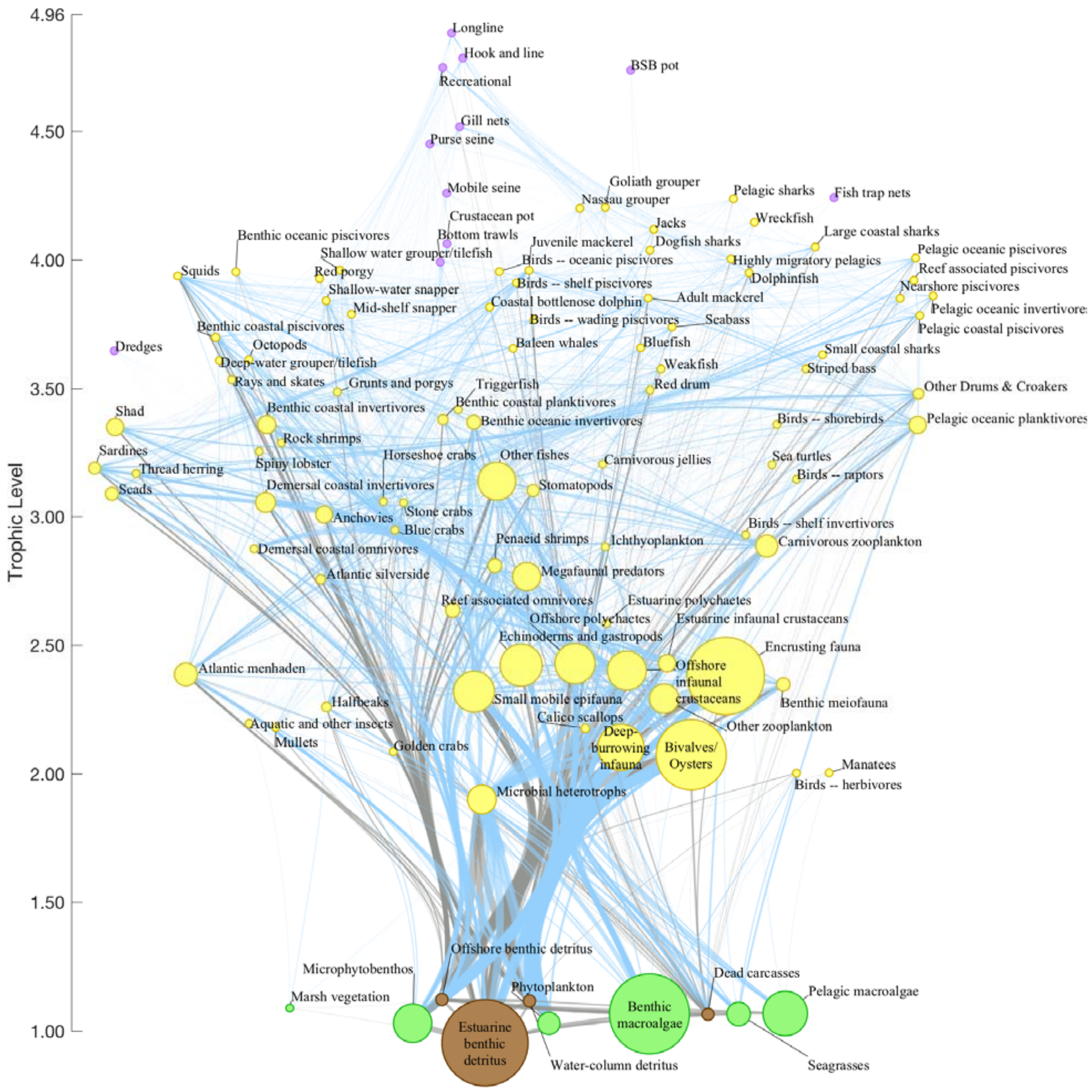

Figure 1-1. The marine food web of the South Atlantic Bight, based on the latest iteration of the SAB Ecopath model as described in Okey et al (2014), based originally on a preliminary model by Okey and Pugliese (2001). Nodes are colored based on type (green = producer, brown = detritus, yellow = consumer, purple = fleet). Blue for all edges except flows to detritus, which are gray. Diagram produced by Kelly Kearney, UW Joint Institute for the Study of the Atmosphere and Ocean and NOAA Alaska Fisheries Science Center, April 2015.

1 Description of South Atlantic Food Webs

1.1 Estuaries

The estuarine food webs of the South Atlantic are typical of temperate and sub-tropical areas. Primary productivity comes in the form of vascular plants, in particular sea grasses and marsh grasses, macroalgae, and to a lesser degree phytoplankton and mangroves. The primary bottom type in South Atlantic estuaries is soft sediment which supports a variety of diverse infaunal invertebrates that rely on phytoplankton and detritus derived from grasses. In turn, the infauna support a variety of mobile epibenthic invertebrates such as Penaeid shrimp and blue crabs, commercially and recreationally important fish such as spot, drum, menhaden, and flounder, and small reptiles such as terrapins and small mammals such as raccoon and fox (add reference). Oysters (*Crassostrea virginica*) are another key component of the estuarine food web that form large reefs and function to filter algae and particulates from the water column. Oyster reefs and the invertebrate communities they support are prey for most other animals in the estuary and may serve an important role in connecting hard and soft bottom food webs in the estuary due to the reefs providing refuge to animals that may move into soft bottom areas to forage.

Larger vertebrates also play an important role in estuarine food webs in the South Atlantic. A variety of birds are common components of estuarine food webs, with wading birds such as herons and egrets consuming benthic invertebrates and demersal fish and pelagic and diving birds such as gulls, terns, and pelicans consuming a variety of fish and invertebrates. Dolphins and manatees are often found in these estuaries, one foraging on fish and the other on algae and seagrasses, respectively. Humans are a major component of estuaries as their activities impact almost every component of the food web due to the proximity between the two (e.g. coastal development, hook and line fishing, net or seine fishing, crab pots).

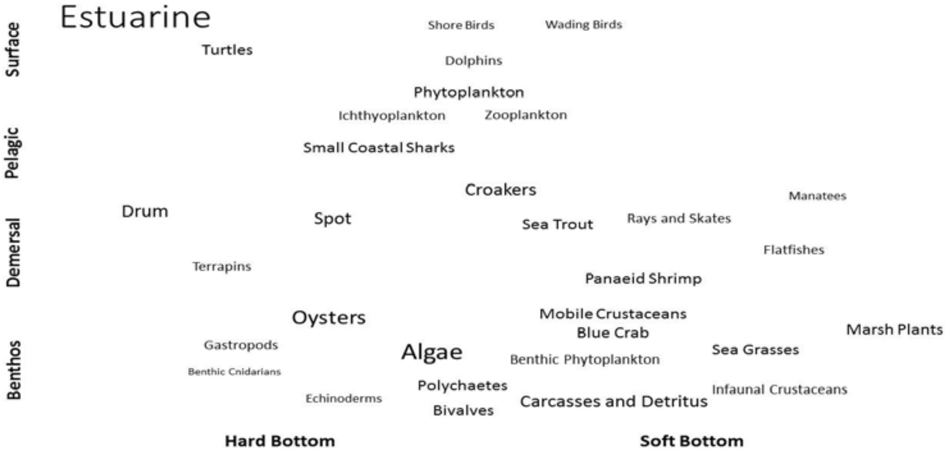

Figure 2-1. Typical components of an estuarine food web.

1.2 Nearshore

Nearshore habitats in the South Atlantic include both soft bottom and hard bottom. In most cases, nearshore hard bottom habitats are low relief, exposed limestone pavement (Henry et al. 1981; Riggs et al. 1996) with attached biota (macroalgae, some corals). In some cases, nearshore hard bottom has moderate relief due to boulders or small ledges (Powles and Barans 1980). The vast majority of the nearshore habitats, however, are soft bottom and support a variety of seagrasses and infaunal and epibenthic invertebrates and fish. Some of the most common mobile and pelagic invertebrates found in nearshore habitats are commercially important such as Penaeid shrimp, blue crabs, and horseshoe crabs. The diversity of fish increases in the nearshore relative to the estuary, although there is a fair amount of overlap in species composition. For example, spot, drum, croaker, weakfish, kingfish, and flounder all utilize nearshore soft bottom areas and are generalist predators that consume diverse diets including fishes, crustaceans, and polychaetes (Willis et al. 2015). Pelagic nearshore waters are inhabited by filter-feeding menhaden consuming phytoplankton and zooplankton, as well as bluefish and juvenile mackerels preying primarily on smaller fishes such as anchovies and atlantic bumper (SEAMAP unpublished data). Small coastal sharks, skates, and rays also comprise a key component of nearshore ecosystems, feeding on fish and benthic invertebrates. Many of the same large mammals and seabirds that utilize the estuary also are found in the nearshore. Dolphins in particular consume fish in this area and humans extract fish and invertebrates with pot or trap fishing and hook and line. Sea turtles also commonly use the nearshore areas and consume seagrasses, sponges, cnidarians and other invertebrates.

Figure 2-2. Components of a nearshore food web.

1.3 Offshore

Live or hard bottom habitats offshore in the South Atlantic support a variety of fish species, including groupers, snappers, grunts, and porgies as the most common. The majority of these species are piscivorous as adults, but many consume diverse diets. For example, Black Sea Bass (a small Serranid grouper) relies heavily on bony fish but nearly a quarter of the diet is comprised of crabs or other crustaceans (Hood et al. 1994). Red Snapper, a relatively large-bodied, fast growing snapper, consume a small fraction of benthic invertebrates as well as other fish (MARMAP, unpublished data). Vermilion Snapper also consume fish, yet are well adapted to feed on small pelagic and planktonic prey such as salps, copepods, and ctenophores (Grimes 1979, Sedberry and Cuellar 1993). Conversely, Red Porgy and Grey Triggerfish prey more heavily upon epifaunal invertebrates such as crabs, barnacles, bivalves, echinoderms, and polychaetes(Goldman et al., in review). Deep-water fish such as Snowy Grouper, Blueline Tilefish and Wreckfish generally prey upon other fish and squid, although diet studies are difficult for these species due to barotrauma during capture (Goldman and Sedberry 2011). Right whales are seasonal but important components of this food web as they rely on mid water zooplankton and can transfer energy along the coast (Lysiak 2009).

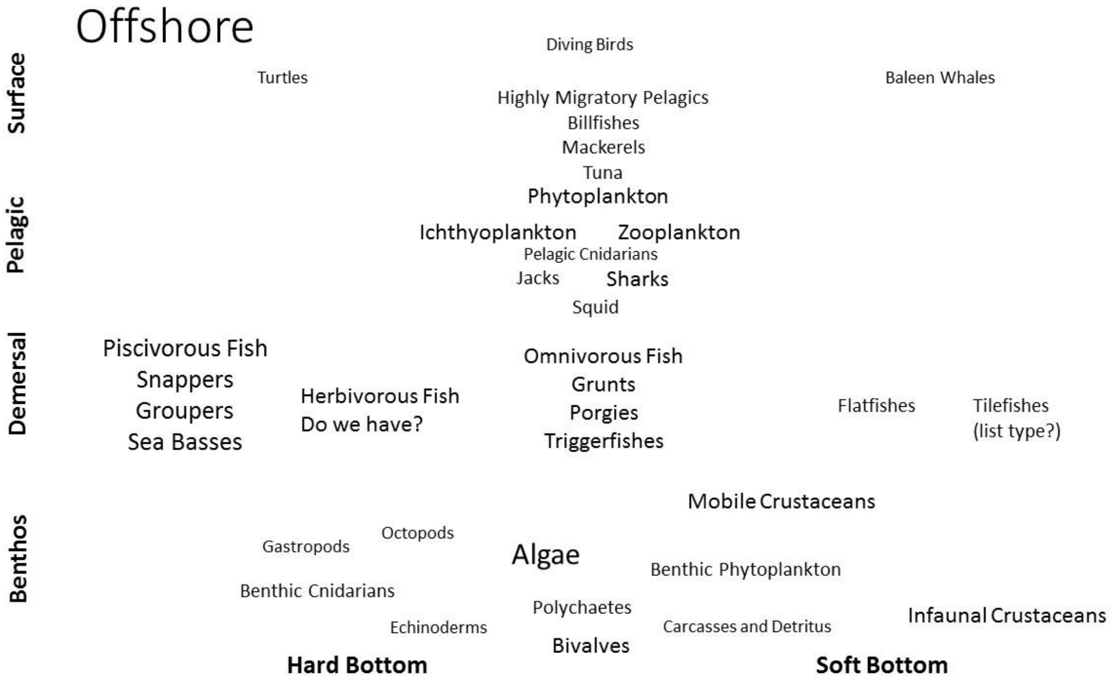

Figure 2-3. Components of the offshore food web

1.4 Species Interactions and Trophic Dynamics

Marine ecosystems are more likely to be impacted trophically by perturbations such as overfishing as the path lengths connecting marine food web components tend to be shorter on average than other ecosystems (Dunne et al. 2004). However, healthy, diverse ecosystems may be more resilient to perturbations due to increased complexity of trophic interactions and redundancy (Martinez 1993 and 1994; Saporiti et al. 2014). Compared to other U.S. marine ecosystems, the SAB standing biomass of ecological and economically important species is low, likely due to limitations in nutrient levels and primary productivity (Hargrave et al. 2009).

1.5 Life History Considerations

Many of the species in the South Atlantic have complex life histories, which often include several changes in habitat during their life cycles. Several endangered or threatened diadromus species are temporary components of one or more of the food webs mentioned above, including the American Eel (estuarine, nearshore, and offshore) and Sturgeon (estuarine and nearshore; add references). Gag Grouper are a large-bodied offshore piscivore as adults but their juveniles are found in oyster and seagrass beds in the South Atlantic estuaries, which are essential for their life cycle (Casey et al. 2007). Round Scad are an example of spatial partitioning in diet among life stages as adults occur either on the inner or outer continental shelf and juveniles are found mid-shelf (Hales 1987). There is a wealth of work supporting the importance of mangroves and marshes to many economically important species for a variety of life history stages (e.g. Kimirei et al. 2011).

1.6 Emerging Trends

There is a paucity of data for offshore fish that are not the most economically important and those that are more pelagic; thus we may be under-representing important links in this food web. This is especially true of species of forage fish that likely provide important links between primary and secondary consumers and large-bodied economically important snappers and groupers and among habitats (but see Sedberry 1985). Nevertheless, Okey et al. 2014 quantitatively characterized and modelled forage species within the South Atlantic Bight Ecopath (food web) model. There is also little known about the potential impacts of invasive species entering the SAB food webs. For example, Lionfish *Pterois* sp., have been shown to reduce recruitment in both nursery areas and on reefs (Barbour 2010) and to compete for both habitat and resources in the Caribbean (Albins and Hixon 2013). Additionally, porcelain crab *Petrolisthes armatus* may reduce predation pressure on native mud crabs (Hollebone and Hay 2008).

2 Energy Pathways

2.1 Basal Food Web Resources

The principal sources of carbon, and energy in marine and estuarine food webs include detritus, salt marsh grasses, seagrasses, phytoplankton, macrophytes, and filamentous algae. In estuarine waters of Sapelo Island, Georgia, *Spartina* detritus, phytoplankton, and benthic diatoms make up the major sources of organic matter that supports secondary production (Haines 1976; Peterson and Howarth 1987). In marine waters, organic carbon is more closely related to phytoplankton than marsh grasses (Rounick and Winterbourn 1986). Seagrass meadows can also constitute a significant source of carbon for certain species (Fry and Parker 1979). In oceanic waters, almost all of the water column and sediment organic matter is derived from phytoplankton production, with less influence from terrestrial inputs as one moves offshore. Therefore, the contribution of carbon from various basal resources varies over space, particularly along the inshore-offshore gradient, and time (or season) as production shifts between primary producers (Radabaugh et al. 2013). Ratios of carbon isotopes ($\delta^{13}C$) vary among primary producers and can be used to determine ultimate sources of dietary carbon in food webs. The ratios of $\delta^{13}C$ measured in organisms reflect long-term dietary patterns and the carbon sources that assimilate into biomass (Layman et al. 2012). Additionally, stable isotope ratios can be applied to evaluate community-wide aspects of food web structure (Layman et al. 2007).

2.2 Top-down and Bottom-up control

The dynamics of food webs are regulated through a combination of environmental, or 'bottom-up' effects, and 'top-down' consumer effects (harvest and predation) (McOwen et al. 2015; Power 1992; Reilly et al. 2013). Bottom-up factors are those that control how primary production enters into the food web over space and time and can include delivery of nutrients or changes in habitat and water quality. In systems where the food web is dominated by bottom-up control, the availability of prey has a strong effect on predator dynamics including migration, survival, and reproduction (Frederiksen et al. 2006). Bottom-up factors are influenced by processes such as nutrient loading (Paerl et al. 1998; Pinckney et al. 2001), large scale climate oscillations (ENSO, AMO) (Barber and Chavez 1983), and circulation patterns (Behrenfeld et al. 2006).

Top-down factors are those that drive consumer abundances and typically include harvest and predation. Top-down controls are therefore altered by processes such as overfishing and introduction of exotic species. Severe depletion of predator populations through fishing can induce trophic-cascades causing increases in their prey and decreases in prey two trophic levels below them (Frank et al. 2005; Steneck 2012). In cases where small fish consume the larval or early juvenile stages of a predator, this can lead to depensatory failures in recruitment of the predator species, and delay stock rebuilding (Walters and Kitchell 2001). Additionally, invasive species can exert top-down control on food webs through direct predation on native prey and competition with native consumers (Albins and Hixon 2008; Albins and Hixon 2013).

Marine food webs are usually regulated by a combination of top-down and bottom-up processes (Mackinson et al. 2009; McOwen et al. 2015) that vary over time and space. When a system is bottom-up limited, the availability of prey has a stronger effect on predator dynamics (Frederiksen et al. 2006). When the system is no longer bottom-up limited, top-down controls become more important. Additionally, the processes can be tightly coupled leading to a false dichotomy between the two (Vinueza et al. 2014). For example, overharvest of herbivorous fishes can lead to phase shifts from coral to algal dominated reef communities (Hughes 1994) and removal of seals has led to overgrazing of kelp forests by sea urchins (Estes et al. 2009). Within a system, the influence of bottom-up versus top-down drivers on various species and functional groups depends on trophic level and how energy flow is mediated by predator-prey interactions (Chagaris and Mahmoudi 2009; Mackinson et al. 2009).

Whether or not fisheries production within large marine ecosystems is driven by bottom-up or top-down forcing depends on oceanographic conditions, historical harvest, targeted species, and food chain lengths (McOwen et al. 2015). Anchovy and sardine fisheries, like those located along the eastern boundaries of the Atlantic and Pacific oceans, are believed to be influenced by bottom-up processes, i.e. the delivery of nutrients via upwelling (McOwen et al. 2015; Ware and Thomson 2005). In relatively low productivity systems such as the tropics and Northern Atlantic, fisheries production is best explained by fishing effort rather than environmental processes (McOwen et al. 2015).

2.3 Energy Pathways and Stability of Food Webs

Fast and slow energy channels refer to the turnover rates of populations (reflecting ecological and life history characteristics), which are related to energy fluxes and interaction strengths. Basal resources in aquatic food webs may be either pelagic (phytoplankton) based or benthic (detritus) based. In a meta-analysis of food webs, turnover rates in the pelagic compartment were found to be consistently higher than benthic compartments (Rooney et al. 2006). Thus the pelagic compartment is considered to be the "fast" channel. Many higher order consumers derive carbon from both channels. Coupling of these channels by consumers leads to more stable system dynamics (Gross et al. 2009). Stability is enhanced when energy flow between the pelagic and benthic channels becomes asymmetric and unsynchronized (more flow from either the fast or slow channel at different times). The fast and slow channels complement one another to produce stable recovery following a strong perturbation (Rooney et al. 2006; Rooney and McCann 2012).

The theory of asymmetry in energy pathways as a stabilizing structure of food webs has implications for management of marine resources. For instance, removal of predatory fish threatens to decouple the fast and slow energy channels and can destabilize the system (Bascompte et al. 2005). Nutrient loading can effectively homogenize production into the pelagic pathway or allow the pathways to become synchronized, also destabilizing the system. The fast channel allows for rapid recovery of predator populations while the slow channel ensures a less variable resource base for predators, allowing for a rapid but muted (i.e. more stable) return to equilibrium (Rooney and McCann 2012).

2.4 Dominant Pathways

The energy pathways in marine ecosystems that connect low and high trophic level species are dominated by forage species that serve as critical links to transfer energy and biomass through marine food webs (Anderson and Piatt 1999, Smith et al 2011, Cury et al. 2011, Pikitch et al. 2012). Some South Atlantic examples of important forage species include sardines, herring, menhaden, scad, shad, silversides, mullet, anchovies, halfbeaks, shrimp, pinfish, and other small pelagic planktivores (Okey et al. 2014). The most important characteristic of forage fish from an ecological and human perspective is that the higher trophic level predators are dependent on them either directly or indirectly for energy intake and biomass consumption. Indeed, the relative abundances of particular forage fish species with different energetic and nutrient contents can directly influence the fitness of predators in the ecosystem, the health of their populations, and subsequently the regulation and organization of biological communities in the ecosystem (Trites and Donnelly 2003, Wanless et al. 2005, Pikitch et al. 2012). In the South Atlantic Bight, forage species serve as important prey resources for popular sport fish species, such as snapper, grouper, mackerel, cobia, dolphinfish, and sailfish. Important commercial fishes such as mackerels, swordfish, amberjack, tuna, snappers, and groupers are also dependent on healthy abundances of forage species to grow and reproduce. Beyond economically important fisheries, many other apex marine predators such as migrating whales, coastal and pelagic sharks, as well as bottlenose dolphins rely on forage species for nourishment, and marine birds such as pelicans, skimmers, terns, and herons feed heavily on forage species and depend on them to successfully rear their chicks (Fins and Feathers Report, 2013).

Forage fish are generally small fast-growing species with high reproductive output and relatively short life-spans giving them the capacity for rapid population growth when environmental conditions are favorable (Checkley et al. 2009). At the same time, their propensity to form large schools make them easy to target and susceptible to overexploitation, especially at small stock sizes when range constricts but catch rates remain stable (Csirke 1989, Prince et al. 2008, Pinsky et al. 2011). Additionally, they may undergo high fluctuations in juvenile recruitment due to environmental variability and strong top down control from predators (e.g. Cisneros-Mata et al. 1995, Baumgartner et al. 1992).

2.5 Emerging Trends

Recent global analyses on the science and management of forage fish populations concluded that conventional MSY catch limits for forage fishes likely reduce the energy pathways that support marine mammals, seabirds, and economically important fish stocks by depleting their food supplies (Pikitch et al 2014, Essington et al. 2015). Thus, conservation and management of forage populations by explicitly accounting for their role as prey in marine food webs is critical to the overall health of marine ecosystems.

3 Connectivity among Food Webs

3.1 Introduction

Daily, seasonal and ontogenetic movements of fishes are often associated with optimal foraging strategies that include following of prey movements, engaging in specific feeding behaviors, and incorporating mechanisms to avoid predators while occupied with feeding (e.g., Fortier and Harris 1989, Sims 2013, Pereira and Ferreira 2013, Catano et al. 2016). Movements to optimal foraging grounds or to areas or times with reduced predator activity connect feeding grounds with areas where fish rest, spawn, and conduct other non-feeding activities. These non-feeding areas may include completely different habitats from feeding habitats, such as water column vs. reef, sand bottom vs. reef, seagrass vs. sand, and many other contrasting habitat connections. To understand how fishes distribute themselves in nature, and are thus available to local fisheries, it is important to know their preferred habitats, the distribution of those habitats, and the reasons why fishes select particular habitats (and not others) at certain times (Sims 2003).

Among reef fishes that dominate fisheries of the South Atlantic region, mobile invertebrate feeders represent the most abundant trophic group in subtropical and temperate environments, preying preferentially on crustaceans, mollusks and polychaetes associated with consolidated hard bottoms or unconsolidated substrate (Pereria and Ferreira 2013). Invertivores of the South Atlantic Bight include very abundant species such as grunts, porgies and smaller snappers that move among habitats and connect differing habitats through their foraging (Randall 1967, Sedberry 1983, Sedberry and Van Dolah 1984, Sedberry 1985, Sedberry and Cuellar 1994, Pereira and Ferreira 2013). These movements may alter predation risk to the invertivores, which often serve as prey for higher trophic levels like large snappers, groupers and sharks (e.g., Randall 1967, Delorenzo et al. 2015). Many predator habitat choices are related to prey availability and prey movements (e.g., Loefer et al. 2007, Pereira and Ferreira 2013). For many reef fishes, these choices include daily foraging excursions off the reef onto adjacent sand or seagrass areas (Sedberry 1985), or into the water column above the reef (Sedberry and Cuellar 1994), to feed at times or in areas where prey is abundant and the foragers are less vulnerable to predation themselves, and there is less competition with other fishes in diverse reef fish assemblages.

In addition to daily or other frequent foraging movements, the early life history and juvenile stages of fishes often move from less productive waters where they were spawned to more productive areas for feeding, rapid growth and predator avoidance. These ontogenetic movements may be superimposed upon seasonal movements that coincide with productivity patterns (Lindeman et al. 2000). As juvenile fishes then mature in nursery habitats, increased energy demands associated with gonad development cause them to move into different habitats where larger and more energy-rich prey organisms are available (e.g., Randall 1967, Sedberry 1983, Mullaney and Gale 1996, Young and Winn 2003, MacNeil et al. 2005). These ontogenetic movements that are associated with feeding connect different geographic areas and a variety of estuarine, coastal and oceanic habitats (Pereria and Ferreira 2013). Feeding movements transfer energy and biomass among habitats, and they couple less productive resting habitats with more productive feeding grounds, or provide trophic or energy subsidies from one habitat and faunal assemblage to another (e.g., Sedberry 1985, Weaver and Sedberry 2001, Goldman and Sedberry 2010).

3.2 Benthic-Pelagic Coupling

Grober-Dunsmore et al. (2008) reviewed benthic-pelagic coupling in regards to the effects of pelagic fishing on benthic communities and the role of MPAs to promote healthy fish stocks. They determined that, because of benthic-pelagic coupling mediated by food web connectivity, recreational pelagic fishing may not be compatible with benthic conservation in (1) high relief habitats; (2) depths shallower than 50–100 m (depending upon the specific location);

(3) major topographic and oceanographic features; and (4) spawning areas. Much of the productive fishing grounds of the South Atlantic regions fall within these descriptions.

Auster and colleagues (Auster et al. 2009, Auster et al. 2011) demonstrated that pelagic piscivores (Great Barracuda, Greater Amberjack and other jacks, Spanish Mackerel) drive pelagic forage fishes toward rocky reef outcrops, where they become prey for demersal predators (Black Sea Bass, Bank Sea Bass, Gag, Scamp). Feeding behavior of mesopelagic piscivorous fishes connects pelagic waters with benthic habitats by inducing responses in prey fishes that produce feeding opportunities for demersal piscivorous fishes. Auster et al. (2009, 2011) described a web of predation behaviors and the responses of prey that indirectly link midwater and demersal piscivorous fishes. These fishes include important components of the Snapper/Grouper management unit.

The linkages between pelagic and demersal fishes can occur by demersal fishes feeding on pelagic prey species and vice versa. It can also occur through ontogenetic shifts in vertical distribution of demersal predators. For example, pelagic and plankton-feeding juvenile stages of Tomtate and other grunts settle to the seafloor to assume a demersal existence and then feed on benthic prey (Sedberry 1985, Pereira and Ferreira 2013). Tomtate are in turn fed on by several species of jack, grouper, snapper, eel and other reef fishes (Randall 1967), further connecting reef, pelagic and sand-bottom habitats.

Many different physical and biological processes contribute to interactions that transfer midwater production to seafloor communities (Grober-Dunsmore et al. 2008, Auster et al. 2009). Physically-mediated processes related to advection of oceanic waters onto the shelf enhance feeding opportunities of deep-reef demersal fishes such as Vermilion Snapper. Vermilion Snapper, a dominant demersal species of mid- and outer-shelf reefs (Sedberry and Van Dolah 1984) have a diet dominated numerically by planktonic species that include copepods, pelagic amphipods, pelagic decapods (including crab larvae), salps and fish larvae. At shelf-edge reefs, advection of oceanic waters and their plankton onto the shelf connects oceanic pelagic species to demersal reef predators. Vermilion Snapper that forage on oceanic plankton advected onto shelf-edge reefs transfer oceanic pelagic biomass to shelf reefs. Vermilion Snapper, in turn, are fed on by other demersal predatory fishes (Randall 1967, Sedberry 1988) and thus may provide trophic links among top-level carnivores and oceanic or shelf plankton, and reef benthos (Sedberry and Cuellar 1993).

Biologically-mediated processes (such as vertical migration behavior) also enhance feeding opportunities of deep-reef demersal fishes such as Wreckfish. Vertically-migrating zooplankton and their pelagic predators provide prey for demersal Wreckfish when daily migrations bring these species in proximity to the sea floor on deep reefs (Weaver and Sedberry 2001, Goldman and Sedberry 2011). Thus, demersal fishes that feed on planktonic invertebrates also couple pelagic and benthic habitats over shelf and shelf-edge reefs of the southeast. The greater biomass and diversity of fishes in rocky reef habitats in the region, compared with sandy areas, may be the result of trophic links through reef-associated fishes, such as Vermilion Snapper and Tomtate, with other ecotopes on the shelf (Sedberry and Cuellar 1993). Pelagic copepods and decapods are important prey in the diet of juvenile Tomtate, which shelter in the reef during the day, transferring energy to the reef in the form of feces and as prey for piscivorous fishes (Sedberry 1985, Auster et al. 2009). Vermilion Snapper, although reef-associated, do not feed heavily on reef species, and may be important in transferring energy from the water column and adjacent sandy areas to the reef (Sedberry and Cuellar 1993).

In summary, trophic links connect planktonic biomass to benthic habitats, and biomass from adjacent sandy areas to hard-bottom reefs. They also connect pelagic forage fishes and their piscivorous predators to demersal piscivores. The links include ontogenetic changes in habitats, and foraging migrations that occur on daily, seasonal and ontogenetic time scales.

3.3 Inshore-Offshore Connections

In subtropical and warm-temperate zones, many reef fishes undergo migrations to spawn at particular reef sites that probably possess hydrographic regimes or biological assemblages that enhance survival of offspring (Sedberry et al. 2006, Farmer et al. in prep.). These migrations often involve cross-shelf movements to spawning sites at the shelf edge or insular drop-offs (e.g., Carter et al. 1994, McGovern et al. 2005, Sedberry et al. 2006). These spawning areas must be hydrographically connected to the habitats where postlarvae settle from the plankton to benthic habitats. Larval durations vary and local settlement near spawning sites is possible; however, for some species such as Gag, larvae must be transported from shelf-edge spawning sites into distant estuaries were small postlarvae settle (Keener et al. 1988, Lindeman et al. 2000, Sedberry et al. 2006). Later in life, these juveniles move out of estuaries and take up residence on offshore reefs (Sedberry and Van Dolah 1984, Mullaney and Gale 1996), eventually returning to the shelf-edge to spawn. The life histories of estuarine-dependent species such as Gag connect inshore coastal and estuarine productivity to offshore habitats. While Gag may be estuarine-dependent, facultative use of estuaries is more common in marine fishes and demersal stages of at least 50 reef fish species show some degree of ontogenetic migration across the shelf (Lindeman et al. 2000).

For some marine fishes exchange of individuals between estuarine and offshore habitats occurs primarily during a pelagic early life history stage (Cowen and Sponaugle 2009), although there may be daily, seasonal, reproductive and ontogenetic movement of fishes between offshore marine and inshore estuarine habitats, particularly in coral reef/mangrove areas. (e.g., Sedberry and Carter 1993, Sedberry et al. 1998, McGovern et al. 2005, Pikitch et al. 2005). Spawning strategies of offshore marine fishes ensure that the pelagic eggs and larvae will be delivered to the appropriate benthic settlement habitats at settlement time, which can be days to months after spawning and may include inshore estuarine areas (Lindeman et al. 2000). Fishes spawn within particular depth and/or latitudinal zones, with concomitant and predictable seasonal circulation patterns, to ensure that this delivery from offshore reefs to estuaries takes place.

3.4 Latitudinal Connections

Because of the complex ocean circulation off the southeastern U.S., there are dominant and predictable mechanisms for long-distance transport of water masses and planktonic stages of fishes. The Florida Current and Gulf Stream transport larvae northward from the tropics. While the Gulf Stream can carry larvae great distances, including expatriation from the region to northeastern North America (Markle et al. 1980, Olney and Sedberry 1983, Hare et al. 2009), Gulf Stream eddies on the western side of the current, where many fishes spawn, set up mechanisms for local retention of some water masses and any larvae they carry from local or more-southern spawning (Govoni et al. 2009, Govoni et al. 2013). These eddies also transport water masses and plankton inshore to coastal and estuarine nursery areas (Govoni et al. 2009). Drifter studies have indicated that transport of pelagic larval stages from south to north (and vice versa) through drift. Drift and active swimming facilitate exchange of eggs and larvae with non-spawning habitats and among MPAs (from north to south) in the region and ensure that postlarvae settle into appropriate habitats (Lindeman et al. 2000, Marancik et al. 2005, Hare and Walsh 2007). Estuarine and coastal waters, where many shelf-spawning fish species spend their early planktonic or juvenile stages (e.g., Lindeman et al. 2000), are also connected hydrographically to offshore adult habitats.

There are a number of MPAs that restrict fishing in the region (Figure). In South Florida, this includes areas within Biscayne Bay National Park, Florida Keys National Marine Sanctuary (FKNMS) and its Tortugas Ecological Reserve. Up the Atlantic coast of the southeast, there are several MPA that restrict all fishing (e.g. the Research Area of GRNMS) or just bottom fishing (SAFMC MPAs and HAPCs). These protected areas include important reef fish spawning sites (Lindeman et al. 2000, Sedberry et al. 2006, Farmer et al. 2013). These MPAs are connected by Gulf Stream flow (Hare and Walsh 2007, Lesher 2008), and these include connections from known spawning areas within and outside of the MPAs. For example, Gag, Scamp, Red Grouper and Gray Triggerfish are common as juveniles and small adults at Gray's Reef National Marine Sanctuary, which has a no-fishing zone off Georgia, but spawn mainly at shelf-edge reefs (around 55 m), including SAFMC MPAs at the shelf edge. As mentioned earlier, Gag use shallow coastal or estuarine waters as nursery areas, but make either an ontogenetic shift or spawning migration to the outer shelf, spending part of that time at inner-shelf reefs like those at Gray's Reef. A combination of shelf-edge (SAFMC), estuarine (e.g., Sapelo Island National Estuarine Research Reserve) and inner shelf (Gray's Reef) protected areas appear to be connected during the life history of species such as Gag, thus maximizing the benefits of each of these MPAs (Green et al. 2015). Larval durations of Gag [31-66 d (Keener et al. 1988)] match well with drift times for water masses from offshore MPAs to coastal nursery habitats (Hare and Walsh 2007).

In addition to drift of early planktonic stages of fishes, there is active meridional migration by demersal stages that are related to many life history factors, including spawning, food availability, temperature preferences (Sedberry et al. 1998, McGovern et al. 2005, MARMAP 2007, mackerel and cobia papers). Gag, Cobia, and Greater Amberjack undertake extensive migrations along the coast, with individuals moving from the Carolinas into the Gulf of Mexico or Caribbean Sea. King Mackerel annually migrate between the Carolinas and south Florida (Sutter et al. 1991, Schaefer and Fable 1994). These migratory species spawn at shelf-edge reefs in depths from 50-100 m and have been (prior to seasonal closures) more easily accessed by fishermen off south Florida than areas north due to the narrow continental shelf from Jupiter Inlet through the Florida Keys. This narrow continental shelf off Florida increased fishing mortality for many other species by "funneling" them close to shore in the vicinity of the high human population (McGovern et al. 2005).

3.5 Seasonal Connectivity

Studies of larval fish assemblages in the South Atlantic region have shown that there is cross-shelf transport of water masses and fish larvae, with seasonal variability. Marancik et al. (2005) found that in spring, summer, and fall, larval fish assemblages determined by ordination of ichthyoplankton collections at a reef site off Georgia were similar to other inner-shelf (13-19 m average depth) stations, and that this grouping was similar to middle-shelf (20-40 m) stations in spring, summer, and winter. Larval fish assemblages at inner and middle-shelf stations were different from outer-shelf stations (40-50 m), indicating perhaps unique assemblages at the shelf edge, under greater influence of the Gulf Stream. The winter station ordination, however resulted in a less distinct cross-shelf pattern and perhaps more mixing in of waters across the shelf in winter. Generally, Marancik et al. (2005) found that assemblages of fish larvae from middle-shelf depths (between the 20- and 40-m isobaths) included taxa that were found across the shelf. Oceanographic studies of the Charleston Gyre indicate that this feature facilitates greater cross-shelf transport in winter than in other seasons, enhancing the cross-shelf transport of species that spawn at the shelf edge in winter but have estuarine-dependent larvae, such as Menhaden, Gag, Spot, Croaker and others (Bane, Govoni Bump and other papers). Seasonality of occurrence of larval fishes probably reflects seasonality of spawning and plankton productivity and spawning, which it timed to productivity pulses.

Recruitment of hard-bottom invertebrates is also seasonal in the South Atlantic region, with seasonal pulses of large numbers of invertebrates in winter (Van Dolah et al. 1988). These pulses may provide additional prey needed for fishes as gonads mature for winter and early spring spawning peaks that occur in most species (Sedberry et al. 2006).

3.6 Emerging Trends

There is evidence of climate change and ocean acidification on the southeast continental shelf. While the effects of this on fish assemblages are not known, experimental studies have shown that rearing juvenile fishes at high temperature (31.5 °C) and control (420 μatm) or moderate (530 μatm) CO_2 concentrations resulted in a reduction of food consumption and foraging activity. In addition, rearing at high temperature and high CO_2 (960 μatm) resulted in an elevation in these behaviors. Maintaining food consumption and foraging activity in high temperature and CO_2 conditions may reduce energy efficiency if the thermal optimum for food assimilation and growth has been exceeded. Maintaining foraging effort needed to thrive might increase predation vulnerability. These results suggest that changes in foraging behaviors caused by the interactive effects of increased temperature and CO_2 could have significant effects on the growth and survival of juvenile reef fishes by late century (Nowicki et al. 2012).

For species like Vermilion Snapper and juvenile Tomtate that forage in the water column (Sedberry 1985, Sedberry and Cuellar 1993), the patchiness of planktonic prey probably determines foraging range and success (Sims 2003). Few plankton studies have been conducted in the region. With newer acoustic technology available, it is possible to more rapidly determine location and residence times of plankton patches that support foraging fishery species like Vermilion Snapper.

In addition to continuing and expanding studies of feeding habits of fishes, we need additional data on available prey in the habitat (Sims 2003). As mentioned, plankton biomass can be obtained acoustically, but additional surveys are needed of benthic communities and infaunal biomass to determine important foraging habitats and prey availability of the many fishes like Tomtate and Scup that forage on infauna and transfer energy among benthic habitats. Testing Optimal Diet Models for predators of mobile prey may be possible by combining fine-scale tracking of individuals with detailed surveys of prey species present across different microhabitats such as hard bottom reefs and adjacent sand areas (Sims 2003). Comparing stomach contents to prey communities is a necessary first step to determining prey vulnerability in the wild (Sims 2003). Knowing what habitats fishes select and why they do so at given times over seasonal scales has obvious practical implications for determining not only catch rates of fisheries in specific regions, but also for their effective regulation (Sims 2003).

4 Impacts on Food Webs

A variety of environmental and human use factors can impact the overall health and integrity of food webs. Some of these impacts are direct, such as overfishing of individual species causing changes in food web dynamics, or the introduction of an invasive species. Other impacts are indirect, including changes in water quality or habitat characteristics which can in turn influence the fish populations and the overall food web. This section provides a brief overview of the relationship between core fishery and non-fishery related impacts on food webs in the South Atlantic. The *Threats to South Atlantic Ecosystems* section of the Fisheries Ecosystem Plan provides additional information on the overarching suite of threats that can impact the region.

4.1 History of change of the system

Not much detail here, hopefully reference other sections in the FEP: histories of the fisheries; habitat change; need to be general and brief; total landings trend, coastal development trend, etc.

4.2 Fishery-related Impacts

Fishing activities can have a variety of impacts on South Atlantic food webs, both with direct impacts to fish populations and through impacts to critical habitats which in turn impact food web dynamics.

4.2.1 Overfishing and Trophic Cascades

Extraction of species from a system can impact community composition, diversity, and trophic structure. In addition to restricting populations of the targeted species, overfishing of a specific species or group of species can modify the broader ecosystem food webs. The role of fishing activities beyond the direct impact on the given population is critical to understanding food web dynamics. Trophic cascades can result when fishing impacts extend beyond a targeted population, influencing the broader food web. The direction of the impact within the food web depends on the trophic level of targeted and non-targeted species. This influence can be top-down, such as the loss of predators within a system, or bottom up, including the loss of forage fish or habitat.

4.2.2 Bycatch

The 2011 *U.S. National Bycatch Report* defines bycatch as discarded catch of any living marine resource plus unobserved mortality due to a direct encounter with fishing gear (NMFS 2011). The limited selectivity of fishing methods and gear results in fisheries affecting nontargeted species, including marine mammals, sea turtles, seabirds, finfish, elasmobranchs and invertebrates. Bycatch can result from incidental take of protected species; regulations on the retention of particular species, sexes, or size ranges; discretionary discards or catch-and release (NMFS 2011). The nontargeted species impacted varies by fishery and associated gear type.

Trawling, for example, is the primary gear used in the shrimp, whelk and jellyfish fisheries A variety of bycatch reduction methods have been put into place to help limit the amount of by catch, including the use of Turtle Exclusion Devices (TEDs) and Bycatch Reduction Devices (BRDs) on trawls in the shrimp fishery, the incorporation of escape panels in pots used in the blue crab fishery and the adoption of non-stainless steel hooks, descending devices and degassing methods the deeper water snapper grouper fishery.

4.2.3 Habitat Alterations

The coastal, nearshore and offshore food web descriptions provided earlier in this chapter highlight the critical role that benthic habitats, including seagrasses, marsh plants, oysters, and hard bottom have in the ecosystem dynamics of the South Atlantic. Fishing activities are amongst a variety of sources human and environmental factors that can influence the extent and health of these critical habitats. Specific connections between fisheries and bottom habitats in the region, include, but are not limited to bottom habitat alteration, particularly sand, from shrimp trawls, loss of fishing gear, and anchor damage. Limitations in the gear types (e.g. trawls) that can be used estuarine, nearshore and offshore areas, are designed to help mitigate the direct destruction of critical habitats.

4.3 Water Quality

The water column is habitat within our estuarine and marine ecosystems. As such, its condition has an impact on the broader food web. Nutrient levels can influence primary productivity, community composition and species diversity; contaminants can negatively impact fish reproduction and endocrine systems and have the potential to bio-accumulate up the food web. The sources of nutrients, pollutants, and contaminants are often land based (e.g. stormwater and agricultural runoff). There is a an broader review of water quality related sources and impacts in the "Threats to the South Atlantic Ecosystem" section of the Fisheries Ecosystem Plan; therefore, this section focuses on the specific relationship with food webs.

4.3.1 Nutrients

Nutrient pollution can result in a variety of ecological impacts. Excessive nutrients in estuarine and nearshore systems can result in fish kills due to oxygen depletion, seagrass die-offs, excessive and sometimes toxic algal blooms, and changes in marine biodiversity (NRC 2000). Studies conducted in southeastern tidal creeks have demonstrated shifts in invertebrate and fish populations with high nitrogen loads (REF). In turn, they may not support food chain and ecological assemblages needed to sustain desirable species and populations. Sources of nutrients include agriculture, silviculture, coastal development and stormwater.

4.3.2 Contaminants

In addition to nutrients, a number of contaminants in the water column can negatively impact fish communities and food webs. While some occur naturally in the environment, anthropogenic activities have resulted in increased concentrations of heavy metals (e.g. mercury), persistent organic carbons (e.g. polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenys (PCBs)) and perfluorinated compounds (PFCs), in coastal and marine ecosystems (Jakimska et al 2011, Houde et al 2011). Excessive levels of these contaminants can result in direct mortality, hormone alterations, immune suppression and bioaccumulation. The latter correlates most directly with food web dynamics, as many of these contaminants undergo biomagnification when transferred across trophic levels, accumulating in the tissues and organs of carnivorous and apex species (Houde et al 2011).

Mercury is an example of a heavy metal found in the marine environment that transfers through trophic levels and raises a significant human health concern. Sources of mercury in the both natural (e.g. degassing of the earth's crust, volcanoes) and anthropogenic (e.g. coal combustion, waste incineration, and metal processing), primarily entering the marine environment through atmospheric deposition. Once in the system can accumulate in bottom sediments where bacteria convert it into methylmercury, a more toxic form of mercury which takes longer for organisms to eliminate (USGS). While there are a variety of local variables that influence methylmercury concentrations, a study on the differences in mercury levels between red and gray snapper in the Gulf of Mexico [MC3] can help inform the discussion of heavy metal bioaccumulation in South Atlantic food webs. *ADD concluding sentence.*

4.3.3 Harmful Algal Blooms

The ecosystem impacts of toxic and nontoxic harmful algal blooms range from loss of species (e.g. shellfish) and habitats (e.g. seagrass beds) to altered food web interactions. For example, brown tides in the Mid-Atlantic and Gulf of Mexico reduced light penetrations, led to seagrass die-offs, and reduced populations of hard clams, scallops and mussels. From a human health standpoint, marine toxins associated with harmful algal blooms can cause neurologic and gastrointestinal disease. Ciguatera, the most common marine toxin disease in the world, is associated with the consumption of subtropical and tropical reef fish such a barracuda, grouper, and snapper. This is a case of bioaccumulation within the food web, toxic dinoflagellates (e.g. *Gambierdiscus toxicus*) adhere to coral, algae and seaweed, are eaten by herbivorous fish, and then by carnivorous fish which are consumed by humans. A 2015 study projects an increase risk from ciguatera in the southeast as a result of climate change and warmer water temperatures (Kibler et al 2015).

4.4 Habitat Alteration

The food web diagrams provided earlier in this chapter highlight the dynamics between fish communities and habitats in estuarine, nearshore, and offshore environments. Many of the habitats on which South Atlantic food webs depend are themselves at risk from a variety of impacts and their loss can alter overall ecosystem dynamics. Discussion of the links between fishing and non-fishing threats and Essential Fish Habitat (EFH) is the crux of threats section of the FEP. This section focuses on a couple of key examples of how habitat alterations can modify broader food web dynamics.

4.5 Invasive Species

The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 defines aquatic nuisance species as “nonindigenous species that threaten the diversity or abundance of native species, the ecological stability of infested waters, and/or any commercial, agricultural, aquacultural, or recreational activities dependent on such waters”. Often referred to as invasive species, they can enter marine ecosystems through shipping activities, such as ballast water discharge or transport on ship hulls, intentional stocking for fisheries, and through the aquarium trade.

Indo-Pacific Lionfish (*Pterois volitans/miles* complex) are the most significant marine invasive when considering larger food web implicationsns in the South Atlantic Bight. Indigenous to coral reefs in the Red Sea, Indian and western Pacific oceans, lionfish are now found throughout the South Atlantic Bight region, from Florida to Cape Hatteras (Whitfield et al 2002, Hare and Whitfield 2003, Meister et al, 2005, Ruiz-Carus et al. 2006, Whitefield et al 2006). They are known to occupy a diverse set of hard bottom habitats, including seagrasses, mangroves, low relief hard bottom, rocky outcrops, and high relief artificial structures, at diverse depths (Whitfield et al 2006, Albins and Hixon 2010). Their already wide distribution in the South Atlantic demonstrates suggests that they are successful marine fish colonizers in the region with the primary limitation to their distribution being minimum bottom water temperature. Recent climate models indicate that changes in sea temperatures will further expand the extent of suitable thermal habitat for lionfish by 45% over the next century covering 90% of the southeast continental shelf (Grieve et al. 2016). With no natural predators, defensive venomous spines, and extraordinary predatory behaviors, lionfish can decrease native prey fish biodiversity and biomass twice as fast as native species, and reduce recruitment of juvenile fishes by >80% including ecologically important reef species (e.g. parrotfish, gobies, damselfish) as well as economically important snappers (e.g. vermillion), groupers (e.g. seabass), flounders, and forage species (e.g. squid & scad) (Albin and Hixon 2008, Morris and Akins 2009, Green et al, 2012, Albins 2013, Dahl and Patterson, 2014).Their exceptionally fast growth rates and continuous year long spawning activities can allow them to reach high densities in newly settled areas, and if left unchecked, can disrupt and alter energy flow pathways within food webs (Fig.# see imbed) (Albins and Hixon 2010, Cerino et al., 2013). Fisheries management plans Utilizing habitats and having similar diets to native reef fish in the should anticipate these potential negative effects of overcrowding, direct predation and competition such as grouper, suggests that lionfish could impact on the South Atlantic Bight ecosystem. through overcrowding, direct predation and competition Extirpation of lionfish is not possible, but mitigating their trophic impacts on South Atlantic food webs will requiren.employing effective management tools and investing in research priorities to inform management (Morris and Green, 2012, Green et al. 2014). Precautionary approaches *inter alia*, such as fishing regulations and marine reserves that protect and conserve native species like groupers that are capable of controlling some lionfish impacts are promising management options (Albins and Hixon 2010, Dodge 2015, National Invasive Lionfish Prevention and Management Plan, 2015).

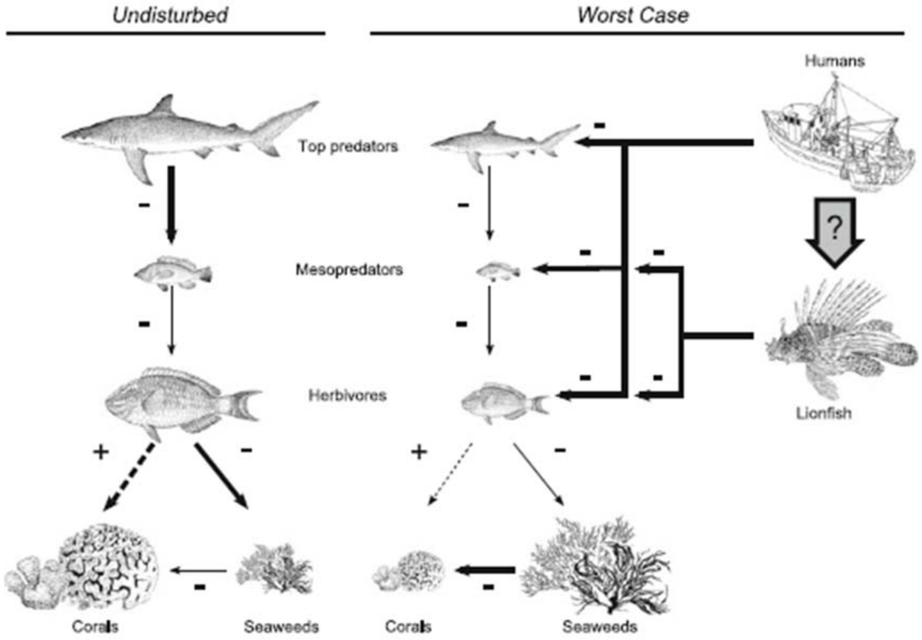

Fig. 2 Worst case scenario for future Atlantic and Caribbean coral-reef ecosystems caused by a combination of human overfishing of larger fishes of all trophic levels and invasive lionfish consuming small fishes and competing with other mesopredators (*right*), compared to an undisturbed system (*left*). The size of each kind of organism represents its relative abundance comparing the two interaction webs, and the thickness of each arrow represents the relative interaction strength between organisms. *Solid arrows* are direct effects representing predation (including fishing), except in two cases: competitive effects of (1) seaweeds on corals and (2) lionfish on other mesopredators and juveniles of some top predators (such as juveniles of large grouper species). The *dashed arrow* is the indirect positive effect of herbivores on reef-building corals. The unknown future effect of humans on lionfish is indicated by a *question mark*, and will be the focus of control efforts. Images courtesy of FAO

4.6 Climate Impacts

An overview of climate change impacts expected in the southeastern U.S. was provided in the 2009 Fisheries Ecosystem Plan of the South Atlantic Region (REF). Anticipated changes include, but are not limited to, increased water temperature, sea level rise, and ocean acidification. The range of climate change impacts in marine ecosystems include decreased ocean productivity, altered food web dynamics, reduced abundance of habitat-forming species, shifting species distributions, and a greater incidence of disease (Hoegh-Guldberg and Bruno 2010). Specific impacts will vary by location. Following are some climate change impacts being observed and tracked in the South Atlantic Bight.

- Coastal habitat shifts and potential loss
    - related to sea level rise, changes in rainfall, obstacles to migration (e.g. development)
- Population/regime shift
    - From FEP: Atlantic Multidecadal Oscillation can cause large scale ecological changes called regime shifts where temperature alterations favor or harm a particular species or groups
- Ocean acidification
    - From FEP (p. 97) Experimental evidence suggests that if these trends continue, key marine organisms, such as corals and some plankton, will have difficulty maintaining their external calcium carbonate skeletons (Orr et al. 2005). acidification of oceans is expected to have negative impacts on marine shell-forming organisms (e.g., corals) and their dependent species.[MC8]

4.7 Combined Effects

(*Hypothetical, used in context of recommendations, likely pull from modeling studies outside the region (California Current IEA, others))*

4.7.1 Synergistic Effects
4.7.2 Antagonistic Effects
4.7.3 Cumulative Effects

4.8 Emerging Trends

4.8.1 Mariculture

(aquaculture may affect food webs. Don’t go too far)

4.8.2 Other Issues

5 Food Web Models

5.1 Models and Principles

Marine food webs and their broader ecosystems are complex, especially those in subtropical and tropical settings, and especially when considering spatial complexity. This high complexity makes such marine ecosystems inherently difficult to understand. Computer models are a useful tool to account for the myriad states and flows in the system, and thus to characterize and examine food web structure, functions, and dynamics. Such models can be used to explore questions relative to ecosystem health, community regulation and stability, ecosystem services, management strategies and policies, and the effects of global, regional, and local pressures on these food webs, ecosystems, and particular resources.

A variety of modeling approaches varying in complexity and theoretical foundation can be used to represent spatially explicit marine ecosystems and trophic interactions. Some examine individual level interactions and responses to environmental heterogeneity, which can scale up to whole populations and ecosystems, while other approaches model the states, flows, and dynamics of aggregate groups of species. These different approaches, while complementary, have very different applications for fisheries management and other conservation planning issues.

In many cases, we need to understand how species are distributed across space to understand and represent food webs and ecosystems. The simplest way to represent species distributions is to extrapolate presence and absence point pattern data to an area of interest by a statistical model. Collectively, the models used for extrapolating point pattern data to continuous areas are called environmental niche models, bioclimatic envelope models, or species distribution models.

There is currently no consensus regarding what bioclimatic envelopes, niche, or species distribution models represent in terms of observed spatial distributions. Recent authors (Soberon 2007, Peterson et al. 2011) suggest a species distribution is governed by physical variables (Grinnell 1917), community status (Elton 1927), and movement. Any combination of these three factors determines an actual distribution or potential distribution, including population sinks due to competitive exclusion or resource limitation.

While the first niche model, as we currently conceptualize them, was probably constructed by Ferrier (1984) to describe birds, these models have exploded in use over the past decade. Bioclimatic envelopes, niche, and species distribution models primarily use raster and GIS data to represent environmental conditions and species co-occurrence. The ease with which these data and methods are accessible via modern computing has renewed a focus in understanding their theoretical underpinnings.

Other models commonly used in fisheries applications are often based on foraging theory. Foraging theory refers to a wide class of explanations that describe individual energy intake and foraging time in terms of rate maximizing. In distribution models, spatial distributions can be quite literal in terms of environmental, dispersal, and competitive gradients. In contrast, distributions based on foraging more explicitly consider individual behavioral decisions due to trophic interactions, predator-prey functional responses, habitat quality, food availability, and vulnerability (e.g. MacArthur and Pianka 1966, Schoener 1971, Charnov 1976, Mangel and Clark 1986).

An early approach to modeling foraging behavior was a Markov state transition model by Marc Mangel (1987). A Markov process is a stochastic process that assumes a lack of process memory. A "state" refers to the current state of the organism and its dynamics (e.g. a population classified by size). A transition occurs between states based on a transfer probability. Mangel used this framework to describe the increase in fitness in an insect due to optimal clutch size on a host. In Mangel's example, he only needed information on survival probabilities to describe state transitions and a measure of fitness to describe current states. Using foraging theory, Mangel ran a series of Monte Carlo simulations to describe optimal oviposition behavior. While Markov models can be relatively simple to parameterize and can help us understand behavior, there are some key assumptions in foraging theory that need to be considered. Optimal foraging assumes that organisms act "optimally" in that they can make non-random decisions considering their fitness. Furthermore, the co-occurrence between predators and prey (or hosts/parasites, etc.) is assumed random, which we know is often not true.

The individual behavioral approach can extend into models that more explicitly consider dynamic systems. Dynamic models represent the full suite of interactions between species, their environment, and external stress as a series of population, trophic dynamic, biogeochemical, and/or hydrodynamic models. In fisheries, two related individual based models have emerged that describe multi-species interactions for natural resource managers: OSMOSE and Invitro.

OSMOSE was developed by Shin, Shannon, and Cury (2004) to explore size based predation rules in the context of trophic interactions. This model describes trophic interactions by assuming a fixed amount of food is required for each individual and a constant predator-prey size ratio exists (e.g., by using data from fishbase.org). In this regard, OSMOSE has theoretical underpinnings in food web ecology, where size selective predation has long been recognized as a complicating factor in describing marine food webs (Shurin et al. 2006). OSMOSE is limited in that it requires a large input of parameters for growth, reproduction, and survival, and does not handle environmental data and lower trophic levels. Furthermore, initial estimates of biomass, natural mortality, and fishing mortality are derived from another model (Ecopath with Ecosim). With the above limitations, this model seems best suited for comparison to other models. Indeed, Shin, Shannon, and Cury (2004) used OSMOSE to compare fishing effects on the Beguela fishing community to Ecosim (Plaganyi 2007).

Invitro, developed by Gray et al. (2006) in Australia, is essentially a model between the individual based OSMOSE and full ecosystem model of Ecopath with Ecosim that more explicitly considers human activities as an ecosystem component. As an agent based model, Invitro can model individuals separately or as aggregates in a group. Agent based flexibility allows the user to represent any one ecosystem component appropriately (even in three dimensions), but comes at a computational cost. Computational costs limit Invitro to 10 to 20 agents and have limited its application. The most well documented use of Invitro thus far is in Australia to evaluate management strategies (Plaganyi 2007).

The first and most common full ecosystem modeling approach is Ecopath with Ecosim (EwE). Ecopath was created by Polovina (1984) as a mass balance accounting system. EwE was further developed by Walters, Christensen, and Pauly (1997) to explore the consequences of foraging arena theory, prey vulnerability, and risk sensitive foraging in exploited food webs. Foraging arena theory (Walters et al. 1997) postulates that trophic interactions occur in restricted arenas where prey will limit growth for survival and predators compete with each other as prey decline in refugia.

The static component of EwE--Ecopath--makes two assumptions regarding functional groups. First, biological production is equal to the sum of fishing mortality, predation, migration, biomass accumulation, and other unexplained mortality. Second, consumption within a function group is the sum of production, respiration, and unassimilated food. The Ecosim component adds temporal dynamics to these assumptions by describing biomass flux between groups as a series of differential equations. The key innovation is the inclusion of a vulnerability term that specifies each predator-prey interaction in terms of foraging arena theory. A final component, Ecospace, runs the differential equations of Ecosim on a cell by cell basis to provide spatially explicit predictions of biomass. Habitat preferences in Ecospace can be parameterized by species distribution models.

While the data requirements for EwE are fairly straightforward (e.g., production, consumption, biomass, diet, etc.), it can be tempting to adjust parameter values with no empirical support. This problem is not unique to EwE, but EwE is the most widely used ecosystem model. Additionally, human activities beyond fishing mortality and potential marine protected areas are not handled in EwE as explicitly as Invitro. However, the computational limitations are substantially less.

The Atlantis model, developed by Fulton et al. (2004), is a different full ecosystem modeling approach that is well suited to include anthropogenic effects. Some Atlantis components are similar to EwE. Most Atlantis sub-models are deterministic differential equations, but the vulnerability term in Atlantis can handle a wider range of functional responses between predators and prey and a wider range of refugia. Additionally, Atlantis explicitly includes biogeochemical cycling and economic models, making it ideal for evaluating management strategies. However, the number of sub-models can be daunting and requires extensive collaboration. Running an Atlantis model requires an extensive amount of time and data, making it only appropriate for selective use.

Ultimately, the use of any one of these models to understand and describe spatially explicit marine ecosystems depends on a tradeoff between complexity and simplicity, deterministic and probabilistic methods, data availability, computational power, and theory. All of these tradeoffs can be viewed through a lens of ever changing and scale dependent management needs. In some cases, computational power has outpaced theory (e.g., niche modeling). In other cases, theory (food web ecology, foraging theory) has provided a strong foundation for complex models to stretch the limits of our computational abilities. While exciting, uncertainty inevitably increases with complexity.

5.2 Case Studies

5.2.1 The South Atlantic Bight Ecopath Model

A whole food web trophodynamic fishery-ecosystem model has been developed for the South Atlantic Bight ecosystem (Figure 1; Okey and Pugliese 2001, Okey et al 2014) using the freely available *Ecopath with Ecosim* (EwE) software. As described in the previous section, Ecopath models were originally developed by Polovina (1984) to describe the food web and trophic structure of the French Frigate Shoals ecosystem. Subsequent development including the capacity of both temporal and spatial dynamics (e.g. Christensen and Pauly 1992, Walters et al. 1997, Walters et al. 1999, Walters et al. 2000, Steenbeek et al 2013) has resulted in a very widely used ecosystem modelling approach for understanding marine ecosystems including the effects of fisheries and other stressors on broad ecosystem components and features, thus increasingly operationalizing ecosystem-based management and policy.

The South Atlantic Fishery Management Council sponsored the development of the first iteration of this South Atlantic Bight (SAB) model (Okey and Pugliese 2001) as part of its initial fishery ecosystem plan (FEP) development. This model was refined soon thereafter during an iterative process involving a broad cross-section of stakeholders and scientists to produce a second generation model during 2002. That refined model was re-structured and refined more recently to explore the importance and roles of forage species in the SAB (Okey et al. 2014).

This latest iteration of the SAB model (Okey et al 2014) is being used as a starting point for developing an updated EwE model, which can form the core of an SAB ecosystem model that will be informed by physical oceanographic and estuarine models and can address broad objectives in fisheries management, habitat protection, climate impact assessment, and understanding cross-system linkages and connectivities. This updating and refinement can be achieved using a wide variety of recently-available resources such as compiled and updated fisheries and diet composition information, fishery independent information, and recent model refinements such as the GOM gag model (Chagaris and Mahmoudi 2013), which was partially based on an original West Florida Shelf model (Okey and Mahmoudi 2002, Okey et al. 2004).

The SAB model domain extends from Cape Hatteras, North Carolina to Biscayne Bay, Florida, and from the intertidal zone to 500 m depth, as described in Okey and Pugliese (2001) and Okey et al 2014). This covers an area of approximately 174,331 km2. An attempt was made to include estuarine components in this overall broad-scale model, but this effort emphasized species assumed to have an influence on the whole spatial domain, and was thus somewhat selective. Some species in this region are distributed beyond and across the model domain boundaries, but the defined area tends to capture the center of distribution for many managed species. The baseline time period characterized by the Ecopath model of the South Atlantic Bight used here is the late 1990s (1995-1998). This is a model initialization period. Now that a variety of time series data are presumably available for this area, potentially over 18 years, the model can be calibrated dynamically.

This current iteration of the SAB model contains 99 functional groups (biomass pools), including 50 fish groups in total, 12 forage groups, 8 fish predators of principle interest to recreational sectors, 5 elasmobranch groups, 7 bird groups, 3 marine mammal groups, sea turtles, 27 invertebrate groups, 4 detritus groups, 6 primary producer groups, 4 zooplankton groups, and microbial heterotrophs. The most recent exploration of the roles and importance of forage species (Okey et al 2014) involved simulations in which the biomasses each of 12 forage groups were both increased and decreased to derive trophodynamic signatures of each of these groups and compare the character of these signatures.

5.2.2 The West Florida Shelf Reef Fish Ecopath Model

A West Florida Shelf (WFS) EwE model has been developed that is centered on regulated species on the WFS including reef fishes, coastal migratory pelagics, and highly migratory pelagics as defined by the GMFMC and the NMFS (Chagaris 2013; Chagaris *et al*. 2015). Gag Grouper, Red Grouper (*Epinephelus morio*), Black Grouper (*Mycteroperca bonaci*), and Yellowedge Grouper (*Epinephelus flavolimbatus*) were each divided into 3 age stanzas and Spanish Mackerel (*Scomberomorus maculatus*), King Mackerel (*Scomberomorus cavalla*), and Red Snapper (*Lutjanus campechanus*) were all divided into juvenile and adult age stanzas. Other reef fishes and pelagics were included either as a single-species biomass group or aggregated into a group of similar species. Coastal and inshore species were included because they interact with reef fish juveniles yet to migrate offshore. Aggregate groups of non-target fishes, invertebrates, zooplankton, and primary producers were necessary for a complete food web. The resulting model consisted of 70 biomass pools including one each for dolphins and seabirds, 43 fish groups (of which 11 are non-adult life stages), 18 invertebrate groups, 4 primary producers, and 3 detritus groups. There are 10 commercial fishing “fleets” and four recreational fishing fleets.

The WFS-EwE Ecosim model was calibrated and capable of reproducing historical trends in abundance and catch from 1950 to 2009. The WFS-EwE model has been used to forecast the ecosystem impacts of various harvest policies in the Gulf of Mexico (Chagaris *et al*. 2015). For example, rebuilding of gag grouper stocks was predicted to have top-down effects and cause potentially large (>10%) declines in biomass of black seabass, other shallow water groupers, and vermilion snapper. A policy optimization search was conducted in Ecosim to quantify the trade-offs between fishery profits and reef fish conservation (Chagaris 2013). Over the long term (40 years), profits were highest when total reef fish biomass was about 40-60% larger than 2009 levels, a realistic and achievable goal. Conditions in 2009 were sub-optimal in regards to reef fish biomass and profits. By simulating policy options in Ecosim and comparing them to the optimal solutions along the tradeoff frontier, the optimization analysis provides a scorecard for which to rank policy choices against broader multi-fleet and multi-species management objectives. Lastly, the Ecosim model was used to simulate the effects of invasive lionfish on native reef fishes and evaluate ways to mitigate such impacts through top down fishing and predation effects (Chagaris *et al.* 2015). In the invasion scenarios, strong negative effects were predicted for lionfish prey groups such as small-bodied reef fishes, small non-reef fishes, and shrimp. Several large bodied predators that support valuable commercial and recreational fisheries were also negatively affected by lionfish through competition for prey. Simulations demonstrated that increased harvest of native reef fish predators is associated with increased lionfish biomass, suggesting that historical overfishing of reef fish may have made the system more vulnerable to species invasions.

The geographic domain of the Ecospace model is 25-30.5 degrees north and 81-87.5 degrees west with a spatial resolution of 10 minutes (= 0.167 degrees or appx. 20 km^2) and has dimensions of 34 rows by 40 columns (Figure 3). This covers an area from the Florida Panhandle south to, but excluding, the Florida Keys and extends from shore out to a depth of 250 m. A bathymetry map was obtained from the NOAA National Geophysical Data Center Coastal Relief Model (NOAA 2014). A rugosity map for the WFS, representing the average elevation change between a grid cell and the eight neighboring grid cells (m/cell), was available from the United States Geological Survey (Robbins et al. 2010). Time-averaged maps for sea surface temperature (11 micron day) and chlorophyll-a from the MODIS aqua satellite were downloaded using the NASA Giovanni Interactive Visualization and Analysis website (Acker and Leptoukh 2007). A salinity map was obtained by subsetting and averaging output from the HYCOM + NCODA Gulf of Mexico hydrodynamic model.

Ecospace was used to simulate the performance of marine protected areas (Chagaris 2013). Existing MPAs (Madison-Swanson, The Edges, Steamboat Lumps, and Middle Grounds) that cover less than 2% of the shelf did very little to enhance grouper and snapper stocks (biomass increase < 5%). Some species were predicted decline under the MPA scenarios due to top-down effects (predation and competition) caused by build-up of predator species. Because biomass of fish spilled over into unprotected areas, some large hypothetical MPA scenarios had little negative impact on the fishery and in some cases provided net economic benefits. The win-win scenarios, where there was gain in both biomass and catch, usually required between 15%-30% of the WFS to be closed to fishing.

5.3 Emerging Trends

6 Food Web Indicators

Ecosystem indicators have been used to assess the health of ecosystems and their components across a wide range of terrestrial and aquatic habitat types (see Jorgensen *et al.* 2010). Food web indicators are a subset of ecosystem indicators that characterize energy flow, ecosystem resilience, and food web structure and functioning (Link 2005; Shin *et al.* 2012). An indicator may be descriptive and serve to track the abundance of a species or suite of species. Or, an indicator may be integrative and describe overall ecosystem attributes such as trophic diversity or resilience. Food web indicators may also serve as proxies for ecosystem-services (Kershner et al. 2011). Many indicators, especially the integrative type, respond slowly to ecosystem change and may appear to be conservative (Cury et al., 2005). Moreover, indicator responses can also be non-linearly related to ecosystem state and pressures (Fulton et al. 2005).

No indicator is all-encompassing and a carefully chosen portfolio of indicators is necessary to determine overall ecosystem status (Cury et al. 2005; Rice and Rochet ref). The International Council for the Exploration of the Sea (ICES) held a workshop in 2014 to identify useful food web indicators (ICES 2014). The goals of the workshop were to develop a short list of suggested food web indicators, with emphasis on pragmatic approaches that are operational now or in the near future. Forty candidate food web indicators were evaluated in categories of food web structure, functioning, and resilience. Each indicator was scored based on its measurability, sensitivity to the underlying pressure, theoretical soundness, ability to be easily communicated, and relevance to management (ICES 2014). Many of the indicators had clear links to food web function. The indicators describing ecosystem resilience scored poorly due to the complexity of measuring food web resilience and recovery, while the structural indicators scored highly and are most readily available. The top scoring indicators from the workshop are summarized in Table 7.1 for each category. The full list of indicators, along with brief descriptions and references, is provided in the workshop report (ICES 2014).

Indicator name	Description	Data needs
Indicators Linked to Energy Flow		
Productivity (production per unit biomass, including seabird breeding success)	survival and reproductive output is affected by food quantity and quality; detects gross structural changes in energy flow	nesting surveys, number offspring, pregnancy rates, spawner abundance
Primary production required to support fisheries	characterizes ecosystem production and conversion of organic matter across trophic levels; difficult to communicate; requires estimates of transfer efficiency that are not readily available	food web model
Productive pelagic habitat index (chlorophyll fronts)	chl-a fronts are areas of efficient energy transfer from low trophic levels to top predators; implications for management are unclear	satellite imagery, oceanographic models
Ecosystem exploitation (fisheries)	useful to describe harvesting patterns and pressure of the fisheries on the food web	catch
marine trophic level (TL) indicators	based on average weighted trophic levels across a suit of species; integrated across the ecosystem; most useful for assessing food web effects of fisheries	food habits data, survey time series, catch, TL estimates
Indicators linked to resilience		
Mean trophic links per species	reflects connectivity and stability; dependent on temporal and spatial characteristics; requires comprehensive diet data	food habits data
Ecological Network Analysis derived indicators (mean overall transfer efficiency)	a descriptor of ecosystem health; average TE varies across ecosystem types; requires comprehensive diet data	food web model
Gini-Simpson dietary diversity index	summarizes contributions of prey resources to consumers; requires comprehensive diet data	food habits data
Indicators linked to structure		
Guild surplus production	productivity of functional guilds	survey biomass; catch
Large fish indicator (LFI)	sensitive to fishing pressure	survey biomass
total biomass of small fish	the amount of energy transferred from zooplankton to higher trophic levels is limited by biomass of small pelagic fish	survey biomass
proportion of predatory fish	captures changes in trophic structure and functional diversity of fish due to fishing and environmental pressures	survey biomass, food habits data
pelagic to demersal ratio	describes changes in trophic energy flow	survey biomass

	and community structure	

7 Management Applications

Fisheries management in the South Atlantic follows the traditional process of setting harvest limits and regulations based on the outcome of single-species stock assessments. There are few, if any, cases where food web properties or predator-prey interactions have been considered under this current framework. Incorporating these processes does not require a complete shift from single-species to ecosystem-based fisheries management. Food web models can in fact make very important contributions at multiple stages of the assessment and management process (Link 2010). This section describes, in a general sense, practical application of food web models and indicators to single-species fisheries assessment and management.

7.1 Informing Stock Assessment

Stock assessment models usually assume that most life history parameters (e.g. natural mortality, growth, fecundity, recruitment) are constant over time or vary according to some simple random deviations. This is usually known not to be true, but lack of empirical evidence has largely prevented a move away from those assumptions. In the absence of such data, ecosystem models can provide estimates of these parameters over time. In particular, food web models predict changes in natural mortality over time as predator abundances vary or food become more or less available (Moustahfid et al. 2009). Alternatively, food availability or environmental conditions may affect growth or fecundity (Schirripa et al. 2009). There is some precedent for including simulated natural mortality time series in stock assessment. The stock assessment of Atlantic menhaden has used natural mortality output from the multi-species virtual population analysis (MSVPA) to account for predator needs (Garrison et al. 2010). In the Gulf of Mexico, natural mortality from two separate Ecosim models was used in sensitivity runs of the gag grouper stock assessment (Chagaris and Mahmoudi 2013; Gray et al. 2013). The increased use of the Stock Synthesis assessment model and similar modeling platforms facilitates these inclusions (Methot and Wetzel 2013).

7.2 Evaluating Policy Options

Harvest policies for one species are likely to have effects on other species due to trophic interactions. However, management decisions are based on projections of single-species stock assessment models that assume a constant environment and ignore any policies that are also being considered for other species. Using ecosystem models, managers (or the SSCs) can simultaneously evaluate multiple policy options for more than one species. For example, if a management goal is to rebuild multiple species that compete with one another for food and/or space (such as in a reef fish community) then rebuilding plans based on single-species models alone may be misinformed. Additionally, projections made with an ecosystem model can explicitly incorporate environmental uncertainty that can then be factored into decision-making (i.e. setting catch limits) following the p-star method. For this to be possible, the food web models must be able to demonstrate similar dynamics to the stock assessment model. To facilitate this, food web models can be calibrated to abundance or biomass trajectories from stock assessment models and derived reference points (Fmsy, MSY, B0) can be compared.

7.3 Using Indicators in Management

How to apply towards fisheries assessment and management; approaches to developing indicators can be complex so focus on describing why they're useful – efficient at measuring overall health and integrity of the system.

7.4 Emerging Trends

8 Summary and Recommendations

The variety of habitats in the South Atlantic support diverse food webs, that also are interconnected by proximity, energy pathways, migration / immigration, and by life history. Many components are shared among habitat-specific food webs, from algae to marine mammals. Ontogenetic, seasonal, and diel migrations, predator avoidance, and foraging behaviors transfer energy and food web participants among the various habitats within the SA. Specific to this report, the paucity of data for offshore, non-commercially important species and pelagic species equate to a difficulty in applying EBFM. As in other sub-tropical to temperate areas, food webs in the South Atlantic rely heavily on grass detritus (marsh or seagrass) and phytoplankton as carbon sources. As one moves offshore, the reliance on phytoplankton increases as terrestrially-derived organic carbon diminishes. SA food webs are regulated by seasonal and long-term environmental variability (bottom-up; e.g. temperature, upwelling, day length, Gulf Stream Index, nutrient loading) and top-down factors such as fishing of large snapper-grouper and natural predation. Ultimately, energy flow within the system is tightly mediated by predator-prey interactions. Forage species (e.g. Menhaden, Shrimp, and Pinfish) are critical links in energy transfer within and among food webs in the SA and thus in stability of these webs. Unfortunately, population dynamics of the vast majority of these critical species are poorly understood. Potential impacts of climate change on consumption rates, foraging behaviors, and the primary producers in the system also are unknown.

Food webs are impacted both directly (fishing, introduction of invasive species) and indirectly (water quality changes, alteration of habitats) and these impacts are often, if not primarily, anthropogenic in origin. Other systems provide well-documented examples of trophic cascades following perturbations and multiple perturbations likely have synergistic or cumulative impacts. Trying to predict impacts, whether they be positive such as the recovery of overfished species or negative such as habitat destruction, increasingly relies on modelling approaches. Modelling approaches often trade-off between being simplistic, needing very little data, but limited in predictive capabilities for whole ecosystems, or complex, needing extensive data sources and computational power, but better able to address multiple questions or hypotheses if uncertainty can be limited.

The goal of understanding food web components, connections, energy, and complexity is to provide useable information to direct management or future research needs. As such, indicators have been employed to summarize the state of knowledge of an ecosystem or food web and serve as a benchmark to inform future actions. Indicators may range from point estimates such as measures of diversity to those that are dynamic such as non-linear relationships between the ecosystem and pressures upon it. Suites of indicators are likely to increase in importance as we move from single-species management and assessment approaches to EBFM. Food web models and indicators are essential tools to predict coupled, synergistic, or cumulative effects of management practices.

Prior to the development or use by managers of tools to characterize, quantify, and predict, the SA region has specific outstanding data needs. Diet, energy, and biomass for non-economically important species must be determined. Uncertainty in complex food web models must be minimized and empirical data such as those mentioned above are crucial to these efforts. Impacts of human activities and climate need to be determined specifically for the SA.

Forage species are a small, but critical piece of the ecosystem puzzle. In order to ensure that the integrity of South Atlantic food webs and the interconnectedness of fish populations and their environments are maintained, prior to any opening of new directed fisheries or expansion of current fisheries for forage species, essential science and monitoring information must be obtained and management plans developed that explicitly account for the dietary needs of predators when establishing management goals and fisheries rules. Also, the abundance of important forage species needs to be monitored and quantified on routine bases for inclusion in stock assessments, ecosystem models, and other scientific tools and processes to enable comprehensive and sound management decisions that incorporate ecosystem considerations and economic tradeoffs.

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