

**DEEP-WATER *OCULINA* REEFS OF FLORIDA:  
SUMMARY OF THE STATE OF KNOWLEDGE OF THE HABITAT, FAUNA,  
GEOLOGY, AND PHYSICAL PROCESSES OF THE ECOSYSTEM**

A Report to the South Atlantic Fishery Management Council  
*Oculina* Evaluation Team Workshop  
August 21-23, 2006  
Port Canaveral, Florida

by  
John K. Reed  
Harbor Branch Oceanographic Institution  
5600 U.S. 1, North, Fort Pierce, FL 34946  
Phone- 772-465-2400 x205, Fax- 772-461-2221  
Email- [jreed@hboi.edu](mailto:jreed@hboi.edu)

August 18, 2006



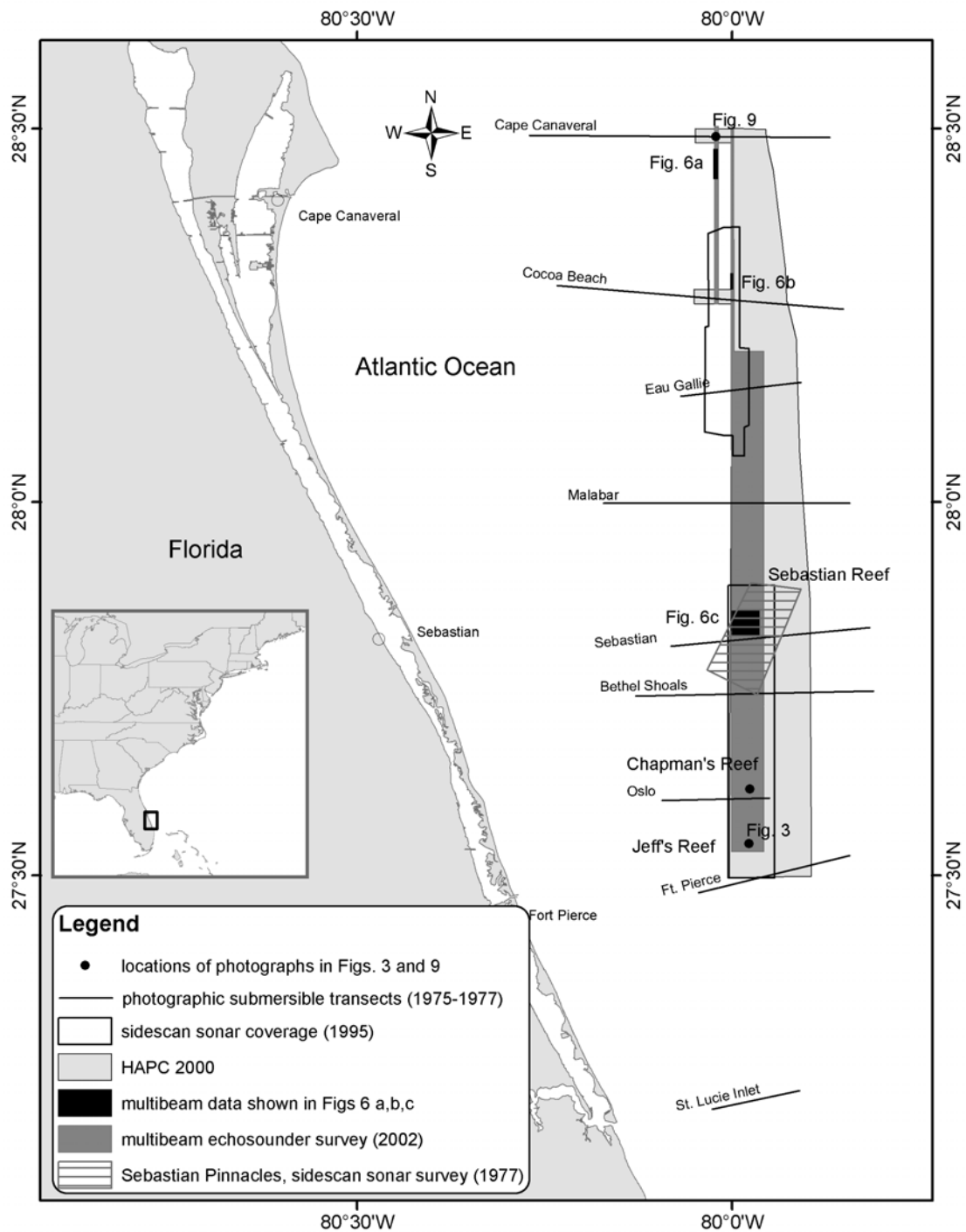


Fig. 1. Light shaded area: 1029 km<sup>2</sup> (300 nm<sup>2</sup>) deep-water *Oculina* Marine Protected Area (MPA) off eastern Florida. The original 315 km<sup>2</sup> (92 nm<sup>2</sup>) *Oculina* Habitat of Particular Concern (OHAPC) that was designated in 1984 (also known as the Experimental *Oculina* Research Reserve) is indicated by the boxed area (1995 sidescan sonar coverage) that extends from the Sebastian Reef area to the south at the Ft. Pierce transect line. (from Reed et al., 2005)



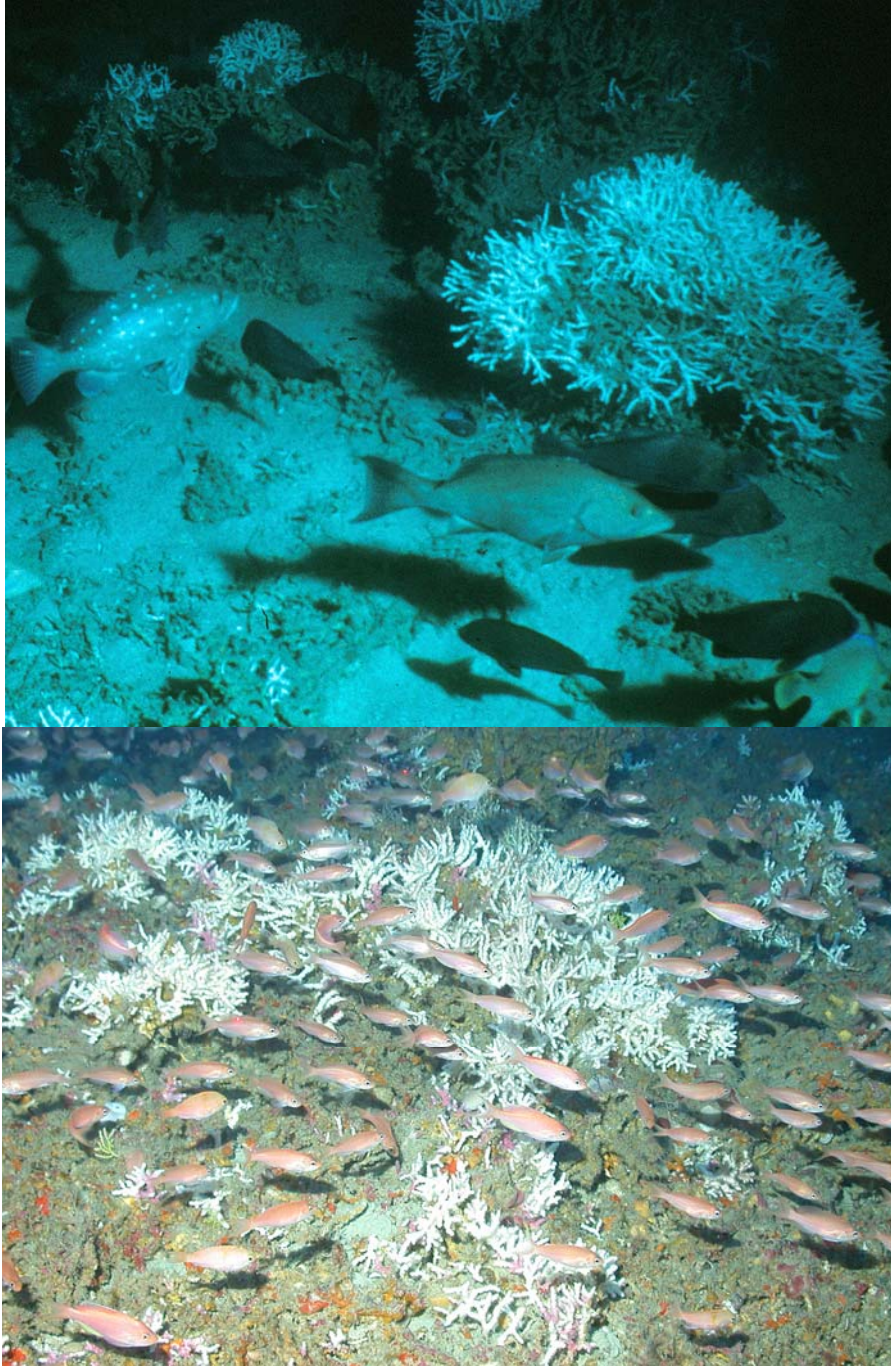


Fig. 2. a. Schools of scamp and gag grouper were abundant on deep-water *Oculina* reefs in 1970s and 1980s (Jeff's Reef, 70-m depth); b. Healthy *Oculina varicosa* coral colony with associated schools of anthiid fish in 2003 (Sebastian Pinnacles, 80-m depth). (from Reed et al., 2005)



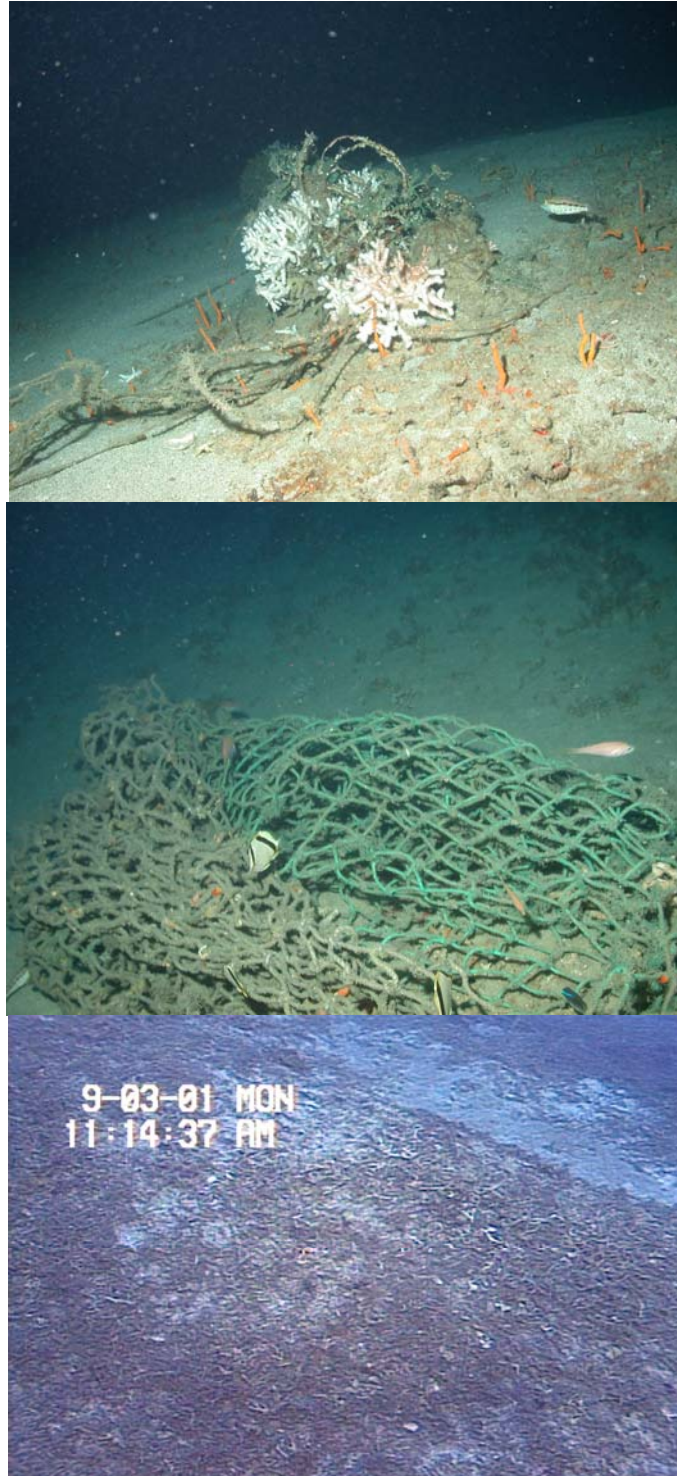


Fig. 3. Damage from fishing gear within *Oculina* MPA: a. longline fishing gear wrapped around colony of *Oculina varicosa* (Sebastian Pinnacles, 80-m depth); b. discarded shrimp trawl net (Sebastian Pinnacles, 80-m depth); c. apparent trawl track at Cape Canaveral Pinnacle site (67-m depth). (from Reed et al., 2005)



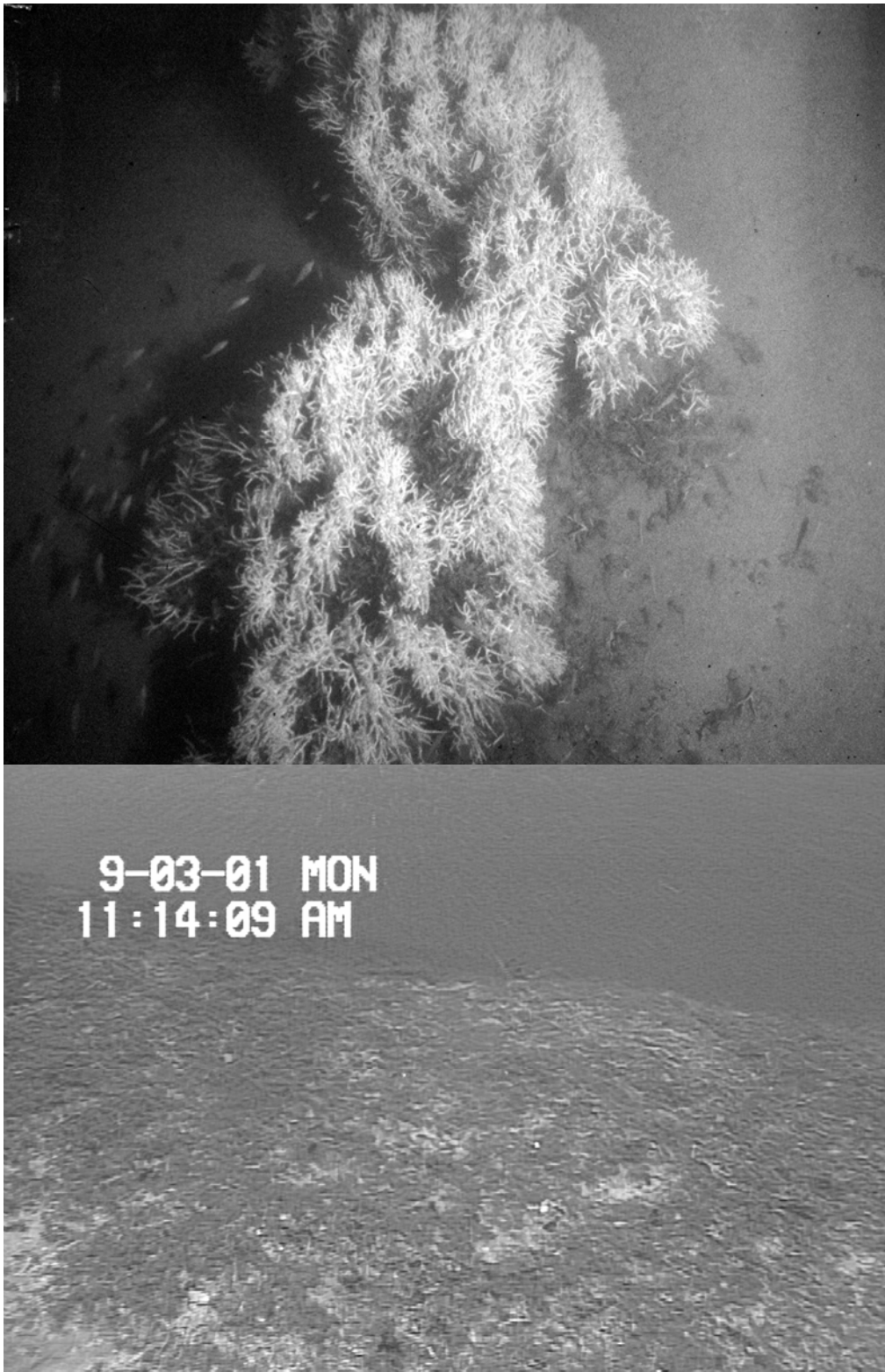


Fig. 4. Peak of 20-m high *Oculina* reef at Cape Canaveral Pinnacle site (67-m depth; 28° 29.8'N, 80° 01.27'W): a. historical photo (JSL II-63) from June 8, 1976; b. same site (Clelia 616) on Sept. 3, 2001, reduced to rubble from apparent trawling. (from Reed et al., 2005)



This report is a review and summary of the state of knowledge regarding the deep-water *Oculina* reefs off eastern Florida since their discovery in the 1970s to the present. A compilation of all known publications (with annotations) about the Florida *Oculina* reefs is listed in the appendix. These references are categorized into the following categories described below:

	<u>Page</u>
Historical habitat and bathymetric surveys-	6
Recent habitat and bathymetric surveys-	7
Physical environment-	8
Coral morphology and distribution-	9
Benthic communities-	10
Fish communities-	11
Artificial habitat modules-	12
Coral reproduction and larval biology-	12
Coral growth-	12
Coral growth and reef age-	13
Deep-water coral reef sediments-	13
Deep-water coral reef geomorphology and development-	14
Deep-water coral reef senescence and bioerosion-	14
Human impacts-	15
Effects of trawling-	16
Conclusions-	18
Appendix- <i>Oculina</i> publications-	20

### **Historical Habitat and Bathymetric Surveys**

#### *1960s Dredge and Commercial Fish Surveys:*

Moe (1963) first described some of the shelf-edge features off eastern Florida based on interviews with commercial fishermen. Macintyre and Milliman (1970) surveyed the physiographic features of the shelf-edge break (80-110 m) from Cape Hatteras, North Carolina (35°N) to Ft. Lauderdale, Florida (26°N) using echosounder profiles, rock dredge, sediment samples, and bottom photographs. Information on coral distribution was also summarized from 57 dredge and trawl records from the R/V Gosnold and R/V Aquarius between 1973 and 1977 (Reed 1980).

#### *1977 Sidescan Sonar Survey:*

The Sebastian Pinnacle site (110 km<sup>2</sup>), within the region now designated as the *Oculina* MPA, was mapped in 1977-78 using a Klein Series 400 sidescan sonar and echosounder (fathometer) tracings (Thompson et al. 1978; Thompson and Gulliland 1980). LORAN C was used for positioning which had navigational accuracy in this region of +36 m in the east-west direction and +850 m north-south. The fathometer had a vertical resolution of 0.25- 1.0 m. Bathymetric maps were plotted with 1-m isobath contours.

#### *1975-1983 Submersible and ROV Surveys:*

Between 1975 and 1983, data were compiled in the region of the deep-water *Oculina* banks using Harbor Branch Oceanographic Institution's (HBOI, Harbor Branch Foundation) *Johnson-Sea-Link* (JSL) I and II submersibles and CORD Remotely Operated Vehicle (ROV). These data



included photographs, videotapes, cruise reports, logs, dive transcripts, hydrographic data, and collections by lockout dives from the submersibles.

From 1975 to 1977, a benthic survey consisting of 12 east-west photographic transects was made with the JSL submersibles at the shelf-edge break within the region that is now designated as the *Oculina* MPA (Avent et al. 1976; Avent and Stanton 1979). The transects were spaced approximately 19 km apart, extended to 300-m depth, and consisted of 55 submersible dives covering 298 km. It was during this survey that the live deep-water *Oculina* banks were first observed and described in detail (Avent et al. 1977). Navigation used LORAN-A which in this region had an accuracy of  $\pm 150$ -300 m. Photographs were taken every 1-2 minutes during each transect and analyzed using a microfilm reader with a grid overlay for estimating percent cover. Photographic data along with hydrographic and navigation information were entered into a computer database (unfortunately the computer tapes are obsolete, but hard copies and photos are archived at HBOI).

JSL dives and echosounder recordings were also conducted from 1979 to 1983 for biological and geological studies within the area of the *Oculina* MPA (C. Hoskin, J. Reed, pers. observations; Reed, 2002). In addition, a time-lapse camera was deployed to document the reef community over several 48-hour periods. Extensive surveys of the fish populations and fish behavior were made concurrently between 1975 and 1983 (G. Gilmore, pers. comm.; Gilmore and Jones, 1992).

Tethered, mixed-gas dives (lockout) were made with the JSL submersibles from 1976 to 1983 on the deep-water *Oculina* banks for studies on biodiversity of animals associated with the coral, coral growth rates, and geology (Reed, 2002). The scientist-lockout diver used a Kirby-Morgan band mask attached to a 30-m umbilical hose which supplied the gas mix (10% oxygen/90% helium) and voice communications from the submersible.

#### *Videotape and Photographic Archives:*

Some of the original videotapes (3/4" and 1/2" open reel) and 30-m rolls of 35-mm Ektachrome film have been recently restored and archived. Unfortunately videotapes of that age are prone to hydrolysis problems. The restoration process stabilizes the polymers of the tape coating. Once stabilized the tapes will be restored and archived onto Beta SP videotapes and copied to digital video disk (DVD) for analyses. The 35-mm photographs were also recently digitized with a Nikon LS-2000 scanner and copied to DVD. These original photographs were recently analyzed for comparison with recent mapping and habitat characterization surveys (Reed et al., 2006).

#### **Recent Habitat and Bathymetric Surveys**

Most of the recent surveys (1995 to present) of the *Oculina* HAPC are a series of continuing research projects to characterize the condition of the coral habitat and fish populations. These surveys have been sponsored largely by NOAA's National Marine Fisheries Service (NMFS), NOAA's National Undersea Research Center at the University of North Carolina at Wilmington (NURC/UNCW), and NOAA's Ocean Service (NOS).

#### *1995 Sidescan Sonar Survey:*

In 1995, the U.S. Geological Survey, using the NOAA ship R/V Chapman, conducted a 100-kHz sidescan sonar survey covering 206 km<sup>2</sup>, and approximately 20% of the *Oculina* MPA (Scanlon et al. 1999). The goal was to provide reconnaissance geologic maps of the



Experimental Oculina Research Reserve (EORR; equivalent to the original 315 km<sup>2</sup> *Oculina* MPA) and an unprotected Control Area north of the reserve (now part of the current 1029 km<sup>2</sup> *Oculina* MPA) to support NMFS studies of grouper populations.

#### *2002-2006 Multi-beam Echosounder Surveys:*

Several multi-beam echosounder surveys primarily from NASA's M/V *Liberty Star* and *Freedom Star*, provided the first high-resolution (1.5-3.0 m) bathymetric map of the coral habitat in the *Oculina* HAPC. Surveys in 2006 will provide additional information within the HAPC but outside the *Oculina* zone (potential tilefish habitat) and also on recently discovered *Oculina* reef areas outside the currently protected OHAPC. Seafloor Systems Inc., Oregon, performed the survey using a 240-kHz RESON 8101 multi-beam echosounder system integrated with the ship's Differential Global Positioning System (GPS) unit, a DMSO 5 TSS motion sensor (quantifies heave, pitch, and roll), a SG Brown gyrocompass (yaw), and HYPACK navigation. All data were compiled in real-time using an ISIS Shipboard Data Acquisition and Image Processing System. Conductivity, temperature and density (CTD) casts were made every six hours. Raw data were post-processed in CARIS software to remove outliers and correct for sound velocity and tidal stage.

#### *1995-2006 ROV, Submersible, and AUV Surveys:*

NOAA/NURC's Phantom S4 ROV and Spectrum II ROV, and HBOI's Clelia submersible were used for habitat and fish surveys in 1995, 2001, 2003, and 2005. These surveys covered approximately 1.13 km<sup>2</sup>, or 0.11% of the *Oculina* MPA. The ROVs and submersible were equipped with digital still cameras and color video cameras with parallel lasers to indicate scale in the images. Objectives included: (1) survey high-, moderate- and low-relief areas to document the various habitats including live coral thickets, dead coral rubble, and hard bottom, and (2) revisit historical sites identified in the 1970s to document any changes in habitat. In 2003, the position of the ship and ROV were overlaid on the 2002 multi-beam map which allowed precise targeting of specific features for exploration during the dives. Photographic and video data from the 2001-2003 ROV surveys have been analyzed for habitat cover and associated fish census (Harter and Shepard, in review). In 2006 a new NOAA NURP AUV will be deployed to complete the multibeam mapping.

#### *Oculina Geographic Information System (OGIS):*

A multi-media geographic information system (GIS) has been developed to allow access and comparison of past and present data in the *Oculina* HAPC (NOAA NURC at UNCW; Manning, 2003). Portions of OGIS are available via the internet for use by resource managers and stakeholders (<http://www.uncw.edu/oculina>). Georeferenced digital photographs and logs from submersible dives complete the multi-media component of OGIS.

### **Physical Environment**

Bottom temperatures averaged 16.2°C and ranged from 7.4 to 26.7°C at the 80-m *Oculina* reef site during a long-term survey (Reed, 1981). Upwelling of bottom water from the Florida Straits produces episodic intrusions of cold water throughout the year at the shelf edge in this region which causes temperatures to drop below 10°C (Smith, 1981; Reed, 1983). During these upwelling periods, levels of nutrients and chlorophyll increase nearly an order of magnitude: nitrates increased from <2 uM during non-upwelling to 9-18 uM during upwelling; phosphate



from  $<0.25$  to  $0.5\text{--}2.0\text{ }\mu\text{M}$ ; and chlorophyll-*a* from  $<1$  to  $1\text{--}9\text{ mg m}^{-3}$  (Reed, 1983). Salinity on the deep reef averages 36.0. The clear, warm water of the northerly flowing Florida Current in the region of the *Oculina* reefs typically only extends down to a depth of 50-60 m. Seldom does this water mass extend to the bottom and the reefs are often inundated with a turbid, bottom nephroid layer. Bottom currents averaged  $8.6\text{ cm s}^{-1}$  but may exceed  $50\text{ cm s}^{-1}$  ( $1\text{ kn}$ ); currents of  $50\text{--}100\text{ cm sec}^{-1}$  due to the Florida Current may affect the peaks of the higher *Oculina* pinnacles and may be strong enough to break the coral branch tips (Reed, 1981; Hoskin et al., 1983).

Long-term light measurements with Lambda quantum meters recorded an average of 0.33% transmittance of surface light which usually does not support macroalgae on the deep-water *Oculina* reefs or zooxanthellae within the coral (Reed, 1981). Sedimentation on the reefs averaged  $53\text{ mg cm}^{-2}\text{ day}^{-1}$ , ranging from 15 to 78 (Reed, 1981). This is slightly higher than typical sedimentation rates for shallow-water coral reefs which average  $1\text{--}10\text{ mg cm}^{-2}\text{ day}^{-1}$  (Rogers, 1999).

### **Coral Morphology and Distribution**

An extensive area of unique deep-water *Oculina* coral reefs stretches over 167 km (90 nmi) along the shelf edge off eastern Florida, at depths of 70-100 m, and ranging from 32 to 68 km offshore (Reed, 1980; Thompson and Gilliland, 1980; Virden et al., 1996; Koenig et al., 2000). These extend from  $27^{\circ}32'\text{N}$  to  $28^{\circ}59'\text{N}$  latitude, in a 2-6 km wide zone, paralleling the  $80^{\circ}\text{W}$  meridian along the western edge of the Gulf Stream (Florida Current). Deep-water *Oculina* reefs are found exclusively here and are not known anywhere else on earth. A single species of a branching scleractinian coral, *Oculina varicosa* Lesueur, 1820, grows on these reefs. The reef system consists of numerous individual coral pinnacles, mounds, and ridges that are high relief structures, ranging from 3 to 35 m in height and up to 100-300 m in width (Figure 2; Reed, 1980). Each pinnacle is actually a veneer of living coral overlying a mound of sand and mud sediment, coral debris, and oolitic limestone base formed during the Holocene transgression (Macintyre & Milliman, 1970; Reed, 1980).

The deep-water growth form of *O. varicosa* has been found in depths of 49-152 m (Reed, 1980), ranging from Florida to North Carolina of the southeastern United States. The high relief *Oculina* banks, however, are only known off central eastern Florida. Colonies are arborescent with highly anastomosed, irregular, dendritic branches which average 6 mm in diameter. Cross sections of the branches show dense, concentric layers of aragonite. Corallites are distributed spirally around the branches, and calyces are generally 2-3 mm in diameter with three cycles (24) of septa. The core of the colony is strengthened by the anastomosed structure while the tapered tips, which are several centimeters in length, are extremely fragile. Living colonies are pure white in color and microscopic examinations have shown that they lack zooxanthellae.

The deep-water form of *O. varicosa* can be divided into three colony types (Reed, 1980). Individual colonies up to 2 m in diameter grow as discrete, branched, spherical heads. These are either unattached on the sand-rubble substrate or attached to limestone pavement. Of these, colonies less than 25 cm in diameter are often 100% alive. Larger colonies are dead in the center, possibly from water stagnation due to the dense branching framework, with only the outer 10-30 cm alive. Some large colonies over 2 m in diameter are broken in half, probably due to their weight and bioerosion, exposing the dead inner branches. The second deep-water colony type is a linear form which is 1-2 m in height and width and attains a length of 3-4 m. Finally, colonies may form massive thickets of contiguous colonies nearly 2 m in height (Reed, 1980).



Extensive banks of this form generally have a steep slope of 30-45 degrees, especially on the south side which faces into the Florida Current. The north slopes are generally less steep and have a greater percentage of dead coral rubble or barren areas. Between 27°45'N and 27°52'N where the prominences reach their maximum density, *Oculina* was mostly found as dead rubble during mapping studies in 1976-1985 (Reed, 1980; Thompson & Gulliland, 1980). Some of these prominences have scattered <1 m live colonies covering up to 10% of the bottom while other banks in this region are 100% dead coral. Usually the dead fragments are <10 cm in length but in some places standing dead colonies <0.5 m in diameter are present (Reed, 1980; Hoskin et al., 1987).

### **Benthic Communities**

Quantitative surveys of the macro-invertebrate fauna associated with the *Oculina* coral discovered that the *Oculina* coral habitat supports very dense and diverse communities of associated invertebrates (Reed et al., 1982; Reed & Mikkelsen, 1987). Live *Oculina* coral colonies of shallow and deep-water growth forms were sampled by placing a Nytex bag with 0.5-mm mesh over each colony. Thus all the macrofauna on and within the coral were collected. In the laboratory, each coral colony was photographed and measured for colony weight, height, diameter, total volume displacement, outer surface area, and branch surface area. Each colony was then broken into live and dead fractions and then further fragmented into 1-2 mm chips to remove all boring, free-living, and epizoid fauna that were retained on a 0.5-mm mesh screen. These studies found over 20,000 individual invertebrates living among and within the branches of 42 small *Oculina* colonies, yielding 230 species of mollusks, 50 species of decapods, 47 species of amphipods, 21 species of echinoderms, 15 species of pycnogonids, 23 families of polychaetes, and numerous other taxa, e.g., sipunculids, nemertines, isopods, tanaids, ostracods, and copepods (Reed et al., 1982; Reed & Hoskin, 1987; Reed & Mikkelsen, 1987; Miller & Pawson, 1979; Child, 1998).

The 42 quantitative *Oculina* coral samples yielded 2,300 decapod crustaceans in 15 families, 35 genera and 50 species (Reed et al., 1982). The community was species rich in xanthid and majid crabs and alpheid shrimp. Numerically it was dominated by hermit crabs (*Pagurus carolinensis*, *P. piercei*), a porcellanid crab (*Megalobrachium soriatum*), and a galatheid crab (*Galathea rostrata*). Densities of most dominant decapod species were positively correlated with the size of the dead, rather than the live, portion of the coral. However, densities of the obligate commensals *Domacia acanthophora* and *Troglocarcinus corallicola* were independent of coral size.

For the molluscan community, the quantitative coral samples yielded 5,132 individuals and 230 species-level taxa in 74 families and 111 genera, including 155 species of gastropods, 68 bivalves, 1 scaphopod, 5 polyplacophorans, and 1 cephalopod (Reed & Mikkelsen, 1987). An additional 32 species were identified from qualitative samples of *Oculina*. Of these taxa, 47% were free living (motile), 32% symbiotic (parasitic or commensal), 18% epilithic (fouling), and 3% endolithic (boring). The pyramidellid gastropods were the most species rich (23 sp.), followed by Cerithiopsidae (15 sp.), Fissurellidae (15 sp.), and Triphoridae (14 sp.). A total of 177 species were numerically rare consisting of less than 10 individuals, 42 species were common, and 11 species were abundant. Three gastropods (*Parviturboides interruptus*, *Costoanachis lafresnayi*, *Metaxia rugulosa*) and three bivalves (*Lithophaga bisulcata*, *Diplothyra smithii*, *Barbatia candida*) comprised 51.5% of the individuals collected. Analysis of the trophic structure of the molluscan community showed that 29% of the species were filter feeders (including suspension feeders and mucoid entrappers), 23.9% parasitic carnivores, 16.8%



non-parasitic carnivores, 15.5% herbivores, 6.7% detritivores, 4.2% scavengers, and 3.8% corallivores (coral eating carnivores). The corallivore genera included *Latiaxis*, *Coralliophila*, *Calliostoma*, and *Heliacus*. The cool bottom temperatures and upwelling may account for the greater numbers of eurythermic tropical, temperate, and boreal species that were found on the 80-m reef site.

### **Fish Communities**

The dense invertebrate community helps support the diverse fish populations (>70 species). The deep-water *Oculina* reefs form impressive breeding grounds for commercially important populations of gag (*Mycteroperca microlepis*) and scamp (*M. phenax*) grouper; nursery grounds for juvenile snowy grouper (*Epinephelus niveatus*); and feeding grounds for these and other fish including black sea bass (*Centropistes striata*), red grouper (*E. morio*), speckled hind (*E. drummondhayi*), warsaw grouper (*E. nigrilus*), goliath grouper (*E. itajara*), almaco jack (*Seriola rivoliana*), greater amberjack (*S. dumerili*), red porgy (*Pagrus pagrus*), red snapper (*Lutjanus campechanus*), gray snapper (*L. griseus*), little tunny (*Euthynnus alletteratus*), giant ocean sunfish (*Mola mola*), Atlantic manta ray (*Manta birostris*), tiger shark (*Galeocerdo cuvieri*), and scalloped hammerhead shark (*Sphyrna lewini*) (G. Gilmore, pers. comm.; NOAA, 1982; Reed & Gilmore, 1982; Gilmore & Jones, 1992; Koenig et al., 2000, 2005; Reed et al., 2006). This shelf-edge structure also may form part of the migration pathway for king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and wahoo (*Acanthocymbium solandri*). The spiny tail stingray *Dasyatis centroura* use the deep-water *Oculina* reefs region for courtship and mating (Reed & Gilmore, 1981), and large populations of the commercially important squid *Illex oxygonius* have been observed spawning on the banks (Reed & Gilmore, 1982).

Dense schools of thousands of small antheids *Hemanthias vivanus* often cover the coral, darting into the recesses of the branches for protection and for feeding on the invertebrates living within. These in turn help support the large populations of larger fish (Reed, 1985; Reed & Hoskin, 1987). Dense populations of gag and scamp grouper were associated with the *Oculina* reefs in the 1970s and early 1980s. Scamp are seasonally abundant (fall to spring) reaching densities of several hundred individuals per hectare (Gilmore & Jones, 1992). Groups of 5-50 individuals of both scamp and gag grouper school 1-20 m above bottom. The deep-water *Oculina* reefs are temporary habitats for gag and scamp since they also occur at shallower reef sites on the shelf. However, spawning aggregations of hundreds of individuals of scamp and gag appear to prefer the shelf-edge coral formations at depths greater than 70 m. These spawning aggregations avoid the reefs when temperatures drop below 10°C during periods of upwelling (Gilmore & Jones, 1992). Unfortunately these large aggregations made perfect targets for both commercial and recreational fishermen, and the populations dropped drastically by the early 1990s.

The abundance and biomass of the economically important reef fish was much higher 30 years ago, and spawning aggregations of gag and scamp grouper have been greatly reduced in size (Koenig et al., 2000, 2005). Surveys of population densities for the dominant fish species were highly correlated with habitat type when comparing healthy intact coral habitat versus dead coral habitat (Koenig et al., 2006). This was true for the serranid basses (e.g., roughnose bass and red barbric); serranid groupers (e.g., gag, scamp, and speckled hind); and pelagics like greater amberjack and almaco jack. Few economically important species occurred in coral rubble (Koenig et al., 2006). Juvenile (yellow phase) speckled hind associated with intact habitat



at average densities of three to five per hectare. Male gag occurred only on Jeff's Reef and on Sebastian Reef near reefball clusters. Intact coral thickets within the EORR (relative to sites outside of the EORR) clearly contribute to improved abundances of gag and scamp, including males of both species on intact reef sites. These areas also appear to serve as juvenile habitat, based on the observation of juvenile speckled hind in association with the *Oculina* thickets of Jeff's and Chapman's Reefs (Koenig et al., 2006). This is a significant finding because the SAFMC considers speckled hind a threatened species (Coleman et al. 2000). Photographic and video data from the 2001-2003 ROV surveys have been analyzed for habitat cover and associated fish census (Harter and Shepard, in review).

### **Artificial Habitat Modules**

In 2000, the first large-scale restoration of *Oculina* reefs on the high-relief features of Sebastian Reef, an area covered with coral rubble and almost completely devoid of intact coral colonies, was initiated (Brooke et al., 2005; Koenig et al., 2005). Reefballs (Reefball Foundation, [www.reefball.org](http://www.reefball.org)), which are perforated dome-like concrete structures one-meter in diameter and 0.7 m high, were deployed to simulate the overall size and aspect of *Oculina* coral colonies. Clusters of reefballs are expected to serve as attachment sites for coral transplants, centers for *Oculina* thicket restoration as the attached coral grows, and structure replacement for reef fish. One hundred and five reefballs were distributed among nine different 500 m<sup>2</sup> areas in clusters of varying density— 5, 10, or 20 reefballs. Thus, there were three replicates of each cluster size arranged in a randomized block design to determine the most efficient cluster size (density) for attracting fish. Each reefball was affixed with a wooden cross on the top attached with a length of jute (both substances being biodegradable), thus providing sufficient drag to ensure that the reefballs would land upright when reaching the bottom. Clusters deployed from the ship platform fell freely to the seafloor. The same fish survey measures used for natural habitat were used for determining fish abundance on these habitat modules.

Koenig (Koenig et al., 2005) surveyed reefballs in September 2002, thirteen months after their original deployment, to record the reef fish populations. The mean species richness and abundance of economically important fish were greater for reefball densities of 10 reefballs per cluster than for five, but did not increase further at densities of 20 per cluster.

### **Coral Reproduction and Larval Biology**

The effect of temperature on embryogenesis, larval survival, and larval swimming speed were examined in the laboratory (Brooke, 1998; Brooke and Young, 2003, 2005). Separate sexes freely spawn gametes during the summer months. The small 120 micron eggs are fertilized externally and develop into swimming lecithotrophic planulae within 6 hours. Larvae swim actively for at least 22 days before initiating settlement. Embryogenesis ceased at 10°C and was inhibited at 17°C, but progressed normally at 25 and 30°C (Brooke and Young, 2005). Newly ciliated larvae swam to the water surface and remained there for ~18 hr, after which they swam throughout the water column, then became demersal. At 14 and 23 days larvae exhibited negative phototactic behavior (Brooke, 1998; Brooke and Young, 2005).

### **Coral Growth**

Long-term growth experiments were conducted on the deep-water *Oculina* coral (80 m depth) using lockout diving from the *Johnson-Sea-Link* research submersibles (Reed, 1981). The growth rates of the deep-water *Oculina* lacking zooxanthellae were compared to the growth of the shallow-



water form of *Oculina* (6 m depth) which had zooxanthellae. Plastic tie wraps were attached to three branch tips on each of 44 coral colonies, and linear growth beyond the bands was measured with calipers every 2-4 months for one year. Additional colonies were stained with alizarin dye and all the branch tips were measured for new growth after a year to determine the variability of intracolony branch growth. Calcification rates were not measured. Control colonies were studied for three years to determine variability of inter-year growth. Additional colonies were transplanted between the 80-m and 6-m reef sites. Analysis of variance was used to compare growth rates within and between stations and stepwise regression analysis to determine the relationship of growth rate and various physical factors such as water temperature, cloud cover, sedimentation rates, light transmittance, and current velocity.

The growth rate of the deep-water *Oculina* coral at 80 m averaged 16.1 mm yr<sup>-1</sup> and was significantly greater compared to the growth at 6 m (11.3 mm yr<sup>-1</sup>; Reed, 1981). Growth rate was significantly positively correlated with water temperature at both sites, but paradoxically the coral growth was faster in deep water where it lacks zooxanthellae. Corals transplanted from 6 m to 80 m lost their zooxanthellae within four months. By the end of one year the morphology of their branch tips became more similar to the deep-water *Oculina* growth form. Typically the deep-water *Oculina* has thinner branches, lower polyp density, but denser skeleta than the shallow-water morph (Reed, 1983). Although environmental factors such as greater sedimentation and sand abrasion from wave surge on the shallow *Oculina* reefs may reduce growth rate, physiological controls resulting from ecotypic variations or differing colony structure may also be factors. The growth rate of the deep-water *Oculina* is comparable to other deep-water ahermatypic scleractinia. Growth rates of 6-15 mm yr<sup>-1</sup> have been estimated for colonies of *Lophelia pertusa* collected from deep-water cables (Teichert, 1958; Wilson, 1979). Studies using stable isotopes have estimated the linear growth rates of *Lophelia* from 5.5 to 20 mm yr<sup>-1</sup> (Freiwald et al., 1997; Mortensen & Rapp, 1998).

### **Coral Growth and Reef Age**

The deep-water *Oculina* reefs, based on a growth rate of 1.6 cm yr<sup>-1</sup> and maximum height of 25 m, may be estimated at a minimum age of 1,526 years. A 6-cm diameter sediment core was taken by the author during a lockout dive half way up the flank of one 16-m high *Oculina* bank. The core consisted of dead coral branch fragments and mud sediment but only penetrated 22 cm; a piece of *Oculina* branch within the core had a radiocarbon age of 480 $\pm$ 70 yr B.P. (Hoskin et al., 1987). Using the radiocarbon date yields an estimate of 980 years for the development of this *Oculina* bank. Considering that the base of these *Oculina* reefs would have been exposed ~15,000 years ago during the low water stand (–80 m) at the height of the Wisconsin glacial period, these deep-water *Oculina* reefs may be relatively young.

### **Deep-water Coral Reef Sediments**

Sediments from deep-water coral reefs and nearby inter-reef areas have been analyzed from both *Oculina* and *Lophelia* reefs (Stetson et al., 1962; Mullins et al., 1981; Hoskin et al., 1987; Freiwald et al., 1997; Paull et al., 2000). Each of these studies reported a greater percentage of mud (silt + clay) in the reef sediments than the non-reef sediments, indicating that the reef structure was trapping the finer sediments. The percentage of gravel, mainly from coral debris, was also generally greater at the reef sites. As the coral dies and erodes, the gravel-size branch fragments remain to form the bank structure.

In addition to the fine sediments produced by bioeroders, the resulting coral rubble is also



subject to physical abrasion resulting in the production of gravel-, sand-, and mud-size particles. Broken *Oculina* coral branches were observed tumbling on the sea floor in 75 cm s<sup>-1</sup> currents. Coral fragments tested in a mechanical tumbler at intervals of 1 to 1000 minutes produced 2-4 mm gravel-size particles and 0.2 mm sand-size (Hoskin et al., 1983). Coral septal fragments comprised the majority of sand-size particles. This abrasion experiment also produced carbonate muds that were 20% of the abrasion products. Natural sediments on the *Oculina* reefs are similarly dominated by mud (17% on the reefs but only 4% in surrounding non-reef shelf areas), gravel-size coral debris (24%), and sand particles (60%) which are primarily fragments of coral, forams, mollusks, barnacles, pellets, and quartz (Hoskin et al., 1987). The mud, which is primarily the product of bioerosion and physical abrasion, is trapped by the baffling effect of the coral and reef structure.

Hoskin et al. (1987) found the sediment components of the deep-water *Oculina* reefs to be more similar to shallow, hermatypic reefs than to other deep-water reefs. Sediments of both deep-water *Oculina* reefs and shallow tropical reefs have a greater percentage of mollusk components whereas the *Lophelia* reefs have higher percentages of planktonic sand components such as foraminifera and pteropods (Paull et al., 2000). The *Oculina* reef sediments, however, lack sand components from calcareous green algae that are abundant on shallow tropical reefs.

### **Deep-water Coral Reef Geomorphology and Development**

The internal structure of deep-water coral reefs is not well documented. Attempts were made on a deep-water *Oculina* reef to determine whether live coral capped a mound of unconsolidated sediment or lithified rock. Using a JSL submersible, the author made a lockout dive at a depth of 71 m in a small flat sand area on the flank and midway between the top and base of the 16-m high *Oculina* reef. A 1.3-cm diameter steel rod was used to probe to a depth of 4 m into the mound without hitting bedrock. Rock outcrops are not apparent on the coral reef itself although rock pavement occurs on the flat sandy bottom areas surrounding the bank. A 6-cm diameter aluminum tube was used to core the flank of the reef. The cores consisted of coral branch fragments and mud sediment but only penetrated 22 cm.

The above results support the hypothesis that deep-water coral reefs are accumulations of coral debris and sediment that are initially built upon a hard substrate. The formation of a deep-water reef may progress through the following hypothetical sequence as proposed in part by Squires (1964) and Mullins et al. (1981): 1) coral larvae initially settle and develop into isolated colonies on rock pavement or outcrops; 2) a coral thicket forms as other colonies grow nearby either by sexual reproduction or by branch fragmentation and regrowth; 3) a coppice stage or mound develops from trapped sediment and coral debris; 4) and finally the coppice develops into a coral bank which is a large structure of unconsolidated coral debris and sediment and is capped with live coral. A final mature phase may result in which the mantle of living coral is relatively negligible to the large volume of dead coral (Newton et al., 1987). This may explain the high frequency of extinct, relict deep-water coral mounds that are common in the Atlantic and Gulf of Mexico. Newton et al. (1987) suggest that a paleoclimatic model may also be a factor for many of these senescent reefs.

### **Deep-water Coral Reef Senescence and Bioerosion**

Extensive areas of dead coral on the *Oculina* reefs as well as their *Lophelia* counterparts (Freiwald et al., 1997) may be due to a combination of events including the natural evolution of the mound as described above along with degradation through bioerosion, hydrodynamic stress from currents (Wilson, 1979b; Reed 1998), and in some regions from dredging and trawling activities by



fishermen (and scientists). Bioerosion of *Lophelia* coral is the result of sponges, foraminifera, bryozoans, polychaetes, sipunculids, mollusks, and various microborers (Newton et al., 1987; Jensen & Frederiksen, 1992; Freiwald & Schönfeld, 1996; Freiwald et al., 1997; Kruttschinn & Freiwald, 1998; Rogers, 1999). Sponges such as *Cliona vastifica*, *Entobia* spp., *Aka labyrinthica*, and *Alectona millar*, and polychaetes such as the sabellid *Perkinsiana socialis* and Paraonidae are the primary borers causing degradation of these deep-water reefs in the eastern Atlantic (Jensen & Frederiksen, 1992). Newton et al. (1987) found large scale borings by lithophagid (?) bivalves, polychaetes, clionid sponges and bryozoans in the Gulf of Mexico's *Lophelia* banks.

For unknown reasons, in the central region of the deep-water *Oculina* reef system, between 27°45'N and 27°52'N, where the *Oculina* pinnacles reach their maximum density, extensive areas of dead *Oculina* rubble were found when the reefs were first discovered in the 1970s. Generally the coral fragments are <10 cm in length and well encrusted with various fouling species. Several unproved hypotheses exist including human damage and natural processes such as bioerosion, physical abrasion, chemical solution, and episodic coral die-off. Our experiments on limestone substrates show that bioerosion is 20 times more intense than either chemical or physical abrasion processes (Hoskin et al., 1986). Bioeroders of *Oculina* in shallow and deep water are dominated by clionid sponges, mollusks, eunicid polychaetes, sipunculids, and boring barnacles. In a detailed survey of mollusks associated with *Oculina* on the deep and shallow reefs, 41 colonies of coral yielded 5,132 individual mollusks and 230 species (Reed & Mikkelsen, 1987). Of these, 47% of the species are free-living on the surface of the coral, 32% symbiotic (parasitic or commensal), 18% epilithic (fouling), and 3% endolithic (boring). The borers comprised 13.1% of all individuals collected. The endolithic bivalve *Lithophaga bisulcata* is the most frequently occurring molluscan species overall. Other endolithic species include *L. aristata*, *Gastrochaena hians*, *Diplothyra smithii*, *Gregariella coralliophaga*, *Rupellaria typica*, and *Rocellaria ovata*. Density of endolithic mollusks decreases from shallow to deep (4.9, 2.6 and 0.9 [N/100-g dry coral wt] at the 6-m, 27-m and 80-m reef sites, respectively). The corallum of *Oculina* is denser and thinner at 80 m than at the 6-m site, possibly accounting for the fewer numbers and species of boring mollusks at 80 m. Significant correlations ( $p < 0.05$ ) exist between the amount of dead coral on the colonies and the endolithic species (*L. bisulcata*,  $r = 0.792$ ; *L. aristata*,  $r = 0.573$ ) but not with the live portion of the colonies.

Weakened by bioerosion the coral becomes susceptible to breakage by peak currents. In our tow tank tests, fresh *Oculina* branches of the deep growth form fractured at current speeds of 140 cm s<sup>-1</sup>. The Gulf Stream that may exceed 5 knots (250 cm s<sup>-1</sup>) sometimes impinges upon the peaks of the pinnacles, possibly causing coral breakage. However, maximum current at the base of the banks is only 58 cm s<sup>-1</sup> and averages 8.6 cm s<sup>-1</sup>. On the lithoherms in the Straits of Florida, Messing et al. (1990) also found peak currents in excess of 100 cm s<sup>-1</sup> on the eastern side of the Straits and Paull et al. (2000) recorded currents of 25-100 cm s<sup>-1</sup> on the western side, which may contribute to the areas of *Lophelia* rubble on these lithoherms. Large 1-2 m *Oculina* and *Lophelia* colonies also occasionally may shear in half possibly due to the weight of the framework structure weakened by bioerosion.

### **Human Impacts**

The exact cause(s) of the extensive areas of dead coral rubble on modern deep-water reefs, including *Oculina* and *Lophelia*, is yet unknown. Bottom trawling and dredging certainly can cause severe mechanical damage as shown on deep-water *Lophelia* reefs in the northeast Atlantic



(Rogers, 1999; Fosså et al., 2000a,b), hard bottom habitats off the southeastern United States (Van Dolah et al., 1987), and deep-water seamounts off New Zealand and Tasmania (Jones, 1992; Koslow et al., 2000; Richer de Forges et al., 2000). Trawling may also cause increased sedimentation on deep reefs which can smother the coral and prevent larval settlement (Rogers, 1990). In addition, most deep-water fish stocks are overfished or depleted. Since most benthic fisheries focus on apex predators such as groupers, snappers, and sharks, removal of these apex predators and other ecologically important species may have severe long-term repercussions (Koenig et al., 2000; Koslow et al., 2000). Natural episodic coral die-off, such as occurs with the shallow-water *Acropora* species also may be an unknown factor on the deep-water coral reefs. We do not yet know whether fungi and other pathogens that attack shallow-water reef corals also affect deep-water ahermatypic coral species. Bioeroders are also an integral component of both *Oculina* and *Lophelia* reefs and are a major producer of sediments. Other hypotheses may account for some of the dead *Oculina* reef areas. One is that German submersibles were known to hide among high relief structures in this region during reconnaissance missions along eastern Florida during World War II (Cremer, 1986). Navy SEAL teams trained here too and the shelf region was bombed extensively as a result. Extensive areas of dead coral on deep-water *Oculina* and *Lophelia* reefs may be the result of a combination of factors: 1) fishing activities and human activities, 2) pathogens, 3) bioerosion, 4) hydrodynamic stress, 5) natural evolution of coral bank development, and 6) paleoclimatic factors.

Apparently commercial fishermen are capable of trawling at these great depths in areas of high relief pinnacles, and shrimp trawlers have been caught and fined for fishing within the *Oculina* Coral Bank Habitat Area of Particular Concern. In the late 1970s roller trawl fishery gear was being used off Georgia and the Carolinas of the southeastern United States and was being considered for fishing off Florida. This type of bottom trawl incorporates wheels along the bottom tickler chain which allows the trawl to be used in rougher bottom topography than the standard bottom trawl. Certainly it would decimate fragile corals like *Oculina*. Other impacts on the *Oculina* reefs are from anchoring, bottom hook and line fishing, and longline fishing. Anchors dropped or dragged through reef areas would certainly destroy coral colonies. From submersible observations we have frequently observed fishing lines draped over some of the deep-water *Oculina* reefs. Since this coral reef system lies within the Gulf Stream and is over 60 m deep, large fishing weights are required for bottom fishing for grouper and snapper. Bottom traps if placed on the reefs would also damage fragile branching coral.

The benthic fisheries that have operated in the region of the deep-water *Oculina* reefs include trawl and dredge fishery for calico scallop (*Argopecten gibbus*), trawl fishery for rock shrimp (*Sicyonia brevirostris*) and penaeid shrimp (*Penaeus* spp.), and hook and line fishery for grouper (*Mycteroperca phenax*, *M. microlepis*), red snapper (*Lutjanus campechanus*), porgy (*Pagrus pagrus*), greater amberjack (*Seriola dumerili*), and various sharks (Koenig et al., 2000). Pelagic fish common to waters above the reefs and in the Gulf Stream include tunas (Scombridae), dolphin (*Coryphaena hippurus*), sailfish (*Istiophorus platypterus*), wahoo (*Acanthocybium solandri*), king mackerel (*Scomberomorus cavalla*), and barracuda (*Sphyrna barracuda*). Sport fisheries for these pelagic species are fished in the upper 30 m or so and typically do not impact the reefs or the coral. Early in the 1970s bottom fishing activity was sparse and the deep-water *Oculina* reefs had large populations of red and grey snapper, and various grouper species including scamp, gag, snowy, speckled hind, and warsaw grouper. By the late 1980s both commercial and recreational fisheries had taken a toll on the fish populations, especially grouper and snapper (Koenig et al., 2000).



## **Effects of Trawling**

Historical photographic records from the 1970s provide evidence of the status and health of the reefs prior to heavy fishing and trawling activities of the 1980s and 1990s (Avent et al., 1977; Avent and Stanton, 1979; Reed, 1980; Reed et al., 2005, 2007). Over 50,000 35-mm photographs were taken during these early submersible transects. Portions of these transects that were over reefs were compared to video transects of the same areas made 25 years later in 2001. Random photographic images from both surveys were quantitatively analyzed by point count to determine changes in percent cover of live *Oculina* coral, standing dead coral and coral rubble. This study has resulted in the restoration, protection and archiving of these rare and invaluable photographic images and data, and also will provide marine managers and scientists a quantitative assessment of the health and percent cover of live coral in the 1970s, prior to intense trawling, compared to the same sites today.

By 2001, only two high-relief bioherm sites (Chapman's Reef and Jeff's Reef) had extensive amounts of live coral remaining (Reed et al., 2007). Except for these two reefs, all 2001 transect sites had less than 0.1% live coral remaining for all *Oculina* habitat types including high relief bioherms, and individual colonies and thickets on moderate to low relief limestone ledges and sand mounds. Overall the loss of mean live coral cover at each transect site was dramatic and statistically significant, varying from 3% to 26%. In addition, the percent loss of live coral was nearly 100% (range 98.4%-100%) for each individual transect site except Chapman's Reef and Jeff's Reef (46.2, 66.4%, respectively). Concurrently, four of the seven transects showed decrease in standing dead coral, and all showed an increase in percent cover of unconsolidated dead coral rubble. Significant declines in both standing live coral and standing dead coral with the concurrent increase of coral rubble suggest that mechanical disruption was the cause of the decline.

### *Habitat Loss- Effects on the Ecosystem:*

The *Oculina* biogenic refuge consists primarily of standing live and dead coral habitat. As long as the coral is standing, the living space within the colony branches supports dense and diverse communities of associated invertebrates (Reed et al., 1982; Reed and Mikkelsen, 1987; Reed et al., 2002 a,b; Reed et al., 2006 in press). However, once reduced to unconsolidated coral rubble, little living space is left except for the boring infauna (Reed, 1998). When the standing coral habitat is lost due to mechanical damage or natural causes, the effects on the ecosystem are dramatic. The decline in fish populations, primarily gag and scamp grouper, on the *Oculina* reefs over that past 20 years is evident (Gilmore and Jones, 1992; Koenig et al., 2000, 2005). This may be attributed to both habitat loss and overfishing. However, population densities of the dominant basses (roughead bass *Holanthias martinicensis* and red barbill *Hemanthias vivanus*), dominant groupers (scamp, gag, and speckled hind *Epinephelus drummondhayi*), and pelagic species (greater amberjack and almaco jack *Seriola rivoliana*) all showed positive association with intact coral habitat (either sparse or dense live coral) compared to unconsolidated coral rubble habitat (Koenig et al., 2005). Scamp grouper density in intact coral habitat was significantly greater ( $p=0.05$ ) than other habitats (sparse live coral or rubble). Only one commercially important species (snapper *Lutjanus* spp.) was primarily associated with the coral rubble habitat.

A hypothetical trophic model of the *Oculina* coral ecosystem shows the plausible interactions of the various invertebrate and fish species that are associated with the coral habitat



(George et al., 2006 in press). Standing live and dead coral provide refuge within the branches for diverse invertebrate communities including polychaete worms, mollusks, crustaceans, sponges and octocorals. These consist of various suspension feeders, detritivores, carnivores and corallivores (Reed, 2002a), which are prey for smaller reef fish and up the food chain to larger benthic and pelagic fish. The economically important grouper complex including gag and scamp grouper and speckled hind are closely associated with the standing intact coral habitat (Gilmore and Jones, 1992; Koenig et al., 2005). The whole system in turn is also linked to physical factors such as food, nutrients, and plankton from the Florida Current (Gulf Stream) and upwelling events which provide influx of cold nutrient rich water (Reed, 1983). Therefore significant loss of habitat, in particular intact live and dead standing coral, will bring dramatic and possibly catastrophic shifts in the ecosystem. As seen with the grouper complex that is associated with the intact coral, the loss of standing coral habitat could result in the loss of several commercially important species that use the *Oculina* ecosystem as spawning and feeding grounds. Several species such as gag grouper also utilize inshore mangrove and grassbed habitat as juveniles then move to the deeper high relief reefs once they are sexually mature (Gilmore and Jones, 1992). Also the effects of overfishing is unknown for the *Oculina* ecosystem. Even if the *Oculina* coral is kept intact, how will the lack of top predators affect the whole reef system? Such a loss could cause dramatic shifts in the entire community structure of smaller food prey and ultimately affect the coral itself.

## CONCLUSIONS

The recent ROV ground-truthing of the multi-beam map provided new information, including: 1) discoveries of isolated thickets of live *Oculina* that exist within the newly expanded *Oculina* MPA; 2) numerous high-relief *Oculina* bioherms that were previously unknown exist outside the *Oculina* MPA; and 3) extensive areas of live-bottom habitat (primarily hard-bottom, rock pavement and ledges) and *Oculina* thickets occur within the low-relief areas. However, ROV surveys are extremely difficult to conduct on these high-current, high-relief reefs and are limited to drifting with the current in most cases. Human-occupied submersibles have consistently proved to be of greater value in surveying the fish populations and mapping the deep-water *Oculina* reefs.

Large gaps still exist in our knowledge of these deep-water *Oculina* reefs. Priorities for habitat mapping and characterization include: 1) complete multi-beam maps of the *Oculina* HAPC and adjacent areas that may contain *Oculina* bioherms; 2) ground-truth these maps with submersible and ROV dives to characterize and document the extent and distribution of the *Oculina* reefs and other habitats; 3) document the extent of damage from recent trawling, both by direct mechanical damage and by indirect damage from resuspension of sediments and smothering of coral; 4) document other potential causes of coral death such as possible temperature changes from global warming, increased nutrient loading, or disease; 5) document the recovery of the fish populations and relationships with artificial reefball structures.

We have little data on when or how the coral rubble was formed, especially the vast areas that were rubble in the 1970s. It is important to know how much of this is from natural causes and how much is man-made. However, the age of dead coral, whether due to trawling versus WWII depth charges, is too young for radiocarbon dating. Also little is known about the rubble ecosystem. For example, what role does it play as habitat for shrimp and other benthic fauna? Characterization should continue and experimental research is needed to quantify the value of



coral thicket habitat (live and dead of various sizes) versus the alternate rubble state.

Certainly, trawling continues to be the primary threat to the ecosystem as evident from recent photographs of trawl nets found on the bottom, destroyed reefball modules, and the documented destruction of the Cape Canaveral Pinnacle reef in the past 25 years (Fig. 4). Since 2000, illegal trawling has been documented within the *Oculina* HAPC, and several poachers have been intercepted by the U.S. Coast Guard. Surveillance and enforcement remain the greatest tasks in protecting the *Oculina* MPA, as well as any deep-water coral reserve. We remain hopeful that the recently mandated use of a vessel monitoring system for the shrimp fishery in this region along with additional enforcement vessels will aid in the long-term protection of the *Oculina* MPA. In addition, proposed projects are envisioned to use surface buoys with satellite relay to monitor the reefs with acoustic devices which could relay real-time data on sounds of boat traffic and illegal trawlers. These could also be used by scientists studying the fish population patterns, and perhaps include arrays of thermographs, current meters, cameras, and other equipment to help understand this remote yet valuable resource.

### ACKNOWLEDGMENTS

This manuscript is dedicated to the memory of Robert Avent who first described these magnificent deep-water *Oculina* reefs using the *Johnson-Sea-Link* submersibles. Appreciation goes to all the individuals in the early years at Harbor Branch Foundation, especially submersible pilots Jeff Prentice and Tim Askew who first discovered Jeff's Reef, and the more recent investigators who have spent countless hours studying various aspects of these reefs. Special thanks goes to Charles 'Skip' Hoskin who provided years of enthusiastic collaboration and leadership. Frank Stanton, John Miller, David Mook, Lee Edmiston, Nat Eisman, Robert Jones, and Mary Rice were also active participants. We gratefully acknowledge Harbor Branch Oceanographic Institution for support of this project. Recent surveys have been sponsored largely by the National Oceanic and Atmospheric Administration (NOAA), including NOAA's National Marine Fisheries, NOAA's Undersea Research Center at the University of North Carolina at Wilmington, and NOAA's Ocean Service. NASA and the United Space Alliance co-funded portions of the shiptime for recent mapping and ROV surveys. We thank the crews of the R/V *Johnson*, R/V *Sea Diver*, R/V *Seward Johnson I* and *II*, M/V *Liberty Star*, M/V *Freedom Star*, *Johnson-Sea-Link I* and *II* and *Clelia* submersibles, and ROV pilots Lance Horn and Glenn Taylor for their exceptional operational support. This is contribution no. 260 from Harbor Branch Oceanographic Institution, Biomedical Marine Research Program.



PUBLICATIONS with ANNOTATIONS  
*OCULINA* CORAL REEFS- 1970- PRESENT  
Compiled by John K. Reed

(in descending order by year)

- 1) Reed, J. K., C. C. Koenig, and A. N. Shepard, 2007. Impacts of bottom trawling on a deep-water *Oculina* coral ecosystem off Florida. *Bulletin of Marine Science* 81: 481–496. (quantitative point count analysis of photo transects between 1975 and 2005)
- 2) Reed, J.K., D. Weaver, S.A. Pomponi. 2006. Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the Southeastern USA: Blake Plateau, Straits of Florida, and Gulf of Mexico. *Bulletin of Marine Science* 78(2): 343-375. (includes *Oculina* fish sp. list and comparison to *Lophelia* reefs)
- 3) Reed, J.K., C. Koenig, A. Shepard. 2006 (in review). Effects of bottom trawling on a deep-water *Oculina* coral ecosystem. Proceeding of 3<sup>rd</sup> International Deep Sea Coral Symposium, *Bulletin of Marine Science*. (quantitative point count analysis of photo transects between 1975 and 2005)
- 4) George, R., T. Okey, J. Reed, M. Sissenwine, R. Stone. 2006 (in review). Ecosystem-based management for biogenic marine habitats: models for deep sea coral reefs and seamounts in US waters. Proceeding of 3<sup>rd</sup> International Deep Sea Coral Symposium, *Bulletin of Marine Science*. (*Oculina* food web and trophic structure)
- 5) Harter, S.L. and A.N. Shepard. 2006 (in review). Deep sea coral ecosystem monitoring: Case study of the *Oculina* Bank. Proceeding of 3<sup>rd</sup> International Deep Sea Coral Symposium, *Bulletin of Marine Science*. (discussion of deep coral assessment methods, and fish census and habitat cover data from 2003-2005 ROV dives).
- 6) Brooke, S. and C.M. Young. 2005. Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*. *Marine Biology* 146(4): 665-675.
- 7) Koenig, C.C., A.N. Shepard, J.K. Reed, F.C. Coleman, S.D. Brooke, J. Brusher, and K.M. Scanlon. 2005. Habitat and fish populations in the deep-sea *Oculina* coral Ecosystem of the western Atlantic. *American Fisheries Society Symposium* 41: 795-805. (fish populations related to coral habitat- living vs dead)
- 8) Reed, J., C. Koenig, A. Shepard. 2005. Effects of bottom trawling on a deep-water coral reef. 3<sup>rd</sup> International Symposium on Deep-Sea Corals Science and Management, Miami, Florida, Abstract Book, p. 240. (quantitative point count analysis of photo transects between 1975 and 2005)
- 9) George, R., T. Okey, J. Reed, R. Stone. 2005. Ecosystem based fisheries management: Food chain models for a northeast Pacific gorgonian forest, the mid-Atlantic Corner Rise Seamount, and the Florida *Oculina* reefs. 3<sup>rd</sup> International Symposium on Deep-Sea Corals Science and Management, Miami, Florida, Abstract Book, p. 139.



- 10) Reed, J.K., A. Shepard, C. Koenig, K. Scanlon, and G. Gilmore. 2005. Mapping, habitat characterization, and fish surveys of the deep-water *Oculina* coral reef Marine Protected Area: a review of historical and current research. Pp. 443-465, In (A. Freiwald, J. Roberts, Ed.), Cold-water Corals and Ecosystems, Proceedings of Second International Symposium on Deep Sea Corals, Sept. 9-12, 2003, Erlanger, Germany, Springer-Verlag, Berlin Heidelberg. (summary of research from 1970 to present on *Oculina* reefs)
- 11) Brooke S, C.C. Koenig, and A.N. Shepard. 2005. *Oculina* banks restoration project: description and preliminary assessment. Proceedings of the 57th Gulf and Caribbean Fisheries Institute p. 607-620. (artificial reef balls and concrete blocks placed in different configurations on *Oculina* rubble areas to assess coral recruitment and use for fish habitat)
- 12) Manning, CB. 2003. *Oculina* Bank Geographic Information System. Masters Thesis, University of North Carolina at Wilmington, Wilmington, NC. 120 pp.
- 13) Reed, J.K. 2003. Deep-water coral reefs off Southeastern USA. National Geographic Society, Classroom Exploration of the Oceans, 2003, Keynote presentation, [<http://www.coexploration.org/ceo>]. (online website with description of deep reefs, lots of photos)
- 14) Shepard, A. and J.K. Reed. 2003. OCULINA BANKS 2003: Characterization of Benthic Habitat and Fish Populations in the *Oculina* Habitat Area of Particular Concern (OHAPC), Mission Summary Report. NOAA/ NURC and South Atlantic Fishery Management Council. 14 pp.
- 15) Brooke, S. and C.M. Young. 2003. Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the southeast Florida shelf. Continental Shelf Res. 23: 847-858. (reproduction and larval development of deep and shallow *Oculina*)
- 16) Reed, J. K. 2002. Deep-water *Oculina* coral reefs of Florida: biology, impacts, and management. Hydrobiologia 471: 43-55. (review of research, trawling impacts, and history of management of *Oculina* reefs)
- 17) Reed, J. K. 2002. Comparison of deep-water coral reefs and lithoherms off southeastern U.S.A. Hydrobiologia 471: 57-69. (comparison and contrast of *Oculina* and *Lophelia* reefs)
- 18) Reed, J. K. 2002. Florida's *Oculina* Reefs, NOAA/ HBOI Cruise. The Slate, American Academy of Underwater Sciences.
- 19) Reed, J. K. 2002. Deep-water *Oculina* coral banks of Florida: an assessment of status, impacts, and management. Pp. 200, In: Proceedings of the First International Symposium on Deep-Sea Corals, July 30- August 3, 2000, Ecology Action Center, Dalhousie University, Halifax, Nova Scotia. (abstract of Hydrobiologia 2002 paper)
- 20) Reed, J. K. 2002. Comparison of deep-water *Oculina* and *Lophelia* coral banks and



- lithoherms off southeastern Florida. Pp. 201, In: Proceedings of the First International Symposium on Deep-Sea Corals, July 30- August 3, 2000, Ecology Action Center, Dalhousie University, Halifax, Nova Scotia. (abstract of Hydrobiologia 2002 paper)
- 21) Koenig, C. C., A. N. Shepard, J. K. Reed, R. G. Gilmore, F. C. Coleman, S. Brooke, J. Brusher, M. Barnette, A. W. David, K. Scanlon. 2002. Florida *Oculina* Banks Marine Protected Area: habitat, fish populations, restoration, and enforcement. National Undersea Research Program, 2<sup>nd</sup> Quarter Milestone. (survey of fish populations in relation to live/dead *Oculina* habitat and reef ball restoration)
  - 22) Shepard, A., P. Orlando, J. Reed, ... 2001. Islands in the Stream Expedition: *Oculina* Habitat Area of Particular Concern, expedition summary report, 10 September 2001. NOAA Ocean Exploration Program, 7 pp.
  - 23) NOAA. 2000. Final rule, Amendment 4 to the Fishery Management Plan for Coral, Coral Reefs, and Live/Hard Bottom Habitats of the South Atlantic Regions (Coral FMP). Federal Register, Vol. 65, No. 115, June 14, 2000.
  - 24) Reed, J. K. 2000. *Oculina* coral banks of Florida: conservation and management of a deep-water reserve. Pp. 2-4, In: Proceedings of the American Academy of Underwater Sciences 20<sup>th</sup> Annual Scientific Diving Symposium, Oct. 11-15, 2000, St. Petersburg, Florida. HBOI Contribution Number 1378.
  - 25) Koenig, C. C., F. C. Coleman, C. Grimes, G. Fitzhugh, K. Scanlon, C. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science* 66: 593-616.
  - 26) Brooke, S. D. 1998. Reproduction and larval biology of the ivory tree coral *Oculina varicosa*. *American Zoologist* 38:100a.
  - 27) Child, C. A. 1998. Nymphon torulum, new species and other Pycnogonida associated with the coral *Oculina varicosa* on the east coast of Florida, *Bulletin of Marine Science* 63, 595-604.
  - 28) NOAA, South Atlantic Fisheries Management Commission. 1998. *Oculina* bank HAPC expanded northward, South Atlantic Update, The South Atlantic Fishery Management Council, 1998. (*Oculina* HAPC expanded from 92 nm<sup>2</sup> to 300 nm<sup>2</sup>)
  - 29) Reed, J. K. 1998. The Gulf Stream. *Florida Naturalist* 71(2): 10-13.
  - 30) Reed, J. K. 1998. An assessment of Florida's deep-water *Oculina* coral banks. Abstract and poster. Atlantic and Gulf Reef Assessment Workshop, June 2-6, 1998, University of Miami, Florida. HBOI DBMR Miscellaneous Publications #31.
  - 31) Reed, J. K. 1998. Bioerosion and sediment production on Florida's deep-water *Oculina* coral Banks. Abstract. 2<sup>nd</sup> International Bioerosion Workshop, Fort Pierce, Florida.



(bioerosion of *Oculina* by mollusks, sipunculans, and sponges and production of sediment as result)

- 32) Perkins, T.H., ..., G. Gilmore, ..., J.K. Reed...1997. Distribution of Hard-Bottom Habitats on the Continental Shelf off the Northern and Central East Coast of Florida. Southeast Area Monitoring and Assessment Program, National Marine Fisheries Service.
- 33) Reed, J. K. and S. Pomponi. 1997. Final Cruise Report. Submersible and scuba collections in the coastal waters of the Bahama Islands and Florida's *Oculina* coral banks: Biomedical and biodiversity research of the benthic communities with emphasis on the Porifera and Gorgonacea. (cruise report- few misc. collections of macroinvertebrates for chemical and biological analyses)
- 34) Reed, J. K. 1996. Preliminary survey of mud deposits on the mid-shelf reefs off Fort Pierce, St. Lucie County, Florida. Unsolicited report submitted to the U.S. Corps of Engineers, E.P.A., Florida Department of Environmental Protection, National Marine Fisheries, and St. Lucie County Port and Airport Authority, 37 pp. (comparison of sediments and foraminifera from *Oculina* reefs and mid to inner shelf areas)
- 35) Virden, W. T., T. L. Berggren, T. A. Niichel, and T. L. Holcombe. 1996. Bathymetry of the shelf-edge banks, Florida east coast, National Oceanographic and Atmospheric Administration, National Geophysical Data Center, National Marine Fisheries Service, Beaufort, North Carolina: 1. (poster of *Oculina* reefs and low resolution bathymetry)
- 36) Gilmore, R. G. and R. S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain, Bulletin of Marine Science 51, 83-103. (detailed studies on mating behavior of gag and scamp grouper with beautiful color plates of fish color patterns)
- 37) Reed, J. K. 1992. Submersible studies of deep-water *Oculina* and *Lophelia* coral banks off southeastern U.S.A. Pp. 143-151, In L. Cahoon (ed.) Diving for Science 1992. Proceedings American Academy of Underwater Sciences, Wilmington, North Carolina.
- 38) Reed, J.K. 1988. Lock-out submersible diving. Pp. 78-81, In N. C. Flemming and H. D. Max (eds.), International code of practice for scientific diving. UNESCO Technical Papers in Marine Science. (details of lock-out diving used for *Oculina* research in 1970s and 80s.)
- 39) Hoskin, C.M., J.K. Reed, and D.H. Mook. 1987. Sediments from a living shelf-edge reef and adjacent area off central eastern Florida. Pp. 42-57, In F. JMR. Maurrasse (ed.), Symposium on south Florida geology, Miami Geological Society Memoirs 3. (first detailed analyses of sediment on *Oculina* banks compared to non-reef shelf areas)
- 40) Reed, J.K. and C.M. Hoskin. 1987. Biological and geological processes at the shelf edge investigated with submersibles. Pp. 191-199, In Scientific applications of current diving technology on the U.S. Continental Shelf, NOAA Symposium Series for Undersea Research, Vol. 2. (quantitative analyses of geological and biological erosion of limestone



substrate from *Oculina* reefs to Bahama reefs)

- 41) Reed, J.K. and P.M. Mikkelsen. 1987. The molluscan community associated with the scleractinian coral *Oculina varicosa*. Bulletin of Marine Science 40(1): 99-131. (quantitative analyses of molluscs living within live and dead colonies of deep and shallow water *Oculina*, 6-80 m)
- 42) Reed, J.K. 1987. The living reef. Pp. 73-77, In Ocean Realm. (description of *Oculina* reefs and discovery for layperson)
- 43) Reed, J.K., et. al. 1986. Shelf-edge *Oculina* coral reefs. Pp. 466-469, In W. Seaman, Jr. (ed.), Florida aquatic habitat and fishery resources, American Fisheries Society, 560 pp.
- 44) Hendler, G. and J.E. Miller. 1984. *Ophioderma devaneyi* and *Ophioderma ensiferum*, new brittlestar species from the Western Atlantic (Echinodermata: Ophiuroidea). Proc. Biol. Soc. Wash. 97(2): 442- 461. (*O. devaneyi*- new species, holotype from *Oculina* banks).
- 45) Reed, J.K. and C.M. Hoskin. 1984. Studies of geological and biological processes at the shelf edge with use of submersibles. In Undersea research and technology - scientific application and future needs - abstracts, Symposia Series for Undersea Research, Vol. 2, NOAA. (Abstract)
- 46) NOAA. 1983. Announcement of Proposed National Marine Sanctuary Program Site Evaluation List. Federal Register, Vol. 48, No. 41, March 1, 1983. (deep-water *Oculina* reefs listed in Federal Register publication of Final Site Evaluation List of potential National Marine Sanctuaries)
- 47) Pawson, D.L. and J.E. Miller. 1983. Systematics and ecology of the sea-urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans. Smithsonian Contributions to the Marine Sciences 20: 1-15. (new subspecies from *Oculina* banks and elsewhere- *C. longispinus rubicingulus*)
- 48) Reed, J.K. 1983. Nearshore and shelf-edge *Oculina* coral reefs: The effects of upwelling on coral growth and on the associated faunal communities. Pp. 119-124, In M. Reaka (ed.), The ecology of deep and shallow coral reefs, Symposia Series for Undersea Research, Vol. 1, NOAA. (qualitative effects of upwelling on *Oculina* ecosystem)
- 49) Hoskin, C.M., J.C. Geier, and J.K. Reed. 1983. Sediment produced from abrasion of the branching stony coral *Oculina varicosa*. Journal of Sedimentary Petrology 53: 779-786. (laboratory quantitative analyses of production of sediment by abrasion and currents on *Oculina* branches)
- 50) Hoskin, C.M., J.K. Reed, and D.H. Mook. 1983. Stony coral bank sediments at 80 m on the eastern Florida shelf-break. Symposium on Geology of South Florida, Miami Geological Society. (Abstract)



- 51) Reed, J.K. and R. Gilmore. 1982. Nomination of a Habitat Area of Particular Concern (HAPC). Pages L-20-42 in J. Brawner, ed. Fishery management plan, final environmental impact statement for coral and coral reefs, Gulf of Mexico and South Atlantic Fishery Management Councils, 337 p. (SAFMC Fishery Management plan listing the deep-water *Oculina* reefs as a HAPC)
- 52) Reed, J.K. and R.S. Jones. 1982. Deep-water coral reefs. Discovery off Florida's Coast. Oceans 15: 38-41. (description and discovery of *Oculina* reefs for layperson)
- 53) Reed, J.K., R.H. Gore, L.E. Scotto, and K.A. Wilson. 1982. Community composition, structure, aerial and trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa* coral reefs. Bulletin of Marine Science 32: 761-786. (quantitative analyses of decapod crustaceans living within live and dead colonies of deep and shallow water *Oculina*, 6-80 m)
- 54) Reed, J.K. and R.G. Gilmore. 1981. Inshore occurrence and nuptial behavior of the roughtail stingray, *Dasyatis centroura* (Dasyatidae), on the continental shelf, east central Florida. Northeast Gulf Science 5(1): 59-62. (description of mating behavior of large stingray from submersible observations)
- 55) Reed, J.K. 1981. In situ growth rates of the scleractinian coral *Oculina varicosa* occurring with zooxanthellae on 6-m reefs and without on 80-m banks. Pp. 201-206, In Proceedings Fourth International Coral Reef Symposium, Vol. 2, May 1981, Manila, Philippines. (insitu quantitative analyses of growth rate of deep and shallow water *Oculina*, 6-80 m, in relation to physical parameters- temperature, light, sedimentation, currents)
- 56) Reed, J.K. 1981. Sedimentology photo and abstract. Journal of Sedimentology Petrology 51(4): 1102. Reprinted In K. Condie. Origin and Evolution of Earth, Burgess Publ. Co. (photograph of deep-water *Oculina* colony with *Holothuria lentigenosa*)
- 57) Reed, J.K. 1981. Nomination of shelf-edge *Oculina* coral banks as a National Marine Sanctuary. Submitted to National Oceanographic and Atmospheric Administration (NOAA), and accepted for Final Site Evaluation List, 31 pp. (deep-water *Oculina* reefs first nominated by J. Reed as a National Marine Sanctuary)
- 58) Reed, J.K. 1981. Nomination of shelf-edge *Oculina* coral banks as a habitat area of particular concern (HAPC) for the Coral and Coral Reef Fishery Management Plan. Submitted to and accepted by Gulf of Mexico and South Atlantic Fishery Management Councils, 24 pp. (deep-water *Oculina* reefs first nominated by J. Reed as a HAPC)
- 59) Reed, J.K. 1981. Research on shelf-edge *Oculina* coral banks off central eastern Florida. Pp. 32-33, In Summary of Results of Reefs and Hardgrounds Workshop, Duke University Marine Lab, Beaufort, N.C. Sept. 1981.
- 60) Reed, J.K. 1980. Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. Bulletin of Marine Science 30(3): 667-677. Part reprinted In W.J.



- Richards (ed.) Proceedings of Marine Recreational Fisheries Symposium. (detailed description of deep-water *Oculina* habitat and distribution of *Oculina* banks along eastern Florida)
- 61) Reed, J.K. 1980. An environmental assessment of the possible effects of deepening the Ft. Pierce Inlet and harbor. Workshop on Navigation Channel Improvement Study for Ft. Pierce Inlet, sponsored by U.S. Army Corps. of Engineers, Ft. Pierce, Fla. Nov. 1980, 10 pp. (possible effects of dredging and sedimentation on nearshore *Oculina* reefs)
  - 62) Smith, N. P., 1981. An investigation of seasonal upwelling along the Atlantic coast of Florida. Proc. 12<sup>th</sup> Internat. Liege Colloque Ocean Hydrodynamics: 79-98. (quantitative analyses of upwelling events on shelf off eastern Florida)
  - 63) Thompson, M.J. and L.E. Gulliland. 1980. Topographic mapping of shelf edge prominences off southeastern Florida, Southeastern Geology 21, 155-164. (first detailed, high-resolution, side-scan-sonar bathymetric maps of high relief *Oculina* reefs off Sebastian region)
  - 64) Miller, J. E. and D.L. Pawson. 1979. A new subspecies of *Holothuria lentiginosa* Marenzeller from the western Atlantic Ocean, Proceedings of Biological Society of Washington 91, 912-922. (new subspecies of holothurian common to deep-water *Oculina* reefs)
  - 65) Avent, R.M. and F.G. Stanton. 1979. Observations from research submersible of megafaunal distribution on the continental margin off central eastern Florida, Harbor Branch Foundation Technical Report #25, 40 pp. (Dr. Robert Avent's qualitative analyses of submersible photographic transects of shelf edge from Cape Canaveral to Palm Beach at depths from 100 to 1000 m)
  - 66) Avent, R.M., M.E. King, and R.H. Gore. 1977. Topographic and faunal studies of shelf-edge prominences off the central eastern Florida coast, Int. Revue ges. Hydrobiol. 62: 185-208. (first detailed description of deep-water *Oculina* reefs, geology, biology and habitat, with echosounder transects across shelf edge)
  - 67) Avent, R.M., F.G. Stanton, and J.K. Reed. 1976. Submersible reconnaissance and research program. Harbor Branch Foundation, Annual Report, 52 pp. (inhouse technical report on Dr. Robert Avent's submersible photographic transects of shelf edge from Cape Canaveral to Palm Beach at depths from 100 to 1000 m; also details of quantitative *Oculina* studies)
  - 68) Avent, R.M. and F.G. Stanton. 1975. Submersible reconnaissance and research program. Harbor Branch Foundation, 1975 Annual Report. (inhouse technical report on Dr. Robert Avent's submersible photographic transects of shelf edge from Cape Canaveral to Palm Beach at depths from 100 to 1000 m)
  - 69) Macintyre, I.G. and J.D. Milliman. 1970. Physiographic features on the outer shelf and upper continental slope, Atlantic continental margin, southeastern United States. Bulletin



American Geological Society 81: 2577-2598. (geology, topography, and sediments from surveys of shelf-edge features from North Carolina to Florida, including region of deep-water *Oculina* reefs)

- 70) Moe, Martin A., Jr. 1963. A survey of offshore fishing in Florida. Professional Papers Series, No.4, Florida State Bd. of Conservation Marine Laboratory, St. Petersburg, Florida. (survey of commercial fisheries from Florida shelf waters- including habitat maps showing high-relief coral areas off eastern Florida = *Oculina* reefs)