Deep-water *Oculina* coral reefs of Florida: biology, impacts, and management

NOTICE: THIS MATERIAL MAY BE PROTECTED BY COPYRIGHT LAW (TITLE 17 U.S. CODE)

John K. Reed

Harbor Branch Oceanographic Institution, Division of Biomedical Marine Research, 5600 U.S. 1 North, Fort Pierce, FL 34946, U.S.A.

E-mail: jreed@hboi.edu

Key words: Oculina, deep-water, coral reef, management, biology

Abstract

Deep-water Oculina coral reefs, which are similar in structure and development to deep-water Lophelia reefs, stretch over 167 km (90 nmi) at depths of 70–100 m along the eastern Florida shelf of the United States. These consist of numerous pinnacles and ridges, 3-35 m in height. Coral growth rates average 16.1 mm yr⁻¹ and biodiversity is very rich. Extensive areas of Oculina rubble may be due to human impacts (e.g. fish trawling and dredging, anchoring, bottom longlines) and natural processes such as bioerosion and episodic die-off. Early in the 1970s, the reefs were teeming with fish. By the early 1990s, both commercial and recreational fisheries, including scallop, shrimp, grouper, snapper and amberjack, had taken a toll on the reefs and especially on populations of grouper and snapper. A 315 km² (92 nmi²) area was designated the *Oculina* Habitat of Particular Concern (HAPC) in 1984, prohibiting trawling, dredging, bottom longlines and anchoring, and legislation was enacted in 2000 for expansion of the Oculina HAPC to 1029 km² (300 nmi²). The United States Coast Guard has been charged with surveillance and enforcement of the ban on bottom fishing and trawling. The primary difficulties in protecting these reefs and other deep-water Marine Protected Areas are their remoteness and time required to engage an enforcement vessel. Education regarding the nature and importance of these rich resources is important for better self regulation and surveillance by the fishing community. Only by bringing deep-water reefs to the public, the fishing community, and enforcement agencies, through video, photos, and education will there be better understanding and acceptance for the need of protection for these unseen resources. This paper reviews the current knowledge on the deep-water Oculina reefs, including the biology, geology, human impacts, and history of conservation and management.

Introduction

Evidence of high relief structures along the edge of the continental shelf off central eastern Florida was first known by fishermen and from dredge surveys from North Carolina to Florida by Macintyre & Milliman (1970). In 1975, during photographic surveys of the continental shelf using the *Johnson-Sea-Link* Research Submersibles, scientists from Harbor Branch Oceanographic Institution discovered that these high relief pinnacles were actually living, deep-water coral reefs composed entirely of the ivory tree coral *Oculina varicosa* Lesueur, 1820 (Avent et al., 1977; Reed, 1980). This coral is unusual in that it is facultatively zooxanthellate; in deep water (>60 m) it generally lacks zooxanthellae, but colonies in shallow water

possess the algal symbiont. Various research studies ensued and included surveys on the distribution of the coral, growth rates of the coral in relation to depth and environmental factors, community structure of associated invertebrates and fishes, effects of upwelling, bioerosion, sediments, geology, reproduction, and taxonomic studies of specific taxa such as fish, decapods, mollusks, echinoderms, sipunculids, pycnogonids, and amphipods (Miller & Pawson, 1979; Thompson & Gulliland, 1980; Reed, 1980, 1981; Reed & Gilmore, 1981; Reed et al., 1982; Reed & Hoskin, 1987; Reed & Mikkelsen, 1987; Gilmore & Jones, 1992; Brooke, 1998; Child, 1998; Koenig et al., 2000).

During the 1970s, these deep-water reefs had large populations of grouper, snapper, and amber-

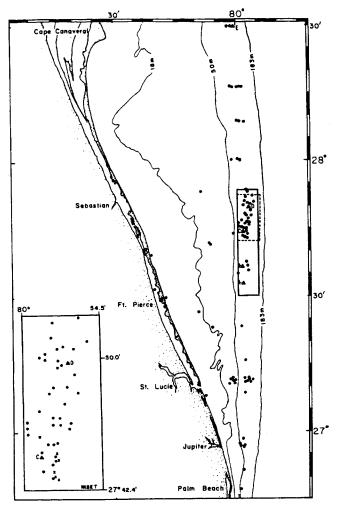


Figure 1. Shaded area- 1029 km² (300 nmi²) deep-water Oculina Bank Habitat Area of Particular Concern (HAPC) off eastern Florida that is protected from bottom longlines, trawling, dredging, pots, and anchoring. Solid rectangle- 315 km² (92 nmi²) Experimental Oculina Research Reserve (EORR) closed to snapper and grouper bottom fishing: Dotted rectangle (inset)- area of high density Oculina pinnacles. Dots indicate Oculina coral communities, triangles indicate Oculina reef study sites (modified from Reed, 1980).

jack (Gilmore & Jones, 1992). Fishing pressure from both commercial and recreational fishermen was intense and by the early 1990s the fish populations had been severely reduced (Koenig et al., 2000). Protection for the reefs began with the Fishery Management Plan (FMP) for Coral and Coral Reefs (NOAA, 1982) which designated a 315 km² (92 nmi²) area as the *Oculina* Bank Habitat Area of Particular Concern (HAPC). This FMP prohibited use of all bottom trawls, bottom long-lines, dredges, and fish traps and pots within the *Oculina* HAPC. In 1994, the National Marine Fisheries closed the *Oculina* HAPC to all snapper and grouper bottom fishing. Recent legislation in 2000 expanded the *Oculina* HAPC to encompass

approximately 1029 km² (300 nmi²) of benthic habitat (Fig. 1).

Reef description

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 & Gilliland, 1980; Virden et al., 1996; Koenig et al., 2000). These extend from 27° 32′ N to 28° 59′ N latitude, in a 2–6 km wide zone, paralleling the 80°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 (Fig. 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 Oculina reefs are sometimes referred to as coral banks since they are below the effective wave base and the coral lacks zooxanthellae, the algal symbiont of shallow-water reef corals (Teichert, 1958; Stetson et al., 1962). These Oculina reefs are similar in structure and development to Lophelia coral reefs found in deeper water (130–900 m) off Norway, Scotland, Gulf of Mexico, and the Blake Plateau north of the Bahamas (Ludwick & Walton, 1957; Teichert, 1958; Moore & Bullis, 1960; Stetson et al., 1962; Milliman et al., 1967; Neumann & Ball, 1970; Emery & Uchupi, 1972; Wilson, 1979; Newton et al., 1987; Mortensen et al., 1995; Freiwald et al., 1997, 1999; Rogers, 1999). Colonies of Lophelia pertusa (Linnaeus, 1758) (= L. prolifera) also form massive, dendritic, bushy colonies, 10-150 cm in diameter, with anastomosing branches, and deep-water Lophelia reefs consist of thickets of living and dead coral that often form mounds of unconsolidated coral debris, sand and mud (see review by Rogers, 1999).

The deep-water growth form of *O. varicosa* has been found in depths of 49–152 m (Reed, 1980),

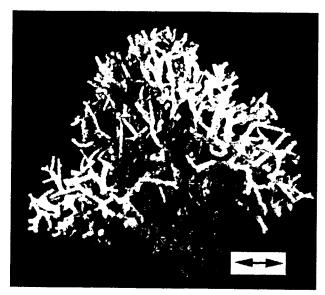


Figure 2. Massive colonies of Oculina varicosa growing on the slopes of a deep-water Oculina coral reef (80 m depth).

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 (Fig. 3). 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 (Fig. 2) (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 found mostly 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).

O. varicosa also grows in shallow water and is known to occur from the Caribbean, Gulf of Mexico, Florida to North Carolina, and Bermuda at depths from 2 to 45 m (Verrill, 1902; Smith, 1971; Reed, 1980). The shallow-water growth form of the coral does not form massive thickets or bank structures like the deep-water form but grows as sparsely scattered, individual colonies. These shallow-water colonies are usually <30 cm in diameter, with stouter branches than the deep-water form, and are golden to dark brown from the presence of zooxanthellae in their tissues. During periods of cold-water upwelling during the summer months along the eastern Florida coast, the shallow Oculina occasionally expel their zooxanthellae for several weeks and become partially or completely white in color (Reed, 1981; Reed, 1983).



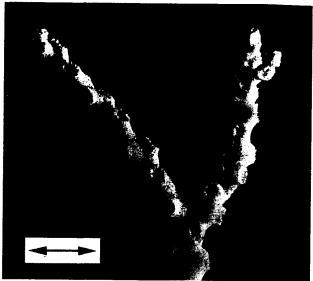


Figure 3. Left-Colony of Oculina varicosa from 80 m depth (scale = 5 cm); Right- branch tip of O. varicosa from 80 m (scale = 1 cm) (from Reed, 1980).

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 $<2 \mu M$ during non-upwelling to 9–18 μM during upwelling; phosphate from <0.25 to 0.5– 2.0 μ M; and chlorophyll-a from <1 to 1–9 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 nepheloid layer. Bottom currents averaged 8.6 cm s⁻¹ but may exceed 50 cm s⁻¹(1 kn); currents of 50–100 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 mg cm⁻² day⁻¹,

ranging from 15 to 78 (Reed, 1981). This is slightly higher than typical sedimentation rates for shallowwater coral reefs which average 1-10 mg cm⁻² d⁻¹(Rogers, 1999). Numerous studies have shown that excessive sedimentation and turbidity may reduce coral growth by either light reduction or smothering of coral (Dodge et al., 1974; Bak, 1978). Light reduction is not a factor for the deep-water Oculina since it lacks zooxanthellae; however, because of its branching morphology and high calical relief it is able to endure this rate of sedimentation. These features were also found important in O: diffusa, a shallowwater species, which is able to reject medium size sand grains (Hubbard & Pocock, 1972). However, the loss of important energy reserves for sediment removal by means of mucus production, polyp extension, and ciliary action could inhibit coral growth (Richman et al., 1975). Other types of deep-water coral reefs such as Lophelia tend to be found in areas with low rates of sedimentation, but precise data of sedimentation rates are lacking (Rogers, 1999). Increased sediment loads from man-made impacts of trawling, dredging or drilling could negatively affect the growth of the coral, kill it by smothering, or prevent recolonization by coral larvae (Rogers, 1999).

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). The biodiversity of the Oculina reefs is equivalent to shallow tropical reefs. 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 epizoic 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 (Miller & Pawson, 1979; Reed et al., 1982; Reed & Hoskin, 1987; Reed & Mikkelsen, 1987; Child, 1998).

The 42 quantitative *Oculina* coral samples yielded 2300 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 *Domecia acanthophora* and *Troglocarcinus corallicola* were independent of coral size.

For the molluscan community, the quantitative coral samples yielded 5132 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



Figure 4. Speckled hind (Epinephelus drumondhayi) on a deep-water Oculina coral reef (70 m depth).

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.

In comparison, Rogers' (1999) review of literature on deep-water *Lophelia* coral reefs recorded 886 species of associated invertebrates. Quantified analyses of live and dead colonies of *Lophelia pertusa* from the Faroe shelf resulted in 298 species, dominated by polychaetes (67 sp.), bryozoans (45 sp.), and poriferans (29 types) (Jensen & Frederiksen, 1992). Although the molluscan community was numerically dominant in this study, only 31 species were recorded compared to 230 species associated with *Oculina* coral.

Fish communities

The dense invertebrate community helps support the dense and diverse populations of fishes (>70 species) (G. Gilmore, pers. comm.; NOAA, 1982; Reed & Hoskin, 1987). 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 (Centropristes striata), red grouper (E. morio), speckled hind (E. drummondhayi) (Fig. 4), warsaw grouper (E. nigritus), jew fish (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, 1985; Reed & Hoskin, 1987; Gilmore & Jones, 1992). 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 (NOAA, 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).

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 (Fig. 5). 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⁻¹ and was significantly greater compared to the growth at 6 m (11.3 mm yr⁻¹; 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⁻¹ 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⁻¹ (Freiwald et al., 1997; Mortensen & Rapp, 1998).



Figure 5. Lockout diver from Johnson-Sea-Link submersible measures coral growth at the base of a deep-water Oculina coral reef (80 m depth).

Human Impacts

The exact causes of the extensive areas of dead Oculina coral rubble is yet unproven. Several hypotheses exist including human impacts from fisheries and natural processes such as bioerosion and episodic coral die-off. 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), in soft bottoms on Georges Bank and Stellwagen Bank (Schmuck et al., 1995), 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).

In the late 1970s, roller trawl fishery gear was being used off Georgia and the Carolinas of the south-

eastern 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. Although it seems unlikely for trawl and dredge fishermen to work in the areas of high relief pinnacles where gear could be lost, shrimp trawlers have recently been caught and fined for fishing within the deepwater Oculina reserve. Other impacts on the Oculina reefs are from anchoring and bottom fishing. Anchors dropped or dragged through reef areas would certainly destroy coral colonies. From submersible observations we have frequently observed fishing lines entangled 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 (Acanthocymbium solandri), king mackerel (Scomberomorus cavalla), and barracuda (Sphyraena 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).

In addition to mechanical damage from trawls, dredges, anchors, and bottom long-lines, 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. Various natural processes also cause reef destruction including bioerosion, physical abrasion from currents, and episodic coral die-off. The rate of bioerosion that destroys corals is typically in dynamic balance with the rate of reef accumulation (Glynn, 1996). However, this may become unbalanced and favor bioerosion if there are factors that detrimentally affect coral growth. Bioeroders of Oculina are dominated by clionid sponges, mollusks, eunicid polychaetes, sipunculids, and boring barnacles (Reed, 1998). For the molluscan community only 3% of the species associated with Oculina coral were endolithic (borers) but comprised 13.1% of the individuals (Reed & Mikkelsen, 1987). 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; Krutschinna & Freiwald, 1998. Rogers, 1999). Finally, episodic coral die-off, such as occurs with shallow-water Acropora coral species may be an unknown factor on deep-water coral reefs too. Do fungi and other pathogens that attack shallow-water reef corals also affect

deep-water coral species? These questions remain unanswered.

Protection and management

Federal and state regulations

In the United States, corals and coral reefs are protected and regulated by various federal and state legislation. The State of Florida has jurisdictional limit of 3 miles in the Atlantic Ocean and bans the taking. destroying or selling of scleractinian corals, fire corals (Millepora spp.), and sea fans (Gorgonia spp.). Beyond the 3-mile limit corals and reefs in federal waters are protected by the Magnuson-Stevens Fishery Conservation and Management Act; enforcement of this legislation is by the National Marine Fisheries Service and the United States Coast Guard. Permits for the harvest of coral for education and research are issued by the National Marine Fisheries Service. Some shallowwater reef areas that are National Marine Sanctuaries are protected by the Marine Sanctuaries and Reserve Act. The Minerals Management Service has jurisdiction in cases of oil/gas/mineral extraction, exploration, and distribution.

Prior to 1984, there was little protection for the deep-water Oculina reefs, which are in federal waters, from trawling or dredging fishing activities. However, protection finally was implemented via various fishery management plans. Fisheries for shrimp, red drum, snapper-grouper, coastal migratory pelagics, golden crab, and spiny lobster; and habitats of coral, coral reefs, and live/hard bottom of the South Atlantic are managed under the South Atlantic Fishery Management Council's Fishery Management Plans (FMP). The FMP are implemented under the authority of the Magnuson-Stevens Fishery Conservation and Management Act which requires the Fishery Management Councils to describe and identify Essential Fish Habitats (EFH) in all FMP, including identification of adverse impacts from both fishing and non-fishing activities on EFH and identification of actions required to conserve and enhance EFH. EFH are defined as those waters and substrates necessary to fish for spawning. breeding, feeding, or growth to maturity. Also created are several Essential Fish Habitat-Habitat Areas of Particular Concern (EFH-HAPC) which are identified based on the following criteria: (1) the importance of the ecological function provided by the habitat; (2) the extent to which the habitat is sensitive to humaninduced environmental degradation; (3) whether, and

to what extent, development activities are, or will be, stressing the habitat type; and (4) the rarity of the habitat type.

Oculina Bank HAPC

A portion of the deep-water Oculina reefs were nominated in 1980 by the author as a Habitat Area of Particular Concern (HAPC) within the Fishery Management Plan (FMP) for Coral and Coral Reefs. The final environmental impact statement for this proposal was published by the National Oceanic and Atmospheric Administration (1982), and the 315 km² (92 nm²) Oculina Bank HAPC was established in 1984 (Federal Register, July 1984). In order to protect the coral, this act prohibited the use of all bottom trawls, bottom long-lines, dredges, and fish traps and pots within the Oculina Bank HAPC. The recommended management goals and objectives were: to protect and conserve the unique and fragile coral habitat; to ensure commercial and recreational fish stocks; to create public awareness, education, and research; and to regulate human activities which could harm the habitat but still allow non-detrimental commercial and recreational usage. The Oculina reefs were also nominated by the author to the National Oceanic and Atmospheric Administration (NOAA) as a National Marine Sanctuary in 1981. The Oculina Coral Bank was listed on NOAA's Site Evaluation List, which is a pool of potential candidates for National Marine Sanctuaries (Federal Register, March 1983), but to date it has not yet been selected.

Experimental fishing ban

Even with over 10 years of protection from trawling, dredging, long-lines and fish traps, the abundance and biomass of the economically important reef fish such as grouper and snapper had been greatly reduced by the early 1990s (Koenig et al., 2000). In 1994, the 315 km² (92 nm²) *Oculina* Bank HAPC was designated as the Experimental *Oculina* Research Reserve (EORR) which banned all bottom fishing for a trial period of 10 years in order to protect the grouper spawning aggregations and to evaluate the benefits of marine reserves (Fig. 1; Federal Register, May 1994). In effect, the EORR prohibits bottom fishing with hook and line in addition to the previous ban on long-lines. This ban on grouper and snapper fishing will be reevaluated in 2004.

Essential Fish Habitat-Expanded Oculina Bank HAPC

In 1998, the South Atlantic Fishery Management Council voted to expand the 315 km² (92 nm²) Oculina Bank HAPC north to Cape Canaveral, Florida, that would encompass approximately 1029 km² (300 nmi²) of shelf-edge habitat (Fig. 1). This proposal was published as Amendment 4 to the Fishery Management Plan for Coral, Coral Reefs, and Live/Hard Bottom Habitats of the South Atlantic Region and the legislation was adopted in 2000 (Federal Register, June 2000). The boundaries of this expanded Oculina Bank HAPC encompass the following: (1) an area bounded on the north by 28° 30' N latitude, on the south by 27° 30′ N latitude, on the east by the 100fathom (183-m) depth contour, and on the west by 80° 00' W longitude; and (2) two adjacent satellite HAPC areas (10 km² each) which encompass dense growth of live Oculina coral (Fig. 1). The expanded Oculina HAPC does not expand the experimental closed area's restrictions on grouper and snapper fishing.

The following restrictions apply to the expanded *Oculina* Bank HAPC, including its two satellite HAPCs: no person may: (i) use a bottom long-line, bottom trawl, dredge, pot, or trap; (ii) if aboard a fishing vessel, anchor, use an anchor and chain, or use a grapple and chain; (iii) fish for rock shrimp or possess rock shrimp in or from the area.

As part of the final environmental impact statement, the National Marine Fisheries Service (NMFS) must consider economic impacts on businesses. If it is shown that the proposal will cause a 5% negative impact on businesses revenue, then the NMFS must prepare an Initial Regulatory Flexibility Analysis (IRFA). The IRFA for Amendment 4 to expand the Oculina HAPC reported that approximately 25 small fishing businesses that have historically participated in the calico scallop industry would be affected (Federal Register, November 1999). In 1997, the calico scallop industry in this region had landings that generated gross revenue of \$1.3 million, or an average gross revenue per vessel of \$52000. Also impacted would be 178 fishermen who historically have fished shark, snapper and grouper in the area. In 1997, 134 052 kg of sharks were taken by bottom long-line gear. based on catch data from the National Marine Fisheries Service accumulative landings system. Many of the shark fishermen also target other species including snapper and grouper. These bottom long-line fishermen in this area typically gross \$5954-7145 per trip with annual revenues of \$34 000–51 000 per boat (Federal Register, November 1999).

Additional Essential Fish Habitats (EFH) which overlap with the *Oculina* HAPC include the EFH for shrimp (penaeid shrimp, rock shrimp, royal red shrimp); coastal migratory pelagics (e.g. king and Spanish mackerel); snapper-grouper complex; and the coral, coral reefs, and live/hard bottom habitats. The HAPC for the snapper-grouper complex includes the *Oculina* HAPC boundaries. These EFH and EFH-HAPCs are considered critical for managed fish species survival, reproduction, and growth to maturity.

Other deep-water coral reef marine protected areas

Although the deep-water Oculina reefs were the first deep-water reefs in the world to be designated as a Marine Protected Area (MPA) or HAPC, the need to protect other deep-water reefs has gained worldwide attention. Recently, Norway enacted its first MPA which is the first MPA to protect deep-water Lophelia coral reefs. The Institute of Marine Research of Norway has documented minor to severe damage of these reefs from trawling fisheries (Fosså et al., 2000 a,b). Based on this research, the Ministry of Fisheries of Norway in 2000 has closed two prominent Lophelia coral reef areas on the shelf to bottom trawling. One area incorporates the Sula reef complex and the other is at Iverryggen north of Haltenbanken. The Institute of Marine Research estimated that of the 2000 km² area of deep-water coral reefs within Norway's EEZ, one-half to one-third may be damaged or affected from trawling (Fosså et al., 2000 a.b).

A deep-water marine reserve was established in 1995 on the continental shelf south of Tasmania over an area of 370 km² protecting 14 deep-water seamounts (Koslow et al., 2000). This is in the vicinity of an orange roughy (Hoplostethus atlanticus) fishery where photographic transects showed that 95% of the bottom was bare rock on a heavily fished seamount compared to 10% on a comparable unfished seamount (Koslow et al., 2000). The seamount community in the western Pacific is often dominated by deep-reef building corals (e.g. Solenosmilia variabilis off Tasmania and Goniocorella dumosa off New Zealand) (Rogers, 1999). These are known to have high diversity and endemism; 24-43% of the Tasmanian seamount fauna are new to science and 16-33% are restricted to this environment (Koslow et al., 2000; Richer de Forges et al., 2000). New Zealand scientists also have plans for a network of Marine Protected Areas on the deep banks

and seamounts off New Zealand (Koslow, in litt.), and in Canadian waters the Northern Coral Forest Marine Protected Area has been proposed for deep-water, soft coral habitats off Nova Scotia (D. Jones, in litt.).

Surveillance and enforcement

The United States Coast Guard (USCG) has been given the task of surveillance and enforcement of the fishing and trawling ban within the Oculina Bank HAPC. The primary difficulties in protecting these reefs, as well as any deep-water Marine Protected Area, are enforcement and surveillance due to: (1) distance offshore and time to engage an enforcement vessel to the area, (2) spotter planes can not enforce the no-fishing zone effectively - they can only report suspicious vessels and then call for surface vessels for enforcement, (3) often spotter planes can not observe or photograph a vessel's registration numbers, and are of no use at night when much of the illegal fishing activities occur, (4) helicopters are necessary for detailed video or photography to effectively prove encroachment but they are very expensive and are restricted by distance and safety requirements for offshore operations, and (5) enforcement depends on actual proof that lines were in the water and verification of the vessel through video or on-site inspection, fish in the boat or illegal gear in the zone. Another problem faced by the USCG is the dual zonation of fishing in the Oculina HAPC. Although anchoring and all bottom fishing are prohibited, trolling for pelagic fish is acceptable. According to the spotter pilots, it is difficult to determine whether someone is fishing hook and line on the bottom or near the surface. It is also impossible to prove where the fish were caught after the fact if boats were inspected on their return to port. Shrimp trawlers have been known to drift outside the borders of the Oculina HAPC during the day but fish illegally at night within the HAPC.

Since the aerial surveys by the United States Coast Guard (USCG) were recently expanded to include the *Oculina* HAPC, a shrimp trawler was seized in 2000 for fishing within the no fishing zone. After the vessel was sighted trawling within the *Oculina* HAPC by a USCG surveillance aircraft, a USCG vessel responded and boarded the vessel, discovering 1343 kg of rock shrimp, 2550 kg of penaeid brown shrimp, and additional bycatch of lobsters and flounder. National Oceanic and Atmospheric Administration's (NOAA) fisheries enforcement agents seized the catch which

NOAA sold, and the owner of the vessel and the fishermen were fined.

To support enforcement efforts in the expanded *Oculina* Bank HAPC, the South Atlantic Fishery Management Council voted to require the use of approved vessel monitoring systems (VMS) in the calico scallop fishery south of the Georgia–Florida border and they will require vessel permits (NOAA, 1998). Also a voluntary pilot program will be implemented with the rock shrimp fishery. The use of VMS in fishery management is growing and gaining acceptance by the fishermen using them. The most important features of this system will be accuracy of pinpointing a vessel's position in relation to the boundaries of a Marine Protected Area, safety, and affordability.

Future

Currently studies are underway on the reproduction of Oculina coral, and artificial substrates have been placed on the deep-water Oculina reefs to see if recruitment of juvenile coral colonies can be enhanced in the dead rubble areas (Koenig, pers. comm.; Brooke, 1998). O. varicosa apparently has separate sexes and externally fertilized eggs which develop into planula larvae that are free swimming for at least 22 days in the lab (Brooke, 1998). Artificial structures on the banks have new coral growth on them, so it may be possible to try to 'seed' the damaged areas with coral recruits. The ban on bottom fishing with hook and line for grouper and snapper will be reevaluated in 2004 to see if the stocks of gag and scamp grouper have recovered sufficiently to allow fishing to resume. The ban on bottom trawling, dredges, fish traps and pots, and anchoring would remain in effect.

Stringent surveillance and enforcement is not likely to be 100% for the Oculina marine reserve or any deep-water Marine Protected Area that is so remote from the coast. The areas are just too large and too far away to be adequately protected. However, random surveillance by various means such as spotter planes along with the occasional helicopter and enforcement vessel may impact the major offenders. Education regarding the importance and delicate nature of these rich resources is also important for both the commercial and recreational fishermen. This will lead to better self regulation and surveillance by the fishing community itself. Although large scale commercial fisheries' impacts could be devastating, the small repetitive impacts from the uninformed recreational fishermen may also have long-term consequences to the health of the reefs. It is also important to educate the enforcement personnel so they have a better understanding what they are protecting and why. These deep-water coral reefs (i.e. *Oculina*, *Lophelia*, and seamounts) are out of sight and can never be visited by the layperson. Only by bringing knowledge of these deep-water coral reefs to the public and the fishing community though videos, photos, and education will we gain their understanding and possible acceptance for the need of protection for these unseen resources.

Acknowledgements

Numerous individuals have contributed to this research over many years. I especially thank Dr Robert Avent who initiated these studies and Dr Charles 'Skip' Hoskin who provided years of enthusiastic collaboration and leadership. Dr Grant Gilmore, John Miller, David Mook, Frank Stanton, Lee Edmiston, Dr Nat Eisman, and Dr Robert Jones were active participants in the research. I gratefully acknowledge the Division of Biomedical Marine Research at HBOI for recent support of this project. The various crew of Harbor Branch Oceanographic Institution's vessels Johnson-Sea-Link and Clelia submersibles are also thanked for their fine efforts. This is contribution no. 1408 from Harbor Branch Oceanographic Institution.

References

Avent, R. M., M. E. King & R. H Gore, 1977. Topographic and faunal studies of shelf-edge prominences off the central eastern Florida coast. Int. Rev. ges. Hydrobiol. 62: 185–208.

Bak, R. P., 1978. Lethal and sublethal effects of dredging on reef corals. Mar. Poll. Bull. 9: 14–16.

Brooke, S. D., 1998. Reproduction and larval biology of the ivory tree coral *Oculina varicosa*. Am. Zool. 38: 100a.

Child, C. A., 1998. *Nymphon torulum*, new species and other Pycnogonida associated with the coral *Oculina varicosa* on the east coast of Florida. Bull. mar. Sci. 63: 595–604.

Cremer, P., 1986. U-boat Commander. Berkley Books. New York: 244 pp.

Dodge, R. E., R. C. Aller & J. Thompson, 1974. Coral growth related to resuspension of bottom sediments. Nature 247: 574– 577.

Emery, K. O. & E. Uchupi, 1972. Western North Atlantic Ocean: topography, rocks, structure, water, life, and sediments. Mem. 17, Am. Ass. petrol. Geol.: 532 pp.

Fosså, J. H., P. B. Mortensen & D. M. Furevik, 2000a. The deep water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. First Internat. Symp. Deep Sea Corals: 25.

Fosså, J. H., P. B. Mortensen & D. M. Furevik, 2000b. *Lophelia*korallrev langs Nordskekysten forekomst og tilstand. Institute of Marine Research, Bergen, Fisken og Havet Nr. 2: 94 pp.

- Freiwald, A. & J. Schönfeld, 1996. Substrate pitting and boring pattern of *Hyrrokkin sarcophaga* Cedhagen, 1994 (Foraminifera) in a modern deep-water coral reef mound. Mar. Micropaleon. 28: 199–207.
- Freiwald. A., R. Henrich & J. Pätzold, 1997. Anatomy of a deep-water coral reef mound from Stjernsund, west Finnmark, northern Norway. Soc. sedim. Geol., SEPM spec. Pub. 56: 141–162.
- Freiwald, A., J. B. Wilson & R. Henrich, 1999. Grounding Pleistocene icebergs shape recent deep-water coral reefs. Sedim. Geol. 125: 1–8.
- Gilmore, R. G. & R. S. Jones, 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. mar. Sci. 51: 83–103.
- Glynn, P. W., 1996. Bioerosion and coral reef growth: A dynamic balance. In Birkland, C. (ed.), Life and Death of Coral Reefs. Chapman & Hall, New York: 68-95.
- Hoskin, C. M., J. C. Geier & J. K. Reed, 1983. Sediment produced from abrasion of the branching stony coral *Oculina varicosa*. J. Sedim. Petrol. 53: 779-786.
- Hoskin, C. M., J. K. Reed & D. H. Mook, 1987. Sediments from a living shelf-edge reef and adjacent area off central eastern Florida. In Maurrasse, F. J. M. (ed.), Proc. Symp. South Florida Geol., Miami geol. Soc. Mem. 3: 42-57.
- Hubbard, J. A. & Y. P. Pocock, 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. Geol. Rund. 61: 598-626.
- Jensen, A. & R. Frederiksen, 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (scleractinia) on the Faroe shelf. Sarsia 77: 53-69.
- Jones, J. B., 1992. Environmenal impact of trawling on the seabed: a review. New Zeal. J. mar. Freshwat. Res. 26: 59-67.
- Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill & M. Grace, 2000. Protection of fish spawning habitat for the conservation of warm-temperate reeffish fisheries of shelf-edge reefs of Florida. Bull. mar. Sci. 66: 593-616.
- Koslow, J. A., G. W. Boehlert, J. D. Gordon, R. L. Haedrich, P. Lorance & N. Parin, 2000. Continetal slope and deep-sea fisheries: implications for a fragile ecosystem. ICES J. mar. Sci. 57: 548–557.
- Krutschinna, J. & A. Freiwald, 1998. Microendolithic succession along live to dead *Lophelia pertusa* (L.) skeletons from an aphotic coral reef. Proc. 2nd Internat. Bioerosion Workshop: 43 pp.
- Ludwick, J. C. & W. R. Walton, 1957. Shelf-edge, calcareous prominences in northeastern Gulf of Mexico. Bull. am. Ass. petrol. Geol. 41: 2054–2101.
- Macintyre, I. G. & J. D. Milliman, 1970. Physiographic features on the outer shelf and upper continental slope, Atlantic continental margin, southeastern United States. Bull. am. geol. Soc. 81: 2577–2598.
- Miller, J. E. & D. L. Pawson, 1979. A new subspecies of *Holothuria lentigenosa* Marenzeller from the western Atlantic Ocean. Proc. biol. Soc. Wash. 91: 912–922.
- Milliman, J. D., F. T. Manheim, R. M. Pratt & E. F. Zarudzki, 1967. ALVIN dives on the continental margin off the southeastern United States, July 2–13, 1967. Tech. Rep., Woods Hole Oceanographic Institution 67-80: 1–48.
- Moore, D. R. & H. R. Bullis, Jr., 1960. A deep-water coral reef in the Gulf of Mexico. Bull. mar. Sci. Gulf Carib. 10: 125-128.
- Mortensen, P. B. & H. T. Rapp. 1998. Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia*

- pertusa (L.) (Anthozoa, Scleractinia): implications for determination of linear extension rates. Sarsia 83: 433-446.
- Mortensen, P. B., M. Hovland, T. Brattegard & R. Farestveit, 1995. Deep-water bioherms of the scleractinian coral *Lophelia pertusal* (L.) at 64° N on the Norwegian shelf: structure and associated megafauna. Sarsia 80: 145–158.
- National Oceanic and Atmospheric Administration, 1982. Fishery Management Plan for Coral and Coral Reefs of the Gulf of Mexico and South Atlantic. Gulf of Mexico and South Atlantic Fishery Management Councils, Tampa, Florida: 342 pp.
- National Oceanic and Atmospheric Administration, 1998. Oculinal bank HAPC expanded northward. South Atlantic Update, The South Atlantic Fishery Management Council, Charleston, South Carolina: 18 pp.
- Neumann, A. C. & M. M. Ball, 1970. Submersible observations in the Straits of Florida: geology and bottom currents. Geol. Soc. am. Bull. 81: 2861–2874.
- Newton, C. R., H. T. Mullins, A. F. Gardulski, A. C. Hine & G. R. Dix, 1987. Coral mounds on the west Florida slope: unanswered questions regarding the development of deep-water banks. Palaios 2: 359–367.
- Reed, J. K., 1980. Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. Bull. mar. Sci. 30: 667–677.
- 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. Proc. 4th Internat. Coral Reef Symp. 2: 201–206.
- Reed, J. K., 1983. Nearshore and shelf-edge *Oculina* coral reefs: the effects of upwelling on coral growth and on the associated faunal communities. National Oceanic Atmospheric Administration, Symp. Ser. Undersea Res. 1: 119–124.
- Reed, J. K., 1985. Shelf edge Oculina reefs. In Seaman, W., Jr. (ed.), Florida Aquatic Habitat and Fishery Resources. Florida Chapter of American Fisheries Society, Kissimmee, Florida: 466–468.
- Reed, J. K., 1998. Bioerosion and sediment production on Florida's deep-water *Oculina* coral banks. Proc. 2nd Internat. Bioerosion Workshop: 54-56.
- Reed, J. K. & 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 Sci. 5: 1-4.
- Reed, J. K. & C. M. Hoskin, 1987. Biological and geological processes at the shelf edge investigated with submersibles. National Oceanic Atmospheric Administration, Symp. Ser. Undersea Res. 2: 191–199.
- Reed, J. K. & P. M. Mikkelsen, 1987. The molluscan community associated with the scleractinian coral *Oculina varicosa*. Bull. mar. Sci. 40: 99–131.
- Reed, J. K., R. H. Gore, L. E. Scotto & K. A. Wilson, 1982. Community composition, structure, areal and trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa* coral reefs. Bull. mar. Sci. 32: 761–786.
- Richer de Forges, B., J. A. Koslow & G. C. Poore, 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405: 944-947.
- Richman, S., Y. Loya & L. Slobodkin, 1975. The rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. Limnol. Oceanogr. 20: 918–923.
- Rogers, A. D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int. Rev. Hydrobiol. 84: 315–406.
- Rogers, C. S., 1990. Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62: 185–202.

- Schmuck, E. A., P. C. Valentine & N. W. Driscoll, 1995. Examples of trawl and dredge marks from side-scan sonar records collected from Stellwagen Bank, Georges Bank, and Block Island Sound, and their geomorphic and sedimentary significance. N.E. Section geol. Soc. Am. 1995, abstract.
- Smith, F. G. W., 1971. Atlantic Reef Corals. Univ. Miami Press. Coral Gables, Florida: 164 pp.
- Smith, N. P., 1981. An investigation of seasonal upwelling along the Atlantic coast of Florida, Proc. 12th Internat. Liege Colloque Ocean Hydrodynamics: 79–98.
- Stetson, T. R., D. F. Squires & R. M. Pratt, 1962. Coral banks occurring in deep water on the Blake Plateau. Am. Mus. Nov. 2114: 1–39.
- Teichert, C., 1958, Cold- and deep-water coral banks. Bull. am. Ass. petrol. Geol. 42: 1064–1082.
- Thompson, M. J. & L. E. Gulliland. 1980. Topographic mapping of shelf edge prominences off southeastern Florida. Southeastern Geol. 21: 155–164.

- Van Dolah, R. F., P. H. Wendt & N. Nicholson. 1987. Effects of a research trawl on a hard-bottom assemblage of sponges and corals. Fisheries Res. 5: 39-64.
- Verrill, A. E., 1902. Papers on corals. Trans. Conn. Acad. Arts Sci. 11: 63–266.
- Virden, W. T., T. L. Berggren, T. A. Niichel & T. L. Holcombe,
 1996. Bathymetry of the shelf-edge banks, Florida east coast.
 National Oceanic and Atmospheric Administration. National
 Geophysical Data Center, National Marine Fisheries Service,
 Beaufort, North Carolina: 1.
- Wilson, J. B., 1979. The distribution of the coral *Lophelia pertusa* (L) [*L. prolifera* (Pallas)] in the northeast Atlantic. J. mar. biol. Ass. U.K. 59: 149–164.

		4