



Comparison of deep-water coral reefs and lithoherms off southeastern USA

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Abstract

Two types of deep-water coral bioherms occur off the coast of southeastern United States: *Oculina* and *Lophelia/Enallopsammia*. The deep-water *Oculina* bioherms form an extensive reef system at depths of 70–100 m along the shelf edge off central eastern Florida. These reefs are comprised of numerous pinnacles and ridges, 3–35 m in height. Each pinnacle is a bank of unconsolidated sediment and coral debris that is capped on the slopes and crest with living and dead colonies of *Oculina varicosa*, the ivory tree coral. In comparison, deep-water reefs of *Lophelia pertusa* and *Enallopsammia profunda* corals occur at depths of 500–850 m (maximum 150-m relief) along the base of the Florida-Hatteras slope in the Straits of Florida. On the western edge of the Blake Plateau off South Carolina and Georgia, 54-m high banks of *Enallopsammia* and *Lophelia* occur at depths of 490–550 m, whereas on the eastern edge of the plateau the reefs form structures 146 m in height and at depths of 640–869 m. The geomorphology and functional structure of both the *Oculina* and *Lophelia* reefs are similar. North of Little Bahama Bank, at depths of 1000–1300 m, a region of bioherms is dominated by the coral *Solenosmilia* sp.; *Lophelia* is reportedly absent. This paper summarizes 25 years of submersible studies on the deep-water *Oculina* reefs, describes submersible reconnaissance of deep-water *Lophelia* reefs off the southeastern United States, and contrasts these types of bioherms with the deep-water lithoherms in the Straits of Florida west of the Bahamas.

Introduction

Deep-water coral reefs typically consist of thickets of live coral, capping mounds of unconsolidated sediment and coral rubble, and are often built upon an underlying lithified base structure. They are found in regions of fairly strong currents or zones of upwelling where the coral structures capture suspended sediment and build up mounds to heights of a few meters to >150 m (see review by Rogers, 1999). Average depths are from 70 m to >1000 m. At these depths the corals lack zooxanthellae, the algal symbiont found in shallow, hermatypic reef corals; however, the deep-water reefs also provide habitat for thriving and diverse reef communities. Deep-water *Oculina* and *Lophelia* coral reefs are sometimes also referred to as bioherms, coral banks, or lithoherms (Teichert, 1958; Stetson et al., 1962; Neumann et al., 1977; Reed, 1980; Paull et al., 2000). Deep-water lithoherms, however, typically

consist of lithified carbonate limestone rather than unconsolidated sediment. Lithoherms also form 50–150-m high structures that are capped with colonies of living *Lophelia* and/or *Enallopsammia* coral. Rogers (1999) has recently suggested that these deep-water coral bioherms fall into the definition of a coral reef, based on their physical and biological characteristics.

Two types of deep-water coral reefs are common off the southeastern United States, primarily between Florida and South Carolina. Deep-water *Oculina* forms an extensive reef system at depths of 70–100 m along the shelf-edge off central eastern Florida (Avent et al., 1977; Reed, 1980). In contrast, deep-water reefs of *Lophelia* and *Enallopsammia* corals occur at greater depths, 490–870 m, in the Straits of Florida and on the Blake Plateau off the coasts of Florida, Georgia and South Carolina (Stetson et al., 1962; Milliman et al., 1967; Uchupi, 1968; Neumann & Ball, 1970; Emery & Uchupi, 1972). This paper compares these two

types of deep-water coral reefs off the southeastern United States and contrasts them with the deep-water lithoherms (Neumann et al., 1977; Messing et al., 1990; Paull et al., 2000) in the Straits of Florida west of the Bahamas.

Methods

Data on the deep-water *Oculina* reefs are based on research over a 25-year period with the *Johnson-Sea-Link* (JSL) submersibles. The four-person JSL submersible is capable of dives to 914 m and is outfitted with an array of photographic and collection equipment including a manipulator arm with clam-shell grab and suction hose; 12-bin rotating collection buckets; environmental data recorder to log temperature, conductivity, salinity, depth and light; a modified Edgerton 35-mm camera with 35- or 80-mm lens and 750 exposure film; and a color video camera system (Tietze & Clark, 1986). Lockout dives to depths of 80 m were utilized on the deep-water *Oculina* reefs. Data on the *Lophelia* reefs and lithoherms were also gathered with Harbor Branch Oceanographic Institution's (HBOI) JSL submersible and *Cord*, a remotely-operated-vehicle (ROV). Additional information was summarized from published literature on submersible dives with *Alvin* (Milliman et al., 1967; Neumann et al., 1977; Griffin & Druffel, 1989; Messing et al., 1990), the *Aluminant* (Neumann & Ball, 1970), the U.S. Navy's submarine NR-1 (Paull et al., 2000), and from surveys using echo-soundings, dredges, and camera sleds (Stetson et al., 1962; Mullins et al., 1981).

Results and discussion

Coral description and distribution

The dominant corals forming deep-water reefs in the western North Atlantic region are *Oculina varicosa*, *Lophelia pertusa*, and *Enallopsammia profunda*, although other branching colonial scleractinia may also occur, including *Solenosmilia variabilis* and *Madrepora oculata*. Numerous solitary coral species are also common (Cairns, 1979).

Oculina varicosa Lesueur, 1820: In deep water (>60 m), *O. varicosa* forms spherical, dendroid, bushy colonies that are 10 cm to 1.5 m in diameter and height (Fig. 1). The branches average 6 mm in

diameter near the tips and frequently anastomose. Individual corals may coalesce forming linear colonies 3–4 m in length or massive thickets of contiguous colonies on the slopes and crests of the deep-water reefs (Reed, 1980). The deep-water form lacks zooxanthellae, whereas in shallow water *O. varicosa* is usually golden brown with the algal symbiont. The shallow-water *O. varicosa* colonies average <30 cm in diameter, with thicker branches, but do not form thickets or coral banks like the deep-water form. *O. varicosa* apparently has separate sexes and externally fertilized eggs which develop into planula larvae that are free swimming for at least 22 days (Brooke, 1998). *O. varicosa* ranges from the Caribbean to Bermuda at depths of 2–152 m (Verrill, 1902; Smith, 1971; Reed, 1980). The deep-water *Oculina* reefs, however, are only known from 27°32' N and 79°59' W to 28°59' N and 80°07' W, and at depths of 70–100 m (Fig. 2, Sites A and A1).

Lophelia pertusa (Linnaeus, 1758) (= *L. prolifera*): Similar in gross morphology to *Oculina*, this coral also forms massive, dendroid, bushy colonies, 10–150 cm in diameter, with anastomosing branches (Fig. 1). Its distribution ranges in the western Atlantic from Nova Scotia to Brazil and the Gulf of Mexico, and also in the eastern Atlantic, Mediterranean, Indian, and eastern Pacific Oceans at depths of 60–2170 m (Cairns, 1979). Along with *Enallopsammia profunda*, it is the primary constituent of deep-water reefs at the base of the Florida-Hatteras slope and at depths of 500–800 m from Miami to South Carolina (Fig. 2, Sites B and C). In addition, over 200 banks have been mapped at depths of 640–869 m (Site D) on the outer eastern edge of the Blake Plateau (Stetson et al., 1962). Elsewhere deep-water *Lophelia* reefs are known from the Gulf of Mexico (Ludwick & Walton, 1957; Moore & Bullis, 1960; Newton et al., 1987) and the eastern Atlantic off Norway and Scotland (Teichert, 1958; Wilson, 1979a; Mortensen et al., 1995; Freiwald et al., 1997, 1999). On the deep-water *Lophelia* reefs in the eastern Atlantic, *Madrepora oculata* commonly occurs with *Lophelia* rather than *E. profunda*.

Enallopsammia profunda (Pourtalès, 1867) (= *Dendrophyllia profunda*): This species also forms dendroid, massive colonies up to 1 m in diameter (Fig. 1). It is endemic to the western Atlantic and ranges from the Antilles in the Caribbean to Massachusetts at depths of 146–1748 m (Cairns, 1979). *E. profunda* occurs with *L. pertusa* at Sites B, C, and D (Fig. 2). It appears to be the primary constituent of the deep-water reefs at Site D except at the tops of the

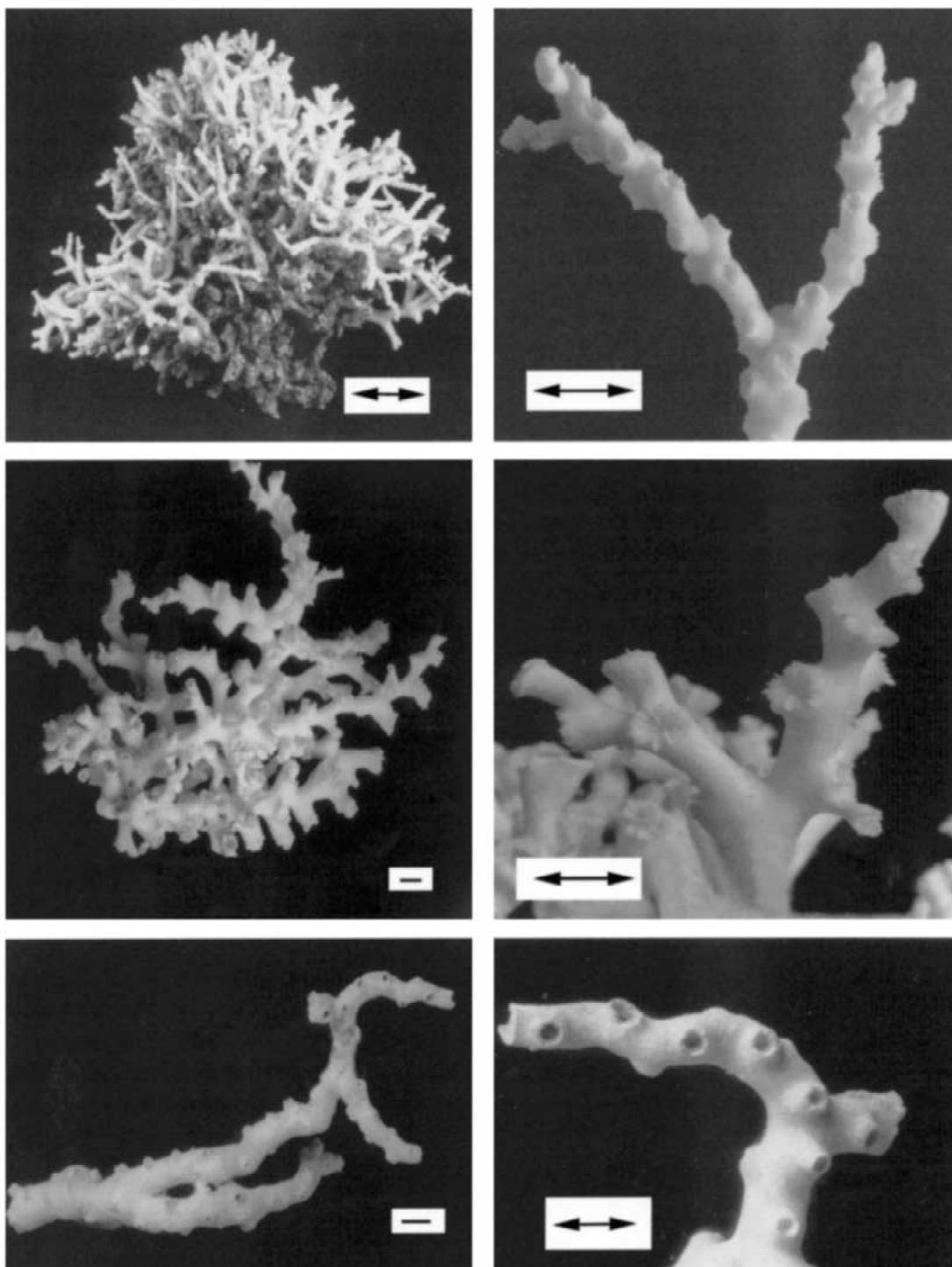


Figure 1. Colony and branch tip for: top, *Oculina varicosa* (80m); middle, *Lophelia pertusa* (490 m); bottom, *Enallopsammia profunda* (585 m). (scale lines = 1 cm; top left fig. scale = 5 cm).

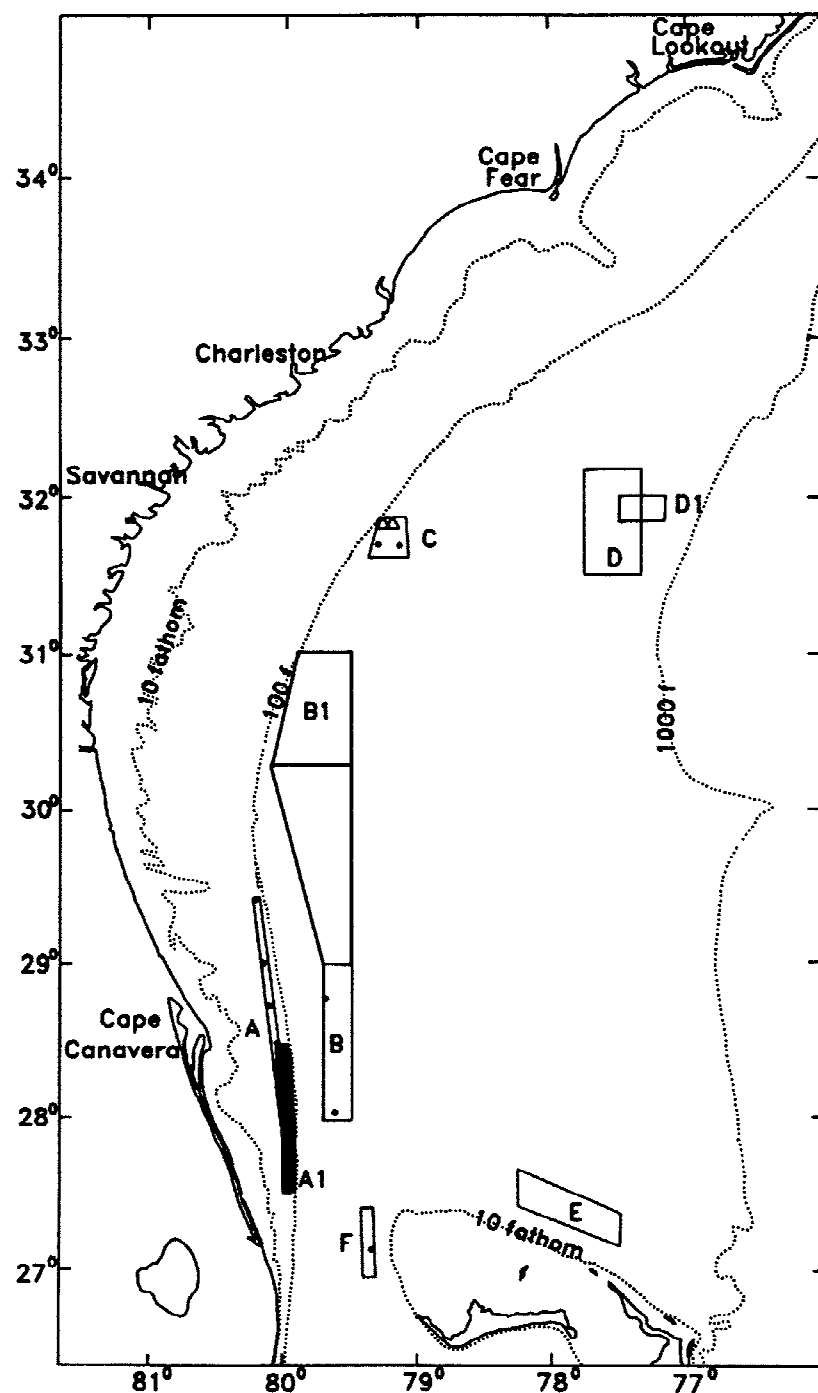


Figure 2. Deep-water coral banks off southeastern U.S.A. (●) Johnson-Sea-Link I and II sites; (▲) Alvin sites. A, *Oculina* coral banks; A1, *Oculina* HAPC site; B-E, *Lophelia/Enallopsammia* coral banks; F, Lithohierms.

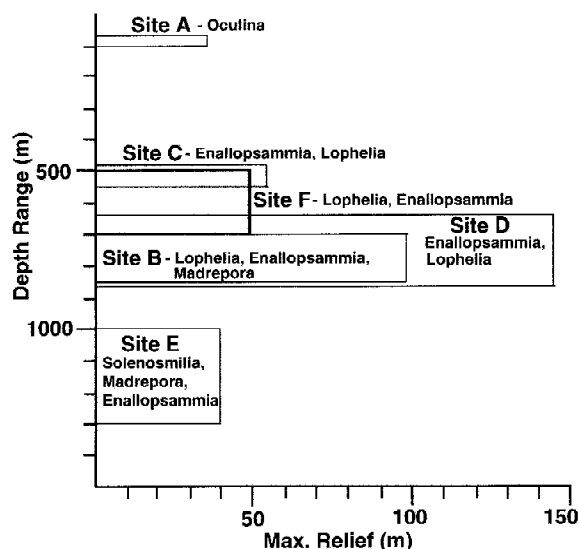


Figure 3. Depth range and maximum relief of deep-water coral banks off southeastern U.S.A. (see Fig. 1 for site locations). Dominant colonial coral listed for each site.

mounds where *L. pertusa* is more prevalent (Stetson et al., 1962).

Site descriptions

Site A

Dozens of isolated pinnacles and mounds of *Oculina varicosa* have been mapped within Site A along a 167 km stretch near the shelf-edge break at 70–100 m depths (Table 1, Figs 2 and 3; Avent et al., 1977; Reed, 1980; Thompson & Gulliland, 1980; Koenig, 2000). A typical reef is a pinnacle-shaped structure with a maximum relief of 35 m and up to several hundred meters in diameter (Fig. 4, top). The tops of the reefs typically have one or more linear ridges with east–west orientation, perpendicular to the prevailing current. Greatest concentration of live coral occurs on the southern face of 30–45° slopes, whereas the northern slopes are often more gradual (<25°) with more dead coral rubble and scattered live colonies, 0.5–2 m in diameter. Some of the reefs are completely covered with dead coral rubble and have no living coral colonies.

Greater growth on the southern facies may indicate exposure to the northerly flowing Gulf Stream (Florida Current); however, the clear, warm waters of this current rarely penetrate below the upper 50 m in this region. Long-term current meter records show average currents of 8.6 cm s^{-1} (0–58.5) which consist of east–west tidal currents, a northerly flow (16% of total flow), and a southerly countercurrent (11% of

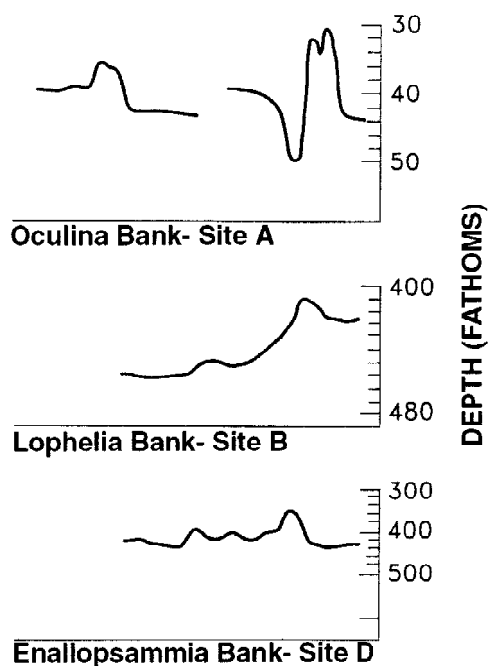


Figure 4. Bottom profiles of deep-water coral banks. Top, *Oculina* coral banks (Site A1); middle, *Lophelia* coral bank (Site B); bottom, *Enallopsammia* coral bank (Site D).

total flow) (Hoskin et al., 1987). Temperatures average 16.2°C and range from 7.4 to 26.7°C (Table 1). Intrusions of cold-water upwelling drop the temperature below 10°C episodically throughout the year (Reed, 1983). Nutrient levels of nitrates also increase nearly 10-fold during upwelling events (nitrates, <2 μM during non-upwelling, 9–18 μM during upwelling; phosphates, <0.25, 0.5–2 μM ; chlorophyll *a*, <1, 1–9 mg m^{-3} , respectively; Reed, 1983).

A 315 km^2 (92 nmi^2) portion (Fig. 2, Site A1) of the deep-water *Oculina* reef system was originally designated in 1984 as a Habitat Area of Particular Concern (HAPC) by the Fishery Management Plan for Coral and Coral Reefs (NOAA, 1982). This was the first Marine Protected Area (MPA) in the world to protect deep-water corals and reefs. It was also selected to the final site evaluation list as a potential National Marine Sanctuary (Federal Register, March 1983). In 2000 the National Marine Fisheries Service and the National Oceanic and Atmospheric Administration (NOAA) issued a final rule to expand the *Oculina* Bank HAPC to an area of approximately 1029 km^2 (300 nmi^2) (Federal Register, June 2000).

Table 1. Site summary for deep-water coral reefs off southeastern U.S.A.

Site Reference	Depth (m)	Max. relief (m)	Temp. (°C)	Current (cm s ⁻¹) (dir. to:)	Salinity (ppt)	Visibility (m)	Coordinates
*(A) Reed, 1980	70–100	35	7.4–26.7 ($\bar{x}$ =16.2)	0–58.5 (N,S) ($\bar{x}$ =8.6)	35.7–36.4	0–30	27°32.8' N, 79°58.8' W to 28°59' N, 80°06' W
(B) JSL I-2474	762–793	30	6.5	15 (315°)		15	28°46.72' N, 79°41.17' W
CORD-85	741–838	97	7.6–8.4				28°02.04' N, 79°36.51' W
Paull et al., 2000	440–914	150		25–100 (NNE)			30°30' N, 79°45' W
(C) JSL II-1690	490–503	13					31°41.23' N, 79°17.46' W
JSL II-1697	541		8.75	25–40 (50°)		15	31°41.82' N, 79°08.60' W
JSL II-1698	499–532	33	7.97–8.4	25–45 (50°)			31°41.5' N, 79°18.06' W
Alvin-203	500–550	54	7.5	35–60 (NE)		30	31°48' N, 79°15' W
(D) Stetson et al., 1962	640–869	146	7–10		35		31°30' N, 77°45' W to 32°10' N, 77°20' W
(E) Mullins et al., 1981	1000–1300	40	4–6	50			27°40' N, 78°15' W to 27°10' N, 77°30' W
(F) Neumann et al., 1977	639–675	50		2–7 (N)			~27°N to 27°25' N, 79°20' W
JSL II-1522, 1523, 1533	610–631		8.25–9.58	0–15 (N)		15–30	26°56.72' N, 79°16.02' W to 27°02.66' N, 79°18.29' W

*Sites A–F (See Fig. 2). JSL and CORD, Harbor Branch Oceanographic Institution's Johnson-Sea-Link Submersibles and CORD ROV. Alvin, Woods Hole Oceanographic Institution's submersible.

Site B

Isolated *Lophelia* reefs at the base of the Florida-Hatteras slope occur at depths of 700–850 m along the western edge of the Florida Straits and 15–25 nmi east of the *Oculina* banks (Table 1, Figs 2 and 3). At a site east of Cape Canaveral (JSL-I dive 2474) a few small (<30 cm) colonies of *Lophelia* and/or *Enalllopsammia* occur on slopes of nearly 100% dead coral rubble. At the southern end of Site B the bathymetry of eight pinnacles was traced (97 m maximum relief; Fig. 4, middle) near a dive site that was documented with a ROV (Cord dive 85). Near the peak a steep 45° slope consists of coral rubble with a 5% cover of live coral colonies, 30–50 cm in diameter. Some upright dead colonies are also present. The northwest slope is muddy with less coral rubble. Temperatures ranged from 6.5 to 8.4°C and currents were northerly at 15 cm s⁻¹.

Further north a continuation of similar structures were reported by Paull et al. (2000) (Fig. 2, Site B1) which they described as lithoherms. No information is available between Sites B and B1 but they estimate that over 40 000 coral lithoherms could be present in this region of the Straits of Florida and the Blake Plateau. Their dives with the *Johnson-Sea-Link* submersible and the U.S. Navy's submarine NR-1 described a region of dense lithoherms forming pinnacles

5–150 m in height with 30–60° slopes that have thickets of live ahermatypic coral (unidentified species, but photos suggest *Lophelia* and/or *Enalllopsammia*). The depths range from 440 to >900 m but most mounds are within 500–750 m. Each lithoherm is 100–1000 m long and the ridge crest is generally oriented perpendicular to the northerly flowing Gulf Stream current (25–50 cm s⁻¹ on flat bottom, 50–100 cm s⁻¹ on southern slopes and crests). Thickets of live coral up to 1 m are mostly found on the southern facing slopes and crests, whereas the northern slopes are mostly dead coral rubble. These are termed lithoherms since the mounds are partially consolidated by a carbonate crust, 20–30 cm thick, consisting of micritic wackestone with embedded planktonic foraminifera, pteropods, and coral debris (Paull et al., 2000).

Further south in the Straits of Florida off Miami, Neumann and Ball (1970) using the *Aluminaut* submersible found thickets of *Lophelia*, *Enalllopsammia* (= *Dendrophyllia*), and *Madepora* growing on elongate depressions, sand ridges and mounds. Large quantities of *L. pertusa* and *E. profunda* have also been dredged from 738–761 m at 26°22' to 24' N and 79°35' to 37' W (Cairns, 1979).

Site C

This is a continuation of the deep-water *Lophelia* coral reefs along the base of the Florida-Hatteras slope from Site B (Table 1, Figs 2 and 3). Site C is at the western edge of the Blake Plateau and occurs in a region of phosphoritic sand, gravel and rock pavement. These deep-water *Lophelia* mounds occur at depths of 490–550 m and have maximum relief of 54 m. *JSL-II* dives 1690, 1697 and 1698 found a coral rubble slope with <5% cover of 30 cm, live coral colonies. On the reef crest are 30–50 cm diameter coral colonies covering ~10% of the bottom. Some areas consist of a rock pavement with a thin veneer of sand, coral rubble, and 5–25 cm phosphoritic rocks. At *Alvin* dive sites 200 and 203, Milliman et al. (1967) reported elongate coral mounds, approximately 10 m wide and 1 km long, that are oriented NNE–SSW. The mounds have 25–37° slopes and 54 m relief. Live colonies (10–20 cm diameter) of *E. profunda* (= *D. profunda*) dominate and *L. pertusa* is common. No rock outcrops were observed. Currents at all dive sites within Site C were to the northeast at 25–60 cm s⁻¹ and temperatures averaged 7–9°C (Table 1).

Site D

This site is on the outer eastern edge of the Blake Plateau at depths of 640–869 m (Table 1, Figs 2 and 3). Over 200 coral mounds up to 146 m in height occur over this 6174 km² area (Stetson et al., 1962; Uchupi, 1968). These are steep-sloped structures with active growth on top of the banks (Fig. 4, bottom). Live coral colonies up to 50 cm in diameter were observed with a camera sled. *E. profunda* (= *D. profunda*) is the dominant species in all areas although *L. pertusa* is concentrated on top of the mounds. Densest coral growth occurs along an escarpment at Site D1 (Fig. 2).

Site E

This is a deeper site (1000–1300 m) north of Little Bahama Bank and consists of 5–40-m high mounds of unconsolidated sediment with coral debris (Table 1, Figs 2 and 3; Mullins et al., 1981). This contrasts with the other sites in that the dominant live branching coral is *Solenosmilia*, whereas *Lophelia* is apparently absent. *Madrepora* and *Enallopsammia* also occur along with various solitary ahermatypic corals.

Site F

On the eastern side of the Straits of Florida, west of Little Bahama Bank, a region of lithohierms occurs at depths of 500–700 m (Table 1, Figs 2 and 3; Neumann

et al., 1977; Mullins & Neumann, 1979; Messing et al., 1990). In contrast with *Lophelia* and *Oculina* reefs which are often unconsolidated, these are mounds of lithified carbonate sediment. Dives with *Alvin* and *JSL* found these 30–50-m high lithohierms to be elongated up to 300 m north–south, in a northerly flowing current which averages <15 cm s⁻¹ but may exceed 100 cm s⁻¹ at their crests. The 20–30° slopes have a thin veneer of sediment. Living colonies of *Lophelia* and *Enallopsammia* are a common component on top of the mounds and on the upcurrent slopes, and coral rubble occurs on the foreslopes. In comparison, the lithohierms described at Site B1 are elongated perpendicular to the current rather than parallel, and the mounds are much larger (Paull et al., 2000).

Deep-water coral reef communities

The deep-water coral reefs support very rich communities of associated invertebrates. Faunal diversity on the *Oculina* reefs is equivalent to many shallow-water tropical reefs. Over 20 000 individual invertebrates were found living among the branches of 42 small *Oculina* colonies from deep and shallow water, yielding 230 species of mollusks, 50 species of decapods, 47 species of amphipods, 21 species of echinoderms, 15 species of pycnogonids, and numerous other taxa (Reed et al., 1982; Reed & Hoskin, 1987; Reed & Mikkelsen, 1987; Child, 1998). A striking difference between the *Oculina* and *Lophelia* reefs is that larger sessile invertebrates such as massive sponges and gorgonians are not common on the deep-water *Oculina* reefs. The *Oculina* coral itself is the dominant component on these reefs. The maximum percentage of live coral coverage is less on the *Lophelia* reefs (5–10% at Sites B and C) compared to the *Oculina* reefs (up to 100% on some reefs); however, both types of reefs have extensive areas where the bottom is covered with 100% dead coral rubble and no living coral.

The *Lophelia* reefs at Site C support large populations of massive sponges and gorgonians in addition to the smaller macroinvertebrates which have not been studied in detail. Dominant macrofauna include large plate-shaped sponges (*Pachastrella monilifera*, Choristida) and stalked, fan-shaped sponges (*Phakellia ventilabrum*, Axinellida), up to 90 cm in diameter and height (Fig. 5). At certain sites (*JSL-II* dive 1697), these species were estimated at one colony/10 m². Densities of small stalked spherical sponges (*Stylodordyla* sp., Hadromerida) were estimated in some

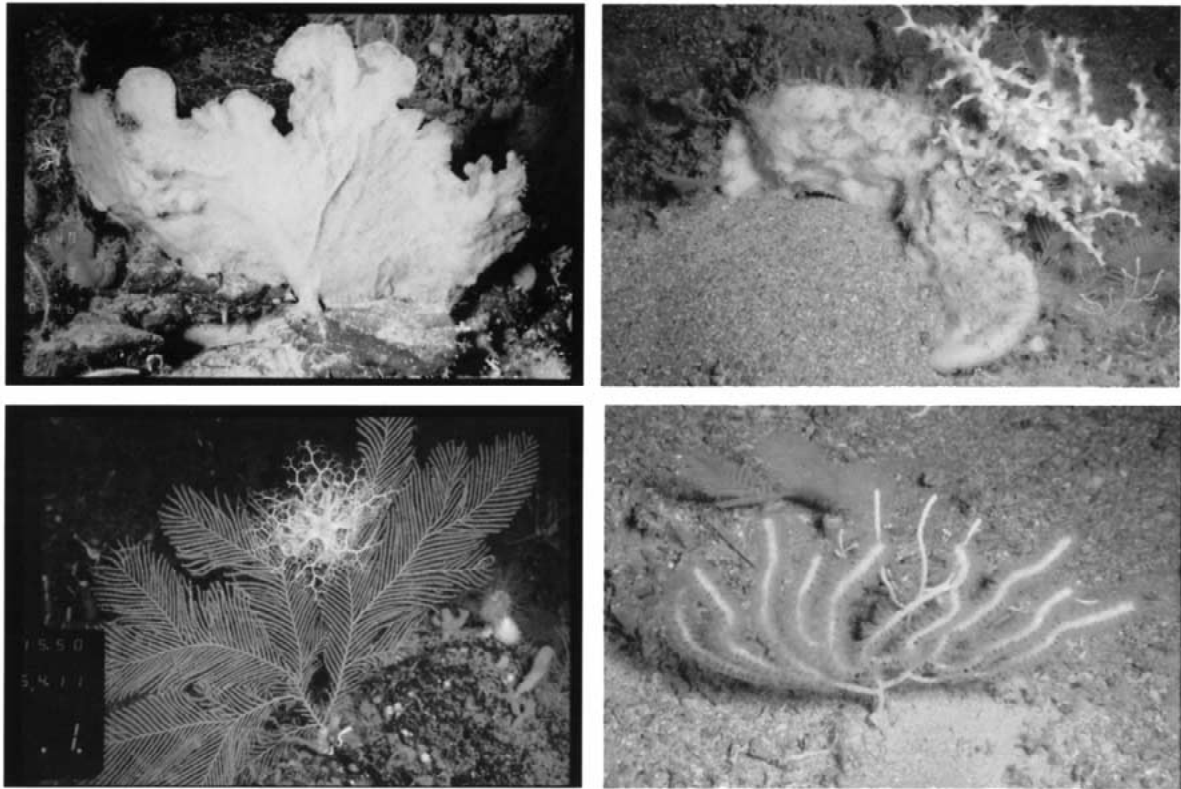


Figure 5. Dominant megafauna associated with deep-water coral banks off southeastern U.S.A. Top left, *Phakellia ventilabrum* (Axinellidae, Porifera); top right, *Pachastrella monilifera* (Pachastrellidae, Porifera) and *Lophelia pertusa*; bottom left, *Plumarella pourtalessi* (Primnoidae, Cnidaria); bottom right, *Eunicella* sp. (Plexauridae, Cnidaria).

areas at 167 colonies/10 m². Hexactinellid (glass) sponges such as *Farrea*? sp. are also common. Dominant gorgonacea include *Eunicella* sp. (Plexauridae) and *Plumarella pourtalessi* (Primnoidae) (Fig. 5). At this same site, colonies of these two species averaged 10–25 cm in height with maximum densities of 33–100 colonies/10 m² and 10 colonies/10 m², respectively. The axes of all these fan-shaped sponges and gorgonians are perpendicular to the current which was constantly to the northeast during all *Alvin* and *JSL* dives. Sediment piles up on the lee side of these colonies.

On the *Lophelia* reefs of Site D, Stetson et al. (1962) reported an abundance of hydroids, alcyonaceans, echinoderms, actiniaria, and ophiuroids, but a rarity of large mollusks. The flabelliform gorgonians were also current-oriented.

The lithoherm reefs at site F (*JSL*-II dives 1522, 1523, and 1533) also share some species of large sessile macroinvertebrates with the *Lophelia* reefs. Large current-oriented fan sponges up to 90 cm in

diameter (*Phakellia ventilabrum*) are common, as well as several species of plate sponges (*Pachastrella* sp., Choristida) and hexactinellid sponges (*Heterotella* sp. and *Farrea* sp.). Fan-shaped gorgonians are common (e.g., *Paragorgia johnsoni*, *Corallium* sp., *Paramuricea* sp., and *Narella* sp.) but are of different genera than those found on the *Lophelia* reefs. Unstalked crinoids are also common on the rock substrate (*Neocomatella pulchella* and *Crinometra brevipinna*). In addition, numerous stalked crinoids (*Neocrinus decorus*, *Endoxocrinus parrae*, *Isocrinus blakei*, and *Diplocrinus maclearanus*) are common on the lithohermes but absent on the deep-water *Oculina* or *Lophelia* reefs at Sites B, C and D. Messing et al. (1990) described three faunal zones on the lithohermes that are determined by current regimes. A zoanthid zone dominates the crest of the mounds in the highest current regime (maximum >100 cm s⁻¹). A zone of living and rubble *Lophelia* coral cover the upcurrent slopes, and a crinoid/alcyonarian zone occurs on the flanks and down-current crests of the lithohermes. The

Oculina reefs do not have such an apparent zonation of associated megafauna.

In comparison, Rogers' (1999) review of literature on deep-water *Lophelia* coral reefs in the northeastern Atlantic recorded 886 species of associated invertebrates. Quantified analyses of live and dead colonies of *Lophelia pertusa* from the Faroe shelf off of Scotland resulted in 298 species, dominated by polychaeta (67 sp.), bryozoa (45 sp.), mollusca (31 sp.), porifera (29 types), and crustacea (15 sp.) (Jensen & Frederiksen, 1992).

Coral growth and reef age

Coral from both the *Oculina* and *Lophelia* deep-water reefs lack zooxanthellae, the algal symbiont that enhances the growth rates of hermatypic corals. Light levels at the *Oculina* site averages 0.33% of transmitted surface light but generally does not support the growth of algae (including zooxanthellae). Average growth rate of *Oculina varicosa* at a depth of 80 m is 16 mm year⁻¹ (Reed, 1981). At this rate a large 1.5-m colony may be nearly a century old. Comparable growth rates of 6–15 mm year⁻¹ have been estimated for colonies of *Lophelia pertusa* collected from deep-water cables (Teichert, 1958; Wilson, 1979a). Studies using stable isotopes estimated the linear growth rates of *Lophelia* from 5.5 to 20 mm year⁻¹ (Freiwald et al., 1997; Mortensen & Rapp, 1998). Mikkelsen et al. (1982) reported rates of 25 mm year⁻¹ for *Lophelia* but this may be an exaggeration due to their sampling methodology (Mortensen & Rapp, 1998). Greatest coral growth for both the *Oculina* and *Lophelia* reefs is on the top or on the current-facing side of the mound. The deep-water reefs are in areas of fairly strong currents (>50 cm s⁻¹) undoubtedly contributing to the growth of the corals in providing particle flux for suspension feeding (Teichert, 1958; Reed, 1981; Messing et al., 1990). Both types of reefs are also often found in areas of upwelling along the shelf edge. The upwelling of nutrient rich water onto the shelf and subsequent increases in phytoplankton and zooplankton may enhance the growth of the coral (Reed, 1983).

The dead *Lophelia* reefs in the Gulf of Mexico were radiocarbon dated at >40 000 years before present (B.P.), dead *Lophelia* from the Straits of Florida (Site F) were dated at 28 170 B.P. (Neumann et al., 1977), and those north of Little Bahama Bank (Site E) yielded radiocarbon dates of 860–940 B.P. (Mullins et al., 1981). At Site B1, the live coral on the crests of deep-water reefs were dated at 700 B.P., the dead coral

rubble was 20 230 B.P., and the carbonate crusts were of Pleistocene age, 17 770 to 33 430 B.P. (Paull et al., 2000). Freiwald et al. (1997) described dying *Lophelia* reef mounds off Norway as clusters of collapsing coral frameworks in which there is an upcurrent growing stage and a downcurrent dying stage. He estimated this 10-m thick reef to be between 526 and 2500 years old.

The deep-water *Oculina* reefs, based on a growth rate of 1.6 cm year⁻¹ and maximum height of 25 m, may be estimated at a minimum age of 1526 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±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 are 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 bio-eroders, 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⁻¹ currents. Coral fragments tested in a mechanical tumbler at intervals of 1–1000 min 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 (Site A1, Figs 2 and 3 top) 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.

Seismic profiles of deep-water *Lophelia*/*Enallopsammia* reefs do not adequately show their internal structure (Stetson et al., 1962; Mullins et al., 1981). The reefs, however, are probably unconsolidated sediment and coral debris associated with underlying hard-bottom. The reefs within Site B are concentrated along the rims of linear depressions that may be erosional features of the Gulf Stream (Emery & Uchupi, 1972). The reefs at Site B1 have live and dead coral debris overlaying a lithified carbonate crust (Paull et al., 2000). The reefs on the Blake Plateau (Site D) are best developed on the crest of an escarpment and also tend to follow bathymetric trends and depressions

which may indicate rock outcrops (Stetson et al., 1962; Uchupi, 1968). In contrast with the deep-water *Lophelia* and *Oculina* reefs, the lithohermes of the eastern Florida Straits (Site F) are primarily lithified, muddy carbonate limestone that is composed of pelagic forams and skeletal remains of coral, mollusks, crinoids, echinoids, and sponges (Neumann et al., 1977).

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 exist with only a few scattered living colonies. 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 5132 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-, 27- 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^{-1} . The Gulf Stream that may exceed 5 knots (250 cm s^{-1}) 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^{-1} and

averages 8.6 cm s^{-1} . On the lithoherms in the Straits of Florida, Messing et al. (1990) also found peak currents in excess of 100 cm s^{-1} on the eastern side of the Straits and Paull et al. (2000) recorded currents of 25– 100 cm s^{-1} 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.

The exact cause of the extensive areas of dead coral rubble on the modern deep-water reefs 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). Apparently commercial fishermen are capable of trawling at these great depths in areas of high relief pinnacles, and shrimp trawlers have recently been caught and fined for fishing within the *Oculina* Coral Bank Habitat Area of Particular Concern. Finally, 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.

Conclusions

The geomorphological structure of the deep-water *Oculina* reefs is similar to that of deep-water *Lophelia* reefs. Their occurrence in high current regimes which provide particulate material for suspension feeding and where fine sand, mud and coral debris are trapped results in similar functioning ecosystems that support rich communities of invertebrates. Lacking zooxanthellae, *Oculina varicosa* and *Lophelia pertusa* have comparable growth rates. The primary difference between these two types of bioherms appears with the species associated with these coral reefs. The deep-water *Oculina* reefs occur on the shelf edge in a region of upwelling that supports a high biodiversity of invertebrates with tropical to temperate and even boreal affinities. However, the *Oculina* reefs lack large sessile invertebrates such as massive sponges and gorgonians that are common to the *Lophelia* reefs and lithoherms. The different faunal assemblages are ap-

parent in the components of the sediment which also differ between the two types of deep-water coral reefs. Bioeroders are an integral component of both *Oculina* and *Lophelia* reefs and are a major producer of sediments. Extensive areas of dead coral on deep-water *Oculina* and *Lophelia* reefs may be the result of a combination of factors: (1) natural evolution of the bank development, (2) paleoclimatic factors, (3) bioerosion, (4) hydrodynamic stress, (5) fishing activities, and (6) pathogens. Degradation due to human factors such as fishing activities can be modified through better understanding of these deep-water coral reefs and with prudent fishing restrictions and regulations to protect the habitat.

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