Reed, J. K., Pomponi, S. A., Weaver, D., Paull, C. K., & Wright, A. E. (2005). Deep-water sinkholes and bioherms of south Florida and the Pourtalés Terrace — habitat and fauna. *Bulletin of Marine Science, 77*(2), 267-296.

BULLETIN OF MARINE SCIENCE, 77(2): 267–296, 2005 CORAL REEF PAPER

DEEP-WATER SINKHOLES AND BIOHERMS OF SOUTH FLORIDA AND THE POURTALÈS TERRACE — HABITAT AND FAUNA

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ABSTRACT

Only a small percentage of deep-water reefs have had their benthic and fish resources characterized. This study surveyed eight deep-water, high-relief, hard-bottom sites off south Florida using human occupied submersibles to characterize habitat and describe the fish and macrobenthic communities: the Naples deep-water sinkhole on the southwest Florida shelf, Jordan and Marathon deep-water sinkholes on the Pourtalès Terrace, and five high-relief bioherms on the Pourtalès Terrace. These submersible dives were the first to enter and explore any of these features. The upper sinkhole rims ranged from 175 to 461 m in depth and had a maximum relief of 180 m. The Jordan sinkhole may be one of the deepest and largest sinkholes known. The high-relief bioherms occurred at depths of 198–319 m, with a maximum height of 120 m. A total of 26 and 16 fish taxa were identified from the sinkhole and bioherm sites, respectively. Species of potentially commercial importance included tilefish, sharks, speckled hind, yellowedge grouper, warsaw grouper, snowy grouper, blackbelly rosefish, red porgy, drum, scorpionfish, amberjack, and phycid hakes. In total, 66 Porifera taxa were identified and four are possible new species. Twenty-one species of Cnidaria included Antipatharia (three spp.), stylasterid hydrocorals (five spp.), octocorals (11 spp.), and one scleractinian. The benthic communities of the Pourtalès Terrace bioherms differed from the bioherms along the northeastern Straits of Florida primarily in that the Pourtalès Terrace communities lacked the scleractinian coral *Lophelia pertusa* (Linnaeus, 1758) and stalked crinoids.

Deep-water reefs are sometimes referred to as coral banks, bioherms, or lithoherms (Teichert, 1958; Stetson et al., 1962; Neumann et al., 1977; Wilson, 1979; Reed, 1980; Friewald et al., 1997; Fosså et al., 2000; Paull et al., 2000). Rogers (1999) has suggested that deep-water coral banks, which are below the effective wave base, fall within the definition of a coral reef based on their physical and biological characteristics. Some deep-water reefs consist of caps of living coral on mounds of unconsolidated mud and coral debris, such as some *Oculina* and *Lophelia* coral bioherms (Reed, 2002b), whereas deep-water lithoherms are defined as high-relief, lithified carbonate limestone mounds rather than unconsolidated mud mounds (Neumann et al., 1977).

Various types of deep-water, high-relief bioherms are common off the southeastern U.S., along the base of the Florida-Hatteras Slope, the Blake Plateau, Straits of Florida, and eastern Gulf of Mexico. The Straits of Florida separate the Florida Platform from the Bahamas and Cuba and is bounded to the north by the northern limit of Little Bahama Bank and to the southwest by the termination of the Florida Keys off the Dry Tortugas (Malloy and Hurley, 1970). The majority of studies of the deep-water reefs in the western Atlantic and southeastern U.S. describe various aspects of their geology. Few studies focus on the ecology or biology of either the macrobenthic or fish communities. Detailed biological studies have concentrated on three areas: the Blake Plateau and, especially, the Charleston Bump (Sedberry, 2001); deep-water *Oculina* reefs off eastern Florida (Reed et al., 1982; Reed and Mikkelsen, 1987; Reed,

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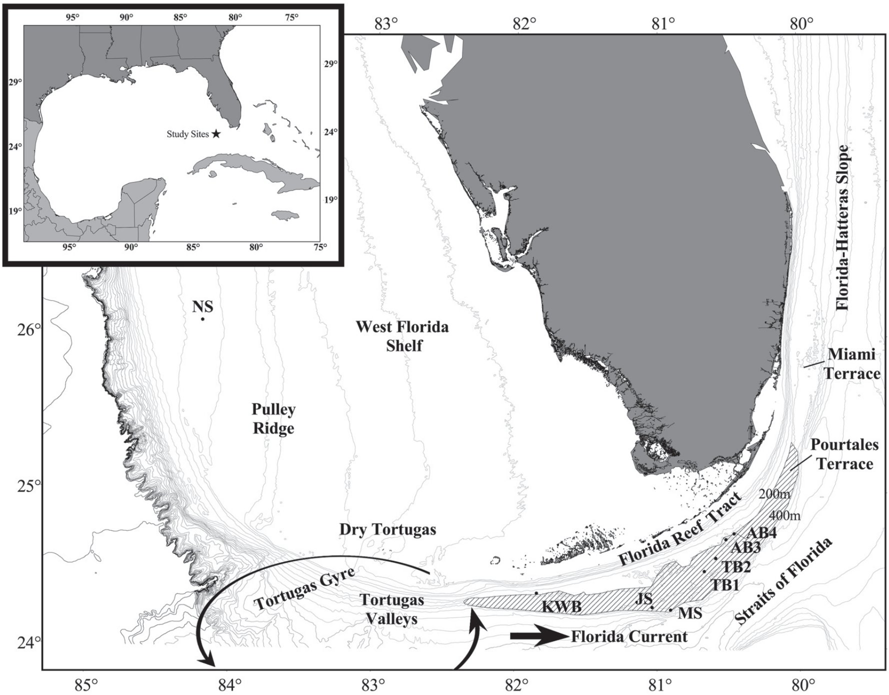

Figure 1. Bathymetry of the Straits of Florida, Pourtalès Terrace, and south Florida shelf with study site locations (NS = Naples sinkhole, JS = Jordan sinkhole, MS = Marathon sinkhole, KW = Key West bioherm, T1 = Tennessee Humps bioherm 1, T2 = Tennessee Humps bioherm 2, A3 = Alligator Humps bioherm 3, A4 = Alligator Humps bioherm 4).

2002a,b; Reed et al., 2005), and the deep-water lithoherms off Little Bahama Bank (Messing et al., 1990). Of these, only the Charleston Bump and *Oculina* studies provide data on associated fish communities. Some geological reports present limited data regarding the benthos: Florida-Hatteras Slope lithoherms (Paull et al., 2000), coral bioherms north of Little Bahama Bank (Mullins et al., 1981), Miami Terrace (Neumann and Ball, 1970; Ballard and Uchupi, 1971), Pourtalès Terrace (Gomberg, 1976), *Lophelia* reefs on the west Florida slope (Newton et al., 1987), and the west Florida Escarpment (Paull et al., 1984, 1990, 1991). Recent funding by NOAA's Office of Ocean Exploration has allowed more extensive surveys of the fish and macrobenthos associated with the deep-water *Lophelia* reefs on the Blake Plateau (J. Reed; S. Ross, UNC, Wilmington; G. Sedberry, S. Carolina Dept. Nat. Res., Columbia).

This study was undertaken to characterize the habitats, fish, and macrobenthic communities associated with deep-water, high-relief, hard-bottoms observed on the Pourtalès Terrace (southern Straits of Florida) and west Florida shelf (Gulf of Mexico). Eight study sites were surveyed with human-occupied submersibles: the Naples deep-water sinkhole on the southwest Florida shelf, Jordan and Marathon deep-water sinkholes on the Pourtalès Terrace, and five high-relief bioherm sites on the Pourtalès Terrace (Fig. 1).

Review of Deep-Water Bioherms off Florida

Deep-water *Oculina* coral reefs occur at depths of 70–100 m along the shelf-edge off central eastern Florida (Avent et al., 1977; Reed, 1980; Reed, 2002a; Reed et al., 2005). In contrast, *Lophelia*, *Enallopsammia*, and *Madrepora* scleractinian corals form reefs at greater depths, 490–870 m, on the Blake Plateau from Florida to North Carolina, in the Straits of Florida, and the eastern Gulf of Mexico (Stetson et al., 1962; Milliman et al., 1967; Uchupi, 1968, 1969; Neumann and Ball, 1970; Emery and Uchupi, 1972; Mullins et al., 1981; Newton et al., 1987; Reed, 2002b; Arendt et al., 2003). At the base of the Florida-Hatteras Slope, off northeastern Florida, Paull et al. (2000) described the geology of an extensive system of deep-water lithoherms with relief of 40–150 m at depths of 440 to > 900 m. They estimated that over 40,000 individual lithoherms may cover ~400 km^2 on the Blake Plateau and Straits of Florida, perhaps exceeding the areal extent of all the shallow-water reefs of the southeastern U.S. Farther south, in the northern Straits of Florida and west of Little Bahama Bank, Neumann et al. (1977) described a region of lithified carbonate mud and sand mounds at depths of 500–700 m. These lithoherms are up to 300 m long and 50 m high and provide habitat to a diverse community of corals, crinoids, and sponges (Messing et al., 1990).

Off southeastern Florida the continental slope is interrupted by two intermediate-depth terraces, the surfaces of which are composed of limestone outcrops of Eocene- to Miocene-age strata: the Miami and Pourtalès Terraces. Each has karst-like, high-relief topography, and deep-water sinkholes. The Miami Terrace is a 65 km long carbonate platform at depths of 200–400 m in the northern Straits of Florida, and consists of high-relief Tertiary limestone ridges, scarps, and slabs that provide extensive hard bottom habitat (Kofoed and Malloy, 1965; Uchupi, 1966, 1969; Uchupi and Emery, 1967; Malloy and Hurley, 1970; Neumann and Ball, 1970; Ballard and Uchupi, 1971). South of this, in the southern Straits of Florida and at the southern end of the Florida carbonate platform, the Pourtalès Terrace provides extensive, high-relief, hard bottom habitat, covering 3429 km^2 (1000 nmi^2) at depths of 200–450 m. The terrace parallels the Florida Keys for 213 km and has a maximum width of 32 km (Jordan, 1954; Jordan and Stewart, 1961; Jordan et al., 1964; Gomberg, 1976; Land and Paull, 2000). The terrace is bounded to the north by the sediment slope to the Florida Reef Tract and terminates to the south along the steep Pourtalès Escarpment (Gomberg, 1976). Louis de Pourtalès discovered the feature in 1867 during a survey aboard the U.S. Coast Survey ship BIBB to lay a telegraph cable from Key West to Havana (Jordan et al., 1964). Alexander Agassiz (1888) named this feature the Pourtalès Platform, and Jordan and Stewart (1961) later renamed it the Pourtalès Terrace.

The complex karst-like topography of the Pourtalès Terrace surface consists of Tertiary limestones. Highly phosphatized, biocalcarenite bedrock of Eocene age cropouts at depths > 350 m, whereas Miocene bedrock forms terraces at depths < 300 m. Unconsolidated Miocene-Pliocene deposits of marine vertebrate bones and cobble are scattered on top of the bedrock (Gomberg, 1976). Unconsolidated Quaternary sediments cover parts of the terrace at depths < 250 m, but the strong Florida Current prevents deposition of more than a thin sediment veneer over most of the terrace (Gomberg, 1976). High-relief, hard-bottom, topographic features consist of: A) a chain of sinkholes extending for ~100 km along the southwest margin; and B) numerous high-relief knolls and ridges on the mid-terrace (Jordan et al., 1964; Malloy and Hurley, 1970; Gomberg, 1976; Land and Paull, 2000).

Jordan (1954) first discovered the large sinkholes on the Pourtalès Terrace. Land and Paull (2000) mapped and described nine of these sinkholes using side-scan sonar, seismic profiler, and echo-sounder profilers aboard the U.S. Navy's submersible NR-1. The largest is the 1.2 km long Jordan sinkhole (first reported by Jordan et al., 1964), which consists of two circular, steep-walled depressions (maximum diameter 680 and 800 m) eroded into the terrace surface at a depth of 350 m. Its maximum vertical relief of 260 m is an order of magnitude greater than terrestrial sinkholes on the Florida Platform but similar in scale to the blue holes on the Bahamas Platform, the largest of which is the 202 m deep Dean's Hole on Long Island (Shinn et al., 1996). The Marathon sinkhole also consists of a pair of holes with 64 m maximum relief at a depth of 460 m.

The high-relief area of the middle and eastern portion of the Pourtalès Terrace is a 55 km long, northeasterly trending band of what appears to be karst topography that consists of depressions flanked by well defined knolls and ridges with maximum elevation of 91 m above the terrace (Jordan et al., 1964; Land and Paull, 2000). Farther to the northeast of this knoll-depression zone is another zone of 40 m high topographic relief that lacks any regular pattern (Gomberg, 1976).

West of the Pourtalès Terrace and near the western end of the Straits of Florida, the Tortugas and Agassiz Valleys exhibit hard-bottom habitats and high-relief escarpments at depths of 512–1189 m (Minter et al., 1975). Deep, hard substrates may also exist in 500–1000 m depths on the Tortugas Terrace, 80 km west of the Dry Tortugas (Uchupi, 1968).

The west Florida shelf in the eastern Gulf of Mexico is a broad carbonate platform that extends 750 km from DeSoto Canyon in the north to the western Straits of Florida and covers ~78,000 km^2 (Holmes, 1981). At the shelf break on the southwest Florida Platform, a series of ancient reef complexes and limestone outcrops of Pleistocene and possibly Miocene ages provide deep-water, hard-bottom habitat: Pulley Ridge forms a 100 km long, moderate relief reef at depths of 60–70 m with zooxanthellate scleractinian plate corals (*Agaricia* sp. and *Leptoseris* sp.) and macroalgae; Howell Hook crests at 130–150 m and a third lies between 210 and 235 m (Jordan and Stewart, 1961; Holmes, 1981; Halley et al., 2003). Seaward of the shelf, on the southwest Florida carbonate-ramp slope, a 20 km long zone of high-relief (10–15 m) Pleistocene coral mounds also provide habitat for coral and hard-bottom communities (Newton et al., 1987; Reed et al., 2004). The slope then grades into the Florida Escarpment, which extends from depths of 2500–3280 m into the eastern Gulf of Mexico. The face of the escarpment has steep vertical limestone cliffs of Cretaceous age, with intervening sediment-covered planes that also provide habitat for dense chemosynthetic communities (Paull et al., 1984; Paull and Neumann, 1987; Paull et al., 1990, 1991).

Materials and Methods

Human-occupied submersibles were used to conduct benthic surveys at eight high-relief bioherm and sinkhole sites on the west Florida shelf and the Pourtalès Terrace south of the Florida Keys. Harbor Branch Oceanographic Institution's (HBOI) R/V Edwin Link (Seward Johnson II) and R/V Seward Johnson supported the Johnson-Sea-Link (JSL) submersible in 1999 and 2004 and the Clelia submersible in 2001. These submersibles have an acrylic sphere (JSL) or hemisphere (Clelia) that provides > 180° visibility to the observers. Each was equipped with a manipulator arm (including a 20-cm clam-shell grab for sediment samples, jaw, and suction hose), twelve 12.7-l Plexiglas buckets, and a CTD data recorder (Seabird SBE 25 Sealogger) that continuously recorded time, temperature, conductivity, salinity, oxygen, and depth. The submersibles were equipped with sonar (Sunwest Technologies Super Search SS300), which employed CTFM (Continuous Transmission Frequency Modulated) sonar techniques to provide rapid scanning and high resolution.

Ship navigation utilized differential GPS (Magnavox MX 200 Global Positioning System), which has an estimated statistical positioning error of 1–5 m. Submersible navigation used Ultrashort Baseline Sonar (USBL) technology which consisted of ORE Trackpoint II Acoustic Positioning System and Integrated Positioning System (IPS) software that integrated the submersible's position relative to the ship and calculated the submersible's real time DGPS position throughout each dive. Analysis of USBL tracking accuracy for a worst-case tracking scenario estimated a maximum statistical positioning error of 9.6 m at a depth of 500 m (J. Kloske, Florida Institute of Oceanography, pers. comm.; Opderbecke, 1997).

At each dive site, profiles of bottom topography were made with the ship's echo sounder (SIMRAD EQ50 video echo sounder 38/50 kHz). Color videotapes (digital mini DV or high 8-mm) were recorded during dives with an external pan and tilt video camera (Sony DX2 3000A with Canon J8X6B KRS lens, 6–48 mm zoom, and 0.3 m minimum focus), which had parallel lasers (25 cm apart) for scale. Samples were photographed in situ with an external Benthos camera with 85-mm lens (Ektachrome ASA 100) on the JSL and with a hand-held Nikon Coolpix 990 digital camera inside the Clelia.

Specimens of dominant macroinvertebrate species (primarily sponges, cnidarians, mollusks, echinoderms, and bryozoans) along with sediment and rock samples were collected using the submersible's manipulator. Documentation of specimens included in situ videotapes and laboratory photographic images, museum voucher specimens, and detailed notes on habitat, which enabled habitat characterization and description of the benthic and fish communities. Taxonomic specimens, photographs, and videotapes are archived at HBOI's Museum for the Division of Biomedical Marine Research (DBMR). The collections of benthic specimens were not quantitative but primarily represented the dominant, large (> 5 cm), sessile organisms at the various sites. These taxa, for the most part, cannot be identified to the species level from the videotapes but generally require microscopic analysis of spicules (e.g., Porifera, Octocorallia). Video transects on some dives allowed for quantitative estimates of densities and sizes of benthic organisms. However, the quantification of densities from the videotapes was primarily at the higher taxa level (e.g., Porifera, stylasterid hydrocorals, Octocorallia). Although the primary objective for all dives was for biomedical research, not all dives recorded video that could be used for quantitative analyses of the benthos. Quantitative analyses of benthic cover was determined from transects in which the submersible was kept close to the bottom (< 1 m) and the video camera with lasers was angled down and zoomed in providing detailed imagery. Random video frames were selected from these transects for analyses, and the video camera's laser dots provided scale in each image to determine density and size of benthic taxa. Maximum and mean densities were calculated for dominant benthic taxa in various habitats (e.g., bioherm peak, bioherm flank and outcrops, sinkhole wall, and terrace pavement). Percent cover of hard substrate was determined by random point counts of grabbed image frames from the video transects. Qualitative estimates of fish populations were made visually by the observer in the submersible; the video camera's lasers were used to estimate size, and identifications were verified from the videotapes.

Results

Naples Sinkhole, Southwest Florida Shelf (Gulf of Mexico).—Three submersible dives (JSL II-3164, 3165, 3173; August 1999) were made in the Naples sinkhole (NS), which lies on the outer southwest Florida shelf, ~204 km (110 nmi) north of the Dry Tortugas and 241 km (130 nmi) west of Naples, Florida (Table 1).

Table 1. Site summary for deep-water sinkholes and bioherms off south Florida. NS = Naples Sinkhole, JS = Jordan Sinkhole, MS = Marathon Sinkhole, KW = Key West Bioherm, T1 = Tennessee Humps Bioherm 1, T2 = Tennessee Humps Bioherm 2, A3 = Alligator Humps Bioherm 3, A4 = Alligator Humps Bioherm 4.

Site reference	Depth (m)	Max. relief (m)	Width (m)	Temp. (°C) (surf.)	Current (cm s^{-1}) (direction to)	Salinity (surf.)	Oxygen (mg L^{-1}) (surf.)	Vis (m)	GPS coordinates
NS	230	–55	152 (152)	14.25 (30.14)	0–5 (180°)	35.87–35.91 (34.85)	2.99 (4.60)	9	26°05.1791′N 84°13.4678′W
JS	546	–180	229 (800)	10.90–11.40 (29.75)	10–15 (240°)	35.19–35.35 (35.60)	2.79–2.99 (4.48)	14	24°16.4241′N, 81°02.1846′W
MS	522	–61	610 (860)	8.60–8.95 (29.75)	5–45 (80°)	35.04–35.09 (35.80)	2.98–3.07 (4.39)	15	24°15.3289′N, 80°54.2705′W
KW	198	12	422	10.95 (30.12)	25–35 (70°)	35.25 (na)	2.93 (3.99)	10	24°21.8038′N, 81°50.7397′W
T1	319	120	574	11.63–12.44 (29.75)	0	35.50–35.60 (35.20)	3.20 (4.25)	15	24°30.1670′N, 80°40.1880′W
T2	213	85	1,613	10.00–12.63 (29.75)	5–15 (180°; 340°); 75–100 (120°)	35.25–35.78 (35.15)	2.95–3.00 (4.11)	15	24°35.2676′N, 80°35.3345′W
A3	217	62	678	10.00–11.50 (29.50)	20 to > 50 (80°)	35.30–35.40 (36.00)	na	15	24°42.4573′N, 80°31.0513′W
A4	213	48	1,778	10.00–10.75 (29.50)	40–60 (90°)	35.40 (35.60)	na	9	24°44.71′N, 80°27.59′W

Depth at base of bioherm or base of sinkhole; width at base of bioherm or base of sinkhole (width at top of sinkhole in parentheses); physical parameters are minimum values near the maximum depth (surface temperature, salinity, and oxygen in parentheses); vis = estimated horizontal visibility from submersible; coordinates are submersible GPS location at peak of bioherm or base of sinkhole; na = data not available.

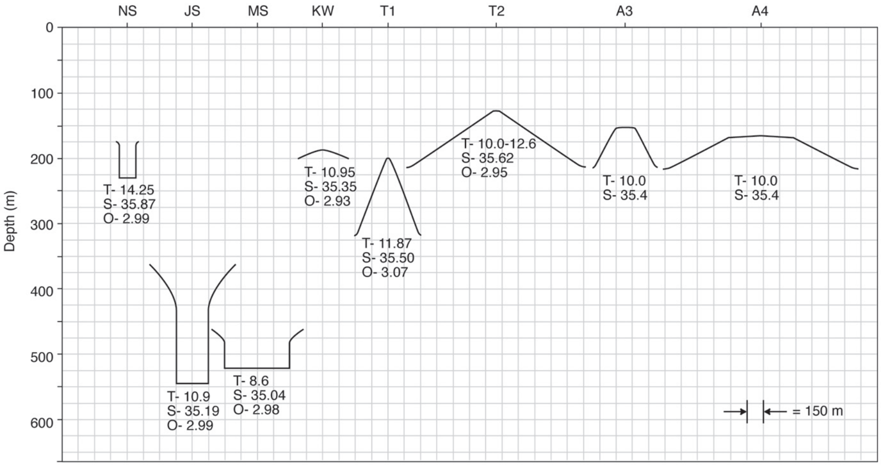

Figure 2. Schematic drawing of sinkholes and high-relief bioherms off south Florida comparing depth and width at top and base of each feature (x-axis grid marks = 150 m each; physical parameters are minimum values at base of feature, T = temperature °C, S = salinity, O = oxygen mg L^{-1}; NS = Naples sinkhole, JS = Jordan sinkhole, MS = Marathon sinkhole, KW = Key West bioherm, T1 = Tennessee Humps bioherm 1, T2 = Tennessee Humps bioherm 2, A3 = Alligator Humps bioherm 3, A4 = Alligator Humps bioherm 4).

Its geomorphology resembled that of shallow-water and terrestrial sinkholes on the Florida peninsula. The sinkhole, which lies on a relatively flat rock and sand bottom at a depth of ~175 m, had steep rocky walls and a maximum depth of 230 m with a maximum vertical relief of ~55 m (Fig. 2). Multiple fixes taken during the submersible's transect around the upper rim revealed a maximum diameter of 152 m from the NW to SW edge and a minimum of 91 m from the E to SW edge. The interior diameter at the maximum depth (230 m) was approximately 152 m as measured by the submersible's sonar.

The bottom of the sinkhole was sand, shell-hash, and rubble with no evidence of rock outcrops or crevices. At the SW base, the depth was shallower (210 m) and the wall had a 3-m rocky overhang at the interface with the flat sand bottom. The south rock wall was steepest with a 70°–90° slope. One rock (sample: 12-VIII-99-2-301), collected at 229 m from a rock outcrop on the vertical wall near the sand bottom, was a conglomerate that was heavily encrusted with serpulid polychaete worm tubes, bryozoans, and thin encrusting sponges. From 224 to 183 m, the rugged, irregular, and near vertical wall was pitted with 10–20 cm oval holes. The upper lip of the hole was vertical rugged rock, with 1–3 m outcrops. Overhangs on the wall occurred at 192–195 and 207 m. From 183 to ~175 m, was a 30°–60° slope with numerous < 1 m rock outcrops or boulders on a muddy-sand bottom. Surrounding the top edge at depths of 172–175 m, was 90% hard bottom, with < 1 m rock outcrops or boulders and 5–10 cm cobble. Further away from the top edge, the bottom was relatively flat silty-sand, with 30–60 cm scattered rock talus.

There was no evidence of salinity or temperature anomalies (such as an active seep or aquifer) within the hole; however, the submersible's CTD sensor was about 3 m off the bottom. In fact, temperature, salinity, and oxygen measurements were stable and consistent from the top to bottom of the hole (Table 1).

Dominant sessile macrofauna were predominately sponges with 14 taxa identified (Table 2). Around the upper edge, the dominant sponges (5–25 cm diameter) included Lithistida (cup-shaped *Corallistes* sp. and frilly-plate *Leiodermatium* sp.), Pachastrellidae, Axinellida, and Hexactinellida. Counts from video transects along the top edge of the sinkhole at 172 m, indicated maximum densities of 5–10 *Corallistes* m^{-2}. In addition, clusters of black comatulid crinoids (15 cm diam.) were common on the surrounding rock boulders along with slit shell gastropods (*Perotrochus amabilis*) and large spider crabs (*Mithrax*? sp., 12 cm carapace). No octocorals or scleractinians were observed along the top, but some stylasterid hydrocorals (5–10 cm tall) were present. Sponge diversity was greatest inside the sinkhole, on the vertical wall, where *Corallistes* spp. dominated along with Hexactinellida glass sponges (cup and trumpet, 25 cm) and various Demospongiae (*Strongylophora* sp., *Spongosorites* sp., Axinellida, and several species of Pachastrellidae). Small stylasterid hydrocorals were also common on the wall.

Fourteen species of fish were identified from the videotapes (Table 3). The largest concentration occurred around the top edge of the sinkhole. Species included schools of greater amberjack (*Seriola dumerili*) and anthiines (*Pronotogrammus martinicensis*, *Hemanthias vivanus*, *Anthias nicholsi*), red porgy (*Pagrus pagrus*), blueline tilefish (*Caulolatilus microps*), snowy grouper (*Epinephelus niveatus*, 50 cm total length (TL)), speckled hind (*Epinephelus drummondhayi*, 60 cm), Warsaw grouper (*Epinephelus nigritus*, 120 cm), green moray (*Gymnothorax* sp., 40 cm), yellowedge grouper (*Epinephelus flavolimbatus*, 80 cm), blackbar drum (*Pareques iwamotoi*), and bigeye soldierfish (*Ostichthys trachypoma*). Congregations of amberjacks and large groupers were estimated at 10–100 and 10–20 individuals, respectively.

JORDAN SINKHOLE.—Two submersible dives (JSL II-3175, 3176; August 1999) were made in the Jordan sinkhole (JS), a massive feature on the southern edge of the Pourtalès Terrace, ~45 km south of the Florida Keys (Table 1). The depth of the northern rim was 366 m, and the maximum depth recorded was 546 m, producing a vertical relief of ~180 m (Fig. 2). The sinkhole floor, ~229 m in diameter (measured by the submersible's sonar), was relatively flat and covered with coarse brown sediment consisting primarily of relatively fresh, unfossilized pteropods, echinoid spines, and mollusk shells (samples: 19-VIII-99-1-201; 19-VIII-99-2-201-203). Forty-one species of benthic mollusks (e.g., limpets, capulids, and vermetids) as well as some pelagic pteropods and heteropods were identified from sediment samples (P. Mikkelsen, American Museum of Natural History, pers. comm.).

On a transect up the north wall (JSL II-3175), a 50° rock slope extended from 546 to 534 m followed by a nearly vertical wall (80°–90°) to ~396 m. The bottom of the wall was fairly smooth, black rock but was rugged with cavities and crevices from 454 m upwards. From 396 to the upper lip of the north wall at 366 m, the substrate consisted of a 30°–50° rock pavement slope with 1 m rock outcrops and hummocks and hills of smooth pavement. On a 400 m long transect heading northeast away from the top edge of the hole from a depth of 366–328 m, the bottom was a 20°–30° rock pavement slope with thin sand veneer and some 1–2 m rock outcrops.

A second transect on the western wall along a heading of 300° (JSL II-3176) revealed a steep slope with 2–3 m boulders from 518 to 509 m followed by a smooth, near-vertical wall from 509 to 476 m. From 466 to 405 m, the wall varied from 70 to 90° slope, and was very rugged with vertical grooves and 1–3 m crevices. It was not possible to ascertain whether these crevices connected to passages into the rock substrate, and no openings were visible at the bottom of the hole. At 396 m, the 80° wall was smooth, without cavities or crevices. The top of the western wall was at a depth of ~375 m and formed a 0°–20° slope of smooth pavement pitted with 1 cm depressions. Near the upper edge, at a depth of 366 m, a 3 m^2 area of bottom was covered with 10–20 cm pieces of smooth, dark brown rock (sample: 19-VIII-99-2-302) that were later identified as lithified dugong rib bones, perhaps belonging to *Metaxytherium floridanum* Hay, 1992 (Dugonidae, Sirenia), a species common in the middle to late Miocene, 6.7–14.2 Ma b.p. (Domning, 1999; D. Domning, Howard University, pers. comm.). The bone fragments ranged from 10 to 13 cm long, 4–4.5 cm wide, and 2.7–3.0 cm thick. They were curved, thoroughly lithified, with a smooth, light and dark brown surface pitted with minute (< 0.5 mm) borings. The ends showed pore holes of the bone. Another boneyard of dugong rib bones was observed at a depth of 357 m. The smooth pavement continued in a series of low terraces to the end of the transect at a depth of 335 m, where the slope flattened out.

Physical parameters within the sinkhole were also relatively constant with no indication of active seeps (Table 1). Surface current was ~130 cm s^{-1} (2.6 kn) to the NE requiring a submersible launch ~1 km up current from the intended bottom target; however, current at the bottom of the hole was 15 cm s^{-1} toward 240° and was similar near the top edge of the hole.

Five cnidarian species and seven sponge species were collected (Table 2, Fig. 3). Along the lower wall, from 546 to 457 m, the rock was almost entirely encrusted with sponges, hydroids, octocorals, ascidians, and serpulid worms. The dominant sponges were yellow encrusting *Siphonodictyon* sp. (15 cm diameter), and various other Demospongiae (2–15 cm) with maximum densities ranging from 10 to 50 m^{-2} (Table 4). Dominant octocorals (5–25 cm tall) were *Plumarella pourtalesii*, *Swiftia casta*, and *Swiftia* new sp., in maximum densities of 1–10 colonies m^{-2} (hereafter col m^{-2}) . Other common invertebrates included anemones, slit shell gastropods (*Perotrochus midas),* cidaroid urchins, asteroids, and decapod crustaceans such as large 15 cm crabs, *Chaceon fenneri* (Manning and Holthuis, 1984), and galatheids. No stylasterids or colonial scleractinians were observed on the wall. On the upper wall, from 457 to ~384 m, where the wall was more rugged and irregular, sponges dominated and were more diverse. However, most were thinly encrusting and were not collected. Small octocorals (5 cm) were common in densities of 1–10 col m^{-2} and were accompanied by antipatharian black coral bushes (up to 1 m tall). The gastropod *P. midas* also occurred in this zone.

Nine species of fish identified in the videotapes were associated with the sinkhole (Table 3). Roughies (three species of Trachichthyidae), blackbelly rosefish (*Helicolenus dactylopterus*), and mora cod (*Laemonema melanurum*) dominated. Also present were cusk eels (Ophidiidae), silky sharks (*Carcharhinus falciformis*), and conger eels (Congridae). The roughies and mora were present at all depths along the sinkhole wall and at the bottom, but most fish were concentrated near the top of the hole. No large groupers were observed. A 2.5 m swordfish (*Xiphias gladius*), bleeding profusely from the stump of its broken spear, was also found lying on the bottom of the sinkhole. Two days earlier at the Key West site, 45 nmi to the west, a swordfish attacked the submersible, and a piece of its sword broke off in the hatch cover. It would have been quite serendipitous if this were the same fish. However, a swordfish with a broken spear was also observed near the bottom during the NR-1 submersible dives (C. Paull, pers. obs.), suggesting that this may not be an unusual phenomenon.

Table 2. Species list of macroinvertebrates associated with deep-water sinkholes and bioherms off south Florida. Sites: NS = Naples sinkhole; JS = Jordan sinkhole; MS = Marathon sinkhole; KW = Key West bioherm; B1–B4 = Bioherms 1–4. Phylum: CNI = Cnidaria; ECH = Echinodermata; MOL = Mollusca; POR = Porifera.

Phy	Taxonomy	Max depth (m)	Min depth (m)	NS	JS	MS	KW	B1	B2	B3	B4
CNI	*Antipathes rigida?* Pourtalès, 1868	319						X			
CNI	*Antipathes* sp.1	375			X						
CNI	*Antipathes* sp.2	470				X					
CNI	*Distichopora foliacea* Pourtalès, 1868	175								X	
CNI	Hydroida	202								X	
CNI	*Keratoisis flexibilis* (Pourtalès, 1868)	378			X						
CNI	*Muriceides* sp.	191					X				
CNI	*Paramuricea multispina* Deichmann, 1936	469	189		X	X	X				
CNI	*Paramuricea placomus* (Linnaeus, 1758)	470	462			X					
CNI	*Placogorgia mirabilis* Deichmann, 1936	212	172					X	X		X
CNI	*Placogorgia* nr. *mirabilis* Deichmann, 1936	172									X
CNI	*Pliobothrus echinatus* Cairns, 1986	175								X	
CNI	*Plumarella pourtalesii* (Verrill, 1883)	527	171		X				X		X
CNI	*Solenosmilia variabilis* Duncan, 1873	470				X					
CNI	*Stylaster erubescens* Pourtalès, 1868	186	175				X			X	
CNI	*Stylaster filogranus* Pourtalès, 1871	200	175					X		X	
CNI	*Stylaster miniatus* (Pourtalès, 1868)	200	175				X	X		X	
CNI	*Swiftia casta* (Verrill, 1883)	525			X						
CNI	*Swiftia* sp. (new sp?)	497			X						
CNI	*Thesea parviflora* Deichmann, 1936	183							X		
CNI	*Trachymuricea hirta* (Pourtalès, 1867)	468	462			X					
ECH	Crinoidea	172		X							
ECH	Holothuroidea	181								X	
MOL	*Entemnotrochus adansonianus* (Crosse and Fisher, 1861)	180							X		
MOL	*Perotrochus amabilis* (F.M. Bayer, 1963)	187	175	X					X		
MOL	*Perotrochus gemma* F.M. Bayer, 1965	174		X							
MOL	*Perotrochus midas* F.M. Bayer, 1965	393	375		X						
POR	*Aka* sp.	214	183							X	
POR	*Auletta* sp.	207	172								X
POR	*Auletta?* sp.	207								X	X
POR	Axinellida + *Plakortis* sp.	210								X	
POR	Axinellida?	201	187	X						X	
POR	Axinellidae	183	168							X	
POR	Axinellidae?	168								X	
POR	*Characella?* sp.	198								X	
POR	*Chondrosia?* sp.	300	297					X			
POR	Choristida	471	462			X					
POR	Choristida?	462				X					
POR	Choristida?, Pachastrellidae?	187							X		
POR	*Corallistes* sp.	261	172	X				X			
POR	*Corallistes* sp. or *Callipelta?* sp.	206							X		
POR	*Corallistes?* sp.	226						X			
POR	Corallistidae	466	186			X					X
POR	Demospongiae	530			X						
POR	Dictyoceratida?	172									X

Table 2. Continued.

Phy	Taxonomy	Max depth (m)	Min depth (m)	NS	JS	MS	KW	B1	B2	B3	B4
POR	*Echinodictyum* sp.	172	171								X
POR	*Echinodictyum?* sp.	172	171							X	X
POR	*Epipolasis* sp.	211								X	
POR	*Erylus transiens* (Weltner, 1882)	262						X			
POR	*Farrea* sp.	384	366		X						
POR	Geodiidae	191	184				X		X		
POR	Hadromerida	181	172	X							
POR	Hadromerida?	181		X							
POR	Halichondrida	260	174					X			
POR	Halichondrida or Haplosclerida	174		X							
POR	Halichondrida?	187		X				X			
POR	Haplosclerida + *Siphonodictyon?* sp.	543	187		X						
POR	Haplosclerida + *Spongosorites?* sp.	187							X		
POR	Haplosclerida?	184					X				
POR	Hexactinellida	464	186	X		X	X		X	X	
POR	*Hymedesmia* sp. 1	172									X
POR	*Hymedesmia* sp. 2	172									X
POR	*Leiodermatium* sp.	312	172	X					X	X	X
POR	*Leiodermatium* sp. or *Vetulina* sp.	312						X			
POR	Lithistida	310	172	X				X	X		
POR	Lithistida?	204		X							
POR	Mycalidae	312	284					X			
POR	*Oceanapia* sp.	172									X
POR	*Pachastrella* sp. or *Poecillastra* sp.	467				X					
POR	Pachastrellidae	470	166	X		X			X	X	X
POR	Pachastrellidae?	470				X		X			
POR	Petrosiidae	206	182					X		X	
POR	Petrosiidae?	182							X		
POR	*Phakellia* new sp. 1	171									X
POR	*Phakellia* new sp. 2	174									X
POR	*Phakellia* new sp. 3	174									X
POR	*Phakellia* sp.	470	171							X	X
POR	*Phakellia?* sp.	328			X	X		X			
POR	*Plakortis* sp.	312	220					X			
POR	*Plakortis?* sp.	312						X			
POR	Poecilosclerida?	212		X				X			
POR	Poecilosclerida	212	132						X	X	
POR	Raspailiidae	336			X						
POR	*Siphonodictyon?* sp.	543	490		X						
POR	Spirophorida	183							X		
POR	*Spongosorites* sp.	490	171	X							
POR	*Spongosorites?* sp.	490			X						X
POR	Stellettidae?	312						X			
POR	*Stellettinopsis?* sp.	198								X	
POR	*Strongylophora* sp.	197	184	X							
POR	Theonellidae	472	470			X					
POR	Theonellidae, new genus, new species	208	199					X	X		
POR	unid. Porifera 1	297						X			
POR	unid. Porifera 2	192							X		

Table 3. Species list of fish associated with deep-water sinkholes and bioherms off south Florida. Sites: NS = Naples sinkhole, JS = Jordan sinkhole, MS = Marathon sinkhole, KW = Key West Bioherm; B1–B4 = Bioherms 1–4.

Taxonomy	Family	Common name	Max depth (m)	Min depth (m)	NS	JS	MS	KW	B1	B2	B3	B4
Anthias nicholsi Firth, 1933	Serranidae (seabasses, groupers)	Yellowfin bass	191		X			X			X	
Antigonia capros Lowe, 1843	Caproidae (boarfishes)	Deepbody boarfish	213	174						X	X	X
Carcharhinus falciformis (Müller & Henle, 1839)	Carcharhinidae (requiem sharks)	Silky shark	522	335		X	X					
Caulolatilus microps Goode and Bean, 1878	Malacanthidae (tilefishes)	Blueline tilefish	198	172	X					X	X	X
Chlorophthalmus agassizi Bonaparte, 1840	Chlorophthalmidae (greeneyes)	Shortnose greeneye	522				X					
Congridae	Congridae (conger eels)	Conger eel	381			X						
Cookeolus japonicus (Cuvier, 1829)	Priacanthidae (bigeyes, catalufas)	Bullseye	171									X
Epinephelus drummondhayi Goode and Bean, 1878	Serranidae (seabasses, groupers)	Speckled hind	183		X							
Epinephelus flavolimbatus Poey, 1865	Serranidae (seabasses, groupers)	Yellowedge grouper	174		X							
Epinephelus nigritus (Holbrook, 1855)	Serranidae (seabasses, groupers)	Warsaw grouper	198	180	X						X	
Epinephelus niveatus (Valenciennes, 1828)	Serranidae (seabasses, groupers)	Snowy grouper	308	174	X			X	X	X		X
Galeus arae (Nichols, 1927)	Scyliorhinidae (cat sharks)	Marbled catshark	518				X					
Gephyroberyx darwinii (Johnson, 1866)	Trachichthyidae (roughies)	Big roughy	518	392		X						
Gymnothorax cf. *funebris* Ranzani, 1840	Muraenidae (moray eels)	Moray	187	174	X							
Helicolenus dactylopterus (Delaroche, 1809)	Sebastidae (rockfishes)	Blackbelly rosefish	381	189		X	X	X			X	
Hemanthias sp.	Serranidae (seabasses, groupers)	Streamer bass	194	174	X						X	
Hemanthias vivanus (Jordan & Swain, 1885)	Serranidae (seabasses, groupers)	Red barbier	191	168	X						X	
Hoplostethus mediterraneus Cuvier, 1829	Trachichthyidae (roughies)	Silver roughy	461			X						
Hoplostethus sp.	Trachichthyidae (roughies)	Roughies	496	189		X		X				
Laemonema melanurum Goode and Bean, 1896	Moridae (codlings)	Codling	546	186		X	X	X	X		X	
Nezumia sp. (3 spp. – *N. bairdii, N. aequalis,* or *N. atlantica*)	Macrouridae (grenadiers)	Grenadier	502	472			X					
Ophidiidae	Ophidiidae (cuskeels)	Brotula	469	375		X	X					
Ostichthys trachypoma (Günther, 1859)	Holocentridae (squirrelfishes)	Bigeye soldierfish	180		X							
Pagrus pagrus (Linnaeus, 1758)	Sparidae (porgies)	Red porgy	175		X							
Pareques iwamotoi Miller and Woods, 1988	Sciaenidae (drums)	Blackbar drum	183		X							
Plectranthias garrupellus Robins and Starck, 1961	Serranidae (seabasses, groupers)	Apricot bass	172									X
Pronotogrammus martinicensis (Guichenot, 1868)	Serranidae (seabasses, groupers)	Roughtongue bass	212	168	X				X		X	X
Scorpaenidae	Scorpaenidae (scorpionfishes)	Scorpionfish	186					X				
Seriola dumerili (Risso, 1810)	Carangidae (jacks)	Greater amberjack	187	175	X					X		
Urophycis sp.	Phycidae (phycid hakes)	Phycid hake	297						X			
Xiphias gladius Linnaeus, 1758	Xiphiidae (swordfishes)	Swordfish	518			X						

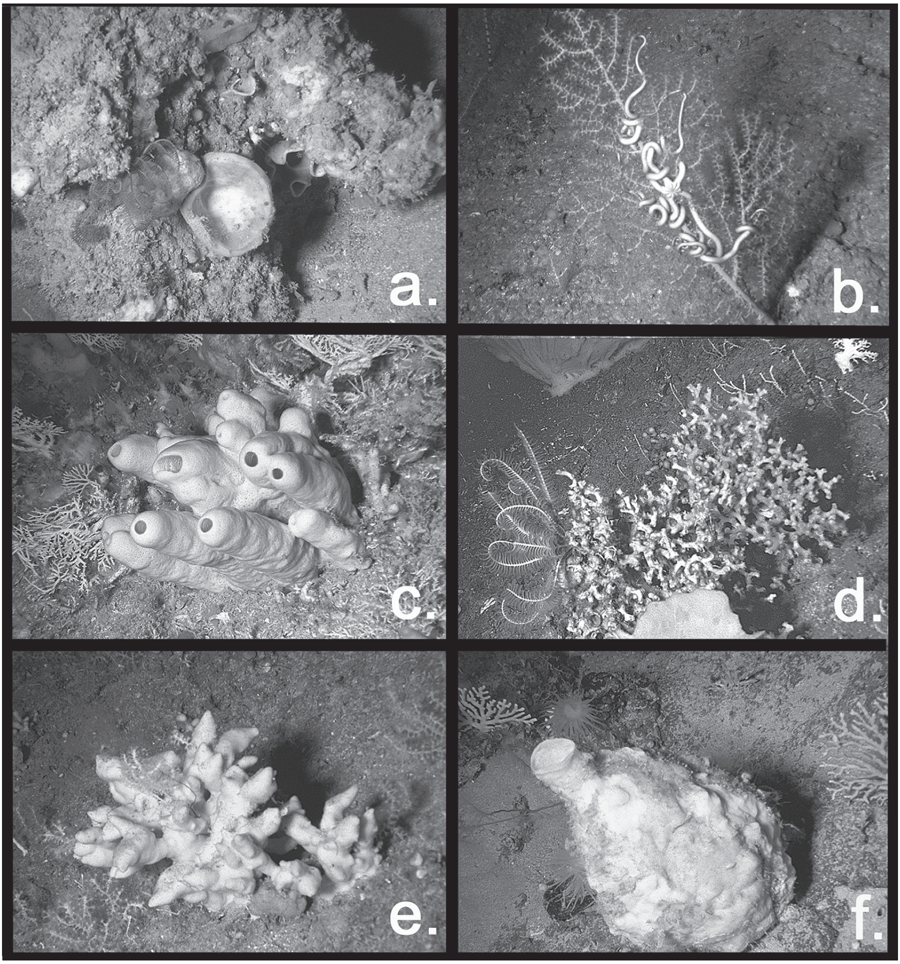

Figure 3. Dense communities of stylasterid hydrocorals, sponges, and octocorals associated with sinkholes and high-relief bioherms off south Florida (a = *Corallistes* sp. cup sponge, top edge of Naples sinkhole, 174 m; b = *Paramuricea multispina* octocoral with *Asteroschema* sp. brittlestar, Jordan sinkhole, 470 m; c = Petrosiidae sponge, bioherm 1, 199 m; d = *Solenosmilia variabilis* coral with crinoid, Marathon sinkhole, 470 m; e = Pachastrellidae sponge, Marathon sinkhole, 468 m; f = Haplosclerida sponge, Key West bioherm, 184 m).

Marathon Sinkhole.—Two submersible dives (JSL II-3177, 3178; Aug. 1999) were made in the Marathon sinkhole (MS), which lies near the outer southern edge of the Pourtalès Terrace, ~7.4 nmi east of Jordan sinkhole (Table 1). The maximum depth in the hole was 522 m. The top edge depth varied from ~461 to 470 m; thus maximum relief was ~61 m (Fig. 2). A fathometer transect from the west to east top edge showed a diameter of 382 m. On dive JSL II-3177, a transect was made down a steep 80° SE wall from 461 to 522 m, across the bottom of the sinkhole on a heading of 320°, and up the NW wall. The submersible's sonar indicated a maximum diameter of 610 m across the base of the hole on this heading. At the base of the NW wall a 15 m long, steep sand slope, was followed by a 20° rock slope to about 503 m. At 488 m the rock wall was very steep (60°–90°), continuing to the top edge where the slope decreased to 20°–30°. The top edge at 470 m was smooth pavement with 50 cm outcrops and ledges of black phosphoritic crust.

Table 4. Maximum densities of macrobenthic taxa associated with deep-water sinkholes and bioherms off south Florida and lithoherms off Little Bahama Bank (number of colonies m^{-2}; P = present but not able to ascertain densities; N = not present; % = Messing et al. (1990) study gives % of frequency of appearance in 35 mm photos).

Site	Adjacent pavement	Terrace slope	Peak plateau	Sinkhole wall	Sinkhole upper rim
Naples sinkhole				5 *Corallistes* Stylasterid - P	5–10 *Corallistes* Stylasterid - P
Jordan sinkhole	1–2 *Phakellia* 5–10 Stylasterid Octocorallia- N			10–50 Porifera Stylasterid - N 1–10 Octocorallia	10 Stylasterid 1–10 Octocorallia
Marathon sinkhole				1 Porifera Stylasterid - P 1–10 *Paramuricea placomus*	1–5 Porifera Stylasterid - P 25 Octocorallia
Key West bioherm		1 Porifera 10 Stylasterid 1–2 Octocorallia			
Tennessee Humps bioherm 1		1–2 Porifera 1–10 Stylasterid 10–80 Octocorallia	1–10 Porifera 10–80 Stylasterid Octocorallia - P		
Tennessee Humps bioherm 2	Porifera- few 1–20 Stylasterid Octocorallia - N	50-80 Octocorallia	Stylasterid - P		
Alligator Humps bioherm 3, North		1–2 Porifera 5–20 Stylasterid	1–2 Porifera 9–10 Stylasterid		
Alligator Humps bioherm 3, South			16–80 Porifera ($x = 27$) 16–96 Stylasterid ($x = 47$)		
Alligator Humps bioherm 4		1–5 Porifera Stylasterid - P	80 *Plumarella pourtalesii* 16–48 *Placogorgia mirabilis* 16–64 Porifera ($x = 30$) 32–80 Stylasterid ($x = 43$) 16–48 Octocorallia ($x = 21$)		
Bahamas lithoherms (Messing et al., 1990)	94.7% Porifera 85.8% Stylasterid	82.3% Porifera 120–150 m^{-2} knob/lump Porifera 73.1% Stylasterid 8–12 m^{-2} Stylasterid 20 m^{-2} *Plumarella pourtalesii*	72.1% Porifera 54.1% Stylasterid		

At a depth of 522 m, the sinkhole floor varied from flat sand and shell hash with some 10 cm sand waves, to areas of flat rock pavement with < 1 m conglomerate boulders and 30 cm ledges. Near the center of the hole the bottom was flat sand with a series of 50 cm tall parallel ridges of sand and cobble that were about 3–6 m apart. The cobble (sample: 20-VIII-99-2-202) proved to be petrified rib bones of dugong. These were dark brown, ~13 cm long, 3.5–4.0 cm wide and 2.5 cm thick. One pile of petrified dugong rib bones was found scattered over an area ~18 m in diameter. Sediment (sample: 20-VIII-99-2-201) from this site was coarse, dark brown sand consisting primarily of echinoid spines, pteropods, foraminiferans, mollusks, and stylasterid coral fragments.

Physical parameters were relatively constant within the sinkhole and were similar but cooler than the Naples and Jordan sinkholes (Table 1). Current at the bottom of the hole was 5 cm s^{-1} to 80°; however, a strong, gusty, and variable current of 25–45 cm s^{-1} was observed near the top lip downwelling into the hole.

Benthic collections resulted in five species of cnidarians and nine sponges (Table 2, Fig. 3). Near the base of the wall (488–518 m), octocorals and sponges were the dominant sessile fauna. Sponges, which occurred at maximum densities of about 1 col m^{-2}, included *Corallistes* spp. (cups and plates, 5–15 cm diameter), *Phakellia* sp. leaf sponges (25 cm), and Astrophorida plate sponges (15 cm). Octocorals (25–75 cm), Antipatharia bushes (0.5–1.0 m tall), and stylasterid hydrocorals (5 cm) were all common. At 488 m on a smooth 80° rock wall, Lithistida plate and cup sponges (10–25 cm) along with octocorals (*Paramuricea placomus,* 10 cm) were abundant (1–10 col m^{-2}; Table 4). On the upper slope and top edge from 471 to 461 m, sponges and octocorals were very abundant. Dominant sponges occurred at maximum densities of 1–5 m^{-2} and consisted of *Theonella* sp. knobs, *Phakellia* sp. fans, Pachastrellidae, and Hexactinellida. Octocorallia (5–30 cm tall) reached densities up to 25 col m^{-2}, and dominant species included *Trachymuricea hirta, P. placomus,* and *Paramuricea multispina*. Other cnidarians were antipatharian black coral (50 cm) and stylasterids (5–10 cm). Several colonies of the scleractinian *Solenosmilia variabilis* (25 cm) along the top edge represented the only colonial scleractinian coral found at any of these dive sites (Fig. 3). Decapod crustaceans included 15 cm galatheids and large crabs, probably *C. fenneri.*

Seven species of fish were identified from the submersible videotapes in and adjacent to the sinkhole (Table 3). Mora cod (*L. melanurum*), marbled catshark (*Galeus arae*), rattails, and grenadiers (Macrouridae) dominated. Also noted were several silky sharks (*C. falciformis*), blackbelly rosefish (*H. dactylopterus*), shortnose greeneye (*Chlorophthalmus agassizi*), and brotulids (Brotulidae). Most of these species were present at all depths of the sinkhole from the top edge to the base of the wall. No large grouper were observed.

Key West Karst Bioherm.—A single submersible dive (JSL II-3174; Aug. 1999) was made on the Key West bioherm (KW), a low to moderate relief mound of hard bottom habitat (Table 1). The total E–W transect was 422 m and ranged from 186 to 198 m depth (Fig. 2). The geomorphology consisted of low (< 1 m) and moderate (2–3 m) relief rock ledges forming a series of terraces mostly from 186 to 191 m. The ledges were eroded features, consisting of thin rock crust (8 cm thick), usually undercut at the edge, with 1–3 m relief on the eroded side. The majority of the bottom was rock pavement with a thin sediment veneer and numerous shallow (2–3 m) apparent sinkholes or karst-like formations with sand-mud bottoms. Percent cover of exposed rock bottom ranged from 30% to 100%. In the flat areas with sediment cover were 20 cm tall sand waves. One rock sample was collected at 189 m in a region of rock pavement, low relief ridges, and karst topography. It was a conglomerate, with irregular surface and encrusted with serpulid polychaete tubes and sponges (sample: 17-VIII-99-1-301).

The predominant macrobenthic species consisted of stylasterids, octocorals, and sponges (Table 2). The greatest densities of these taxa were on the rock terraces and near the ledge edges. Orange and white stylasterids (5–25 cm tall), *Stylaster erubescens* and *Stylaster miniatus*, reached maximum densities of 10 col m^{-2} (Table 4, Fig. 4). Dominant octocorals (20 cm tall) included *Muriceides* sp. and *P. multispina* in densities up to 1–2 col m^{-2}. Sponges, in densities up to 1 m^{-2}, consisted of Geodiidae (20 cm diameter), Haploslcerida, and at least two species of Hexactinellida glass sponges (one a mass of tubes and one clusters of stalked spheres).

The few fish identified from the videotapes were mostly associated with the relief structures such as the ledges or karst features and included snowy grouper (*E. niveatus*), yellowfin bass (*A. nicholsi*), blackbelly rosefish (*H. dactylopterus*), roughies (*Hoplostethus* spp.), Scorpaenidae, and Moridae (Table 3).

TENNESSEE HUMPS, BIOHERM 1.—Bioherms 1–4 are high-relief, hard-bottom features that are spread over 37 km (20 nmi) of the central and eastern portion of the Pourtalès Terrace, approximately 37 km south of Long Key and south of Tennessee Reef. Two submersible dives (JSL II-3179, 3180; Aug. 1999) were made on bioherm 1 (T1) (Table 1). It had a minimum depth of 199 m and maximum depth of 319 m at the eastern base, and thus a maximum relief of 120 m (Fig. 2). The width of the mound at the base from north to south was ~574 m. At the base were slabs of broken rock, 2–3 m diameter and 30 cm thick on a very rugged, karst-like topography, with 1–2 m relief. The lower flank of the eastern face was a 10°–20° slope of smooth rock pavement with 5–10 cm deep erosional features and < 1 m boulders. A series of terraces started at a depth of 284 m on a 20°–30° rock pavement slope, with 1–2 m vertical faces below each terrace. The terraces were pock-marked with 10–20 cm erosional features similar to karst topography. Near the top of the mound, from 203 to 199 m, the bottom was nearly flat, irregular rock with 50 cm relief, and was covered with piles of live and dead stylasterid coral. A 30° slope continued down the opposite side of the mound.

On the lower slope and base from 319 to 274 m, the dominant cnidarians were stylasterids (5–15 cm tall; 1–10 col m^{-2}, max. density) and *Antipathes rigida* (75 cm tall). Sponges of 10–25 cm diameter occurred in maximum densities of 1 col m^{-2} and included Pachastrellidae, *Leiodermatium* sp., *Chondrosia* sp., *Plakortis* sp., Stellettidae, Mycalidae, and various Lithistida (Tables 2 and 4; Fig. 4). On the upper slope and terraces from 274 to 213 m, sponge densities were 1–2 m^{-2} and included *Erylus* sp. (possibly a new species), *Corallistes* sp., *Plakortis* sp., *Leiodermatium* sp., Halichondrida, and Poecilosclerida. At 206 m, octocorals became dominant on the rocky slope with dense populations of *Placogorgia mirabilis* (10 cm) and Primnoidae (15 cm; 10–80 col m^{-2}, max. density). Fields of stylasterids covered the top of the mound at 197 m, accompanied by a few octocorals. Thick piles of dead and live 5–15 cm tall *S. miniatus* and *Stylaster filogranus* covered nearly 100% of the bottom in some areas, and densities of live colonies ranged from 10 to 80 m^{-2}. Also on the top of the mound, sponges occurred in densities of 1–10 col m^{-2}; dominant species were large

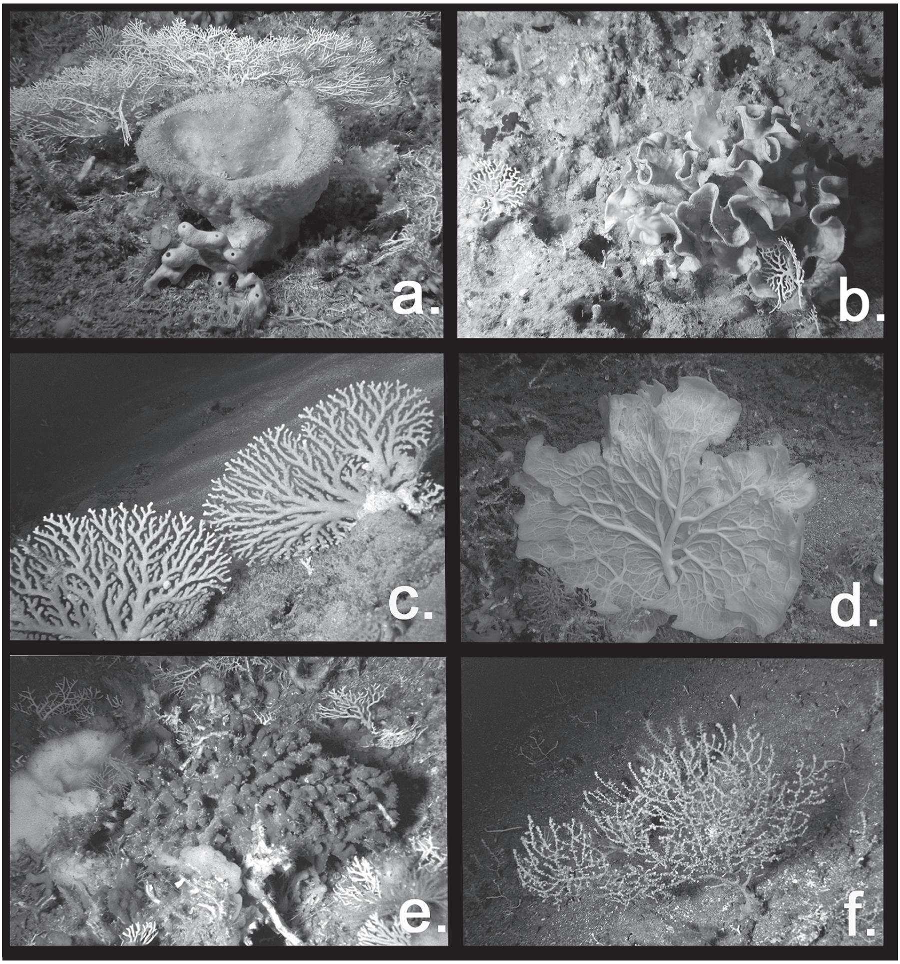

Figure 4. Dense communities of stylasterid hydrocorals, sponges, and octocorals associated with sinkholes and high-relief bioherms off south Florida (a = Choristida vase sponge, *Stylaster filogranus* hydrocoral, bioherm 1, 173 m; b = *Leiodermatium* sp. sponge, bioherm 1, 295 m; c = *Stylaster miniatus* hydrocoral, Key West bioherm, 186 m; d = *Phakellia* sp. sponge, bioherm 4, 171 m; e = Theonellidae new genus, new sp. sponge, bioherm 1, 200 m; f = *Paramuricea placomus* octocoral, Marathon sinkhole, 462 m).

Phakellia sp. fan sponges (~1 m in width), *Geodia* sp. (50 cm), Petrosiidae, and a new species of Theonellidae.

The few fish observed on the submersible's videotapes consisted of four species: a snowy grouper (*E. niveatus*) and phycid hake (*Urophycis* sp.) near the base of the mound, and roughtongue bass (*P. marinicensis*) and mora (*L. melanurum*) in rock cavities near the top (Table 3).

Tennessee Humps, Bioherm 2.—Bioherm 2 (T2) is a high relief, double peaked, hard bottom mound that lies ~13 km NE of bioherm 1. Three dives were made on the North and South Peaks (JSL II-3181 and 3182, Aug. 1999; Clelia 599, Aug. 2001). The top of South Peak was 128 m, North Peak was 131 m, and the linear distance between the two peaks was 1538 m (Table 1; Fig. 2). Maximum relief was ~85 m. The slope of the mound varied from ~10° to 20° at 183 m to 40° to 50° on the upper flanks and consisted mostly of hard bottom with low relief ledges. The South Peak had a rounded peak of stylasterid debris, ~15 m in diameter (Fig. 3). The eastern base of the mound was 213 m, the west base was 198 m, and the E–W width was 1613 m. The bottom adjacent to the mound was relatively flat and consisted of rock pavement with coarse sand, low ridges of < 30 cm relief, and some areas of parallel, linear 1 m tall ridges covered almost entirely with stylasterid coral.

Minimum bottom temperature was 12.6° in August of 1999 and 10.0 °C in August of 2001 (Table 1). A strong thermocline was encountered on the flank of the mound where the temperature jumped from 12.8 °C at 184 m to 15.27 °C at 182 m. This site is near the axis of the Florida Current and surface currents exceeded 150 cm s^{-1} (3 kn). Bottom currents were quite variable; dive JSL II-3181 reported bottom current at the base of the mound at 5 cm s^{-1} to the south and the second dive reported 15 cm s^{-1} to 340° whereas CLELIA 599 had to abort the dive when bottom currents exceeded ~100 cm s^{-1} (2 kn) to 120°. Currents on the flank and top of the mounds ranged from 40 to > 50 cm s^{-1}. The strong currents on the upper flanks and top of the mound also prevented submersible operations except for a brief look.

Significant areas of exposed hard bottom with low relief outcrops surrounded the mound. Some areas had parallel 1 m high ridges covered with stylasterid coral rubble and live colonies (5–20 cm) in densities of 1–20 m^{-2}. These flats had no octocorals and only a few sponges (Table 2). Areas of rock pavement on the lower flanks from 218 to 183 m were dominated by octocorals, stylasterids, and sponges. In this region the octocoral populations were dense (50–80 col m^{-2}, max. density) and included *P. mirabilis*, *P. pourtalesii*, and *Thesea parviflora*. Thirteen taxa of sponges were identified including a possible new species of Theonellidae, *Corallistes* sp., *Pachastrella* sp., Lithistida, Geodiidae, and *Neofibularia* sp. (1 m diameter). The upper slope also included *Leiodermatium* sp. frilly plate sponges, Hexactinellida vase sponges, Petrosiidae, and Spirophorida. Motile invertebrates included slit shell gastropods (*P. amabilis*, *Entemnotrochus adansonianus*), spider crabs, and sea stars. Only four fish species were identified from the videotapes, all on the lower mound flanks: deep-body boarfish (*Antigonia capros*), snowy grouper (*E. niveatus*), blueline tilefish (*C. microps*), and greater amberjack (*S. dumerili*, 10–20 individuals; Table 3).

ALLIGATOR HUMPS, BIOHERM 3 AND 4.—Bioherms 3 (A3) and 4 (A4) are among dozens of bioherms that lie in a region ~5.6 × 18.5 km (3 × 10 nmi) called "The Humps" by local fishers, ~26 km south of the Florida Keys and south of Alligator Reef (Table 1; Fig. 2). Three dives were made on A3 (CLELIA 597, 598, 600; Aug. 2001), approximately 16 km NE of bioherm 2. A3 consisted of two peaks 1.9 km apart with a maximum relief of 62 m. The North Peak's minimum depth was 155 m (submersible DGPS: 24°42.4573′N, 80°31.0513′W) and was 653 m wide at the base, which was 217 m deep at the east base and 183 m at the west side. The minimum depth of South Peak was 160 m and was about 678 m in width E–W at the base. The surrounding habitat adjacent to the mounds was flat sand with about 10% cover of rock pavement. From 213 m to the top, generally on the east flank of the mound, were a series of flat rock pavement terraces at depths of 210, 203, 198, 194, 183, and 171 m and the top plateau was at 165 m. Between each terrace was a 30°–45° slope consisting of either rock pavement or coarse sand and rubble. Below each terrace was a vertical scarp of 1–2 m where the sediment was eroded away leaving the edge of the terrace exposed as a horizontal, thin, rock crust overhang of < 1 m and 15–30 cm thick. The top of the bioherm was a broad plateau of rock pavement with 50%–70% exposed rock, few ledges or outcrops, and coarse, brown sand. Less time was spent on the western side, which was more exposed to the strong bottom currents. The west side of South Peak sloped more gradually than the eastern side, had more sediment, and no ledges were observed.

A4 is 7.4 km NE of A3 and consisted of a very complex geomorphology. Four fathometer transects revealed three adjacent plateaus; East Peak, West Peak, and North Peak, each about 168–183 m on top, and separated by a narrow valley cut to depths of 213–229 m. North Peak was the smallest with a minimum depth of 177 m on top. East Peak was a broad t-shaped plateau with a minimum depth of 171 m that was at least 1.8 km in width, E–W, and had a sharp escarpment to 229 m on the east side. East Peak and West Peak were ~0.8 km apart and separated by a narrow channel 213 m deep.

Two submersible dives (Clelia 601, 602; Aug. 2001) were made on the West Peak of A4. The plateau of West Peak was 733 m long, N–S, with a minimum depth of 165 m. Between West Peak and East Peak was a 200–300 m wide valley, which was likely an erosional feature, and consisted of a flat sand bottom with some rock pavement and rubble. The eastern face of West Peak, from 213 to 183 m, was a 10°–20° slope of rubble, rock, and sand with a series of 15 m wide terraces. The terraces were generally flat, smooth, rock pavement with a thin veneer of coarse, brown sand. Some areas had 1–2 m slabs of rock with 30–60 cm relief that apparently had slumped down-slope. The upper slope was steeper, from 45° to 60°, with rock slabs and rubble. The eastern edge along the top of the plateau at 174 m consisted of a 15–30 cm thick rock crust, which was undercut from erosion and extended out 1–2 m from the edge. Below this was a 2–3 m vertical escarpment, which graded into the eastern slope. The wide plateau on top of A4 was generally flat rock pavement, with few low relief ledges or outcrops, and coarse, brown sand. Video counts on top indicated an average of 21% cover (range 0%–50%) of exposed rock pavement.

Physical parameters for both A3 and A4 were similar (Table 1). No oxygen sensors were available for these dives. Bottom currents were 20–30 cm s^{-1} to 80° at the base of the mound and 40 to > 50 cm s^{-1} at the peak.

The benthos at both A3 and A4 was dominated by sponges, octocorals, and stylasterids (Table 2; Fig. 4). No colonial scleractinians were encountered. Sponges identified from collections included 28 taxa. The five species of stylasterids were *Distichopora foliacea*, *Pliobothrus echinatus*, *S. erubescens*, *S. filogranus*, and *S. miniatus*. On the flat pavement adjacent to the base of the mounds, stylasterids and antipatharian black coral bushes were common along with sea urchins and sea stars. On North Peak of A3, the benthos cover on the lower slope at 213 m was < 10% and consisted of small sponges, including *Phakellia* sp., Pachastrellidae, and Hexactinellida, along with octocorals, stylasterids, and rock shrimp. The first terrace at 210 m had stylasterids (5–20 cm tall; 20 col m^{-2}, max. density) and Demospongiae (5–20 cm diameter; 1–2 m^{-2}). Another terrace at 203 m was dominated with bushy clumps of hydroids (10 cm; 1–5 m^{-2}). From 198 to 168 m the terraces had 10%–30% of live cover, including Petrosiidae tube sponges, *Leiodermatium* sp. frilly plates, clusters of Hexactinellida tube sponges, Pachastrellidae plates, and spherical sponges, *Aka* sp. and *Geodia* sp. No octocorals, black coral, or colonial scleractinians were encountered in this region. The flat top at 165 m of A3's North Peak was covered with dense populations of sponges and stylasterids, all oriented perpendicular to the prevailing current from the SW. Video counts showed live cover ranging from 10% to 50%, and exposed rock pavement was 50%–70%. Stylasterid (5–25 cm tall) maximum densities ranged from

9 to 10 col m^{-2}, and densities of Demospongiae (5–25 cm) were 1–2 m^{-2}. Also present were large axinellid fan sponges (60 cm wide and 20 cm tall), *Echinodictyum* sp. lacey fans, and *Auletta* sp. tube sponges.

On South Peak of A3, a 250 m wide plateau was encountered at 198 m. Video counts on top of this plateau showed live cover ranging from 0% to 90%. Dominant benthic species were 3–4 taxa of stylasterid corals, bushy hydroids, and at least six species of large Demospongiae including *Phakellia* sp., *Hymedesmia* sp. (yellow and blue species encrusting on dead stylasterids), Axinellida, and Pachastrellidae. Maximum densities of stylasterids ranged from 16 to 96 col m^{-2}. Demosponge densities ranged from 16 to 80 m^{-2}; Table 4).

On the east-facing slope of West Peak of A4, most of the sponges were associated with the terraces or slumped rock slabs. On the steep scarp just below the top plateau and also attached to the underside of the plateau's crust edge were various Lithistida sponges including *Leiodermatium* sp. On the plateau top, between 171 and 174 m, the dominant sponges were 25–50 cm tall Axinellida, a possibly new species of *Phakellia* sp. fan sponge, *Spongosorites* sp. yellow cake sponges, *Echinodictyon* sp. lacy fans, *Auletta* sp. tubes, *Oceanapia* sp. vase sponges, *Geodia* sp., and blue and yellow encrusting *Hymedesmia* sp. Dominant octocorallia included *P. pourtalesii* (80 col m^{-2}, max. density) and *P. mirabilis* (16–48 m^{-2}; Table 4). Video counts from transects on top of the plateau found stylasterid corals in maximum densities of 32–80 col m^{-2}, 16–64 col m^{-2} of Demospongiae, 16–48 col m^{-2} of octocorallia, and clusters of 10 cm tall hydroid bushes (16–80 m^{-2}). Percent live cover on exposed hard bottom was 0%–50%. Other motile macroinvertebrates that were common on the plateau included large *Rochinia* sp. crabs and the sea urchin *Coelopleurus floridanus* Agassiz, 1872.

Twelve species of fish were encountered during dives at the A3 and A4 (Table 3). The dominant species included large Serranidae, Warsaw (*E. nigritus*, 50 cm), and snowy groupers (*E. niveatus*); small serranids including yellowfin bass (*A. nicholsi*), red barbier (*H. vivanus*), apricot bass (*Plectranthias garrupellus*), and roughtongue bass (*P. martinicensis*); also deepbody boarfish (*A. capros*), blackbelly rosefish (*H. dactylopterus*), mora (*L. melanurum*), and blueline tilefish (*C. microps*, 40–50 cm). Most of the snowy grouper (5–10 individuals) were seen along the sharp scarp of the eastern edge of the top plateau, and the tilefish resided in holes eroded into the rock on the slope face.

Discussion

Sinkhole Geomorphology.—These submersible dives were the first to enter and explore the insides of these deep-water sinkholes. During the geological surveys by Land and Paull (2000), the NR-1 submarine dived ~50 m above the seafloor adjacent to the sinkholes and visual observations were not made inside either the JS or MS. Although this earlier report provided excellent details of the bathymetry of the holes from side-scan and echo-sounder surveys, differences in tracking and navigation of the NR-1 and our submersibles resulted in some variation in the exact coordinates of the sinkholes between the two studies.

Land and Paull (2000) reported that the maximum depth of the JS west lobe was 610 m and the east lobe was 520 m, whereas we found the greatest depth was 546 m. Because of the depth and steep interior walls of the hole, echo-sounder records of the

NR-1 had numerous side echoes, which obscured the actual bottom reflections. At the top of the sinkhole, the long axis of the holes were 680 and 800 m, respectively, or a total of 1480 m in diameter (Land and Paull, 2000). We found the internal diameter at the base of the hole to be 229 m in diameter. Thus the JS may be the largest and deepest marine sinkhole in the world.

The MS is also a massive feature, with a maximum width of 860 m at the top of the hole (Land and Paull, 2000) and 610 m diameter at the bottom (present study). The NR-1 recorded a maximum depth of 524 m for the MS; in the present study a maximum depth of 522 m (61 m of relief) was recorded. Both of these holes apparently have partially filled in with Recent sediments and Tertiary deposits from the surrounding terrace. The sediment samples from the base of the hole consisted primarily of relatively fresh pteropod, echinoid, and mollusk skeletal grains. The presence of the petrified dugong rib bones in the center of the MS, however, is difficult to explain. This area had piles of cobble and bones but was distant from the edge where the Tertiary lag deposits could have slumped. Scattered throughout the Pourtalès Terrace are Miocene-Pliocene deposits of marine vertebrate bones (dugong), shark teeth, coprolites, and phosphatized limestone cobble (Gomberg, 1976) and our dives also found dugong bones on the terrace slope adjacent to the sinkholes. It is not likely that currents could move these heavy deposits. In contrast to the JS and MS, the NS occurred at a shallower depth (175 m), but it was smaller in diameter (152 m at the bottom), and no dugong deposits were found.

Whether these sinkholes are still active or when they ceased development is uncertain. There was no evidence of salinity or temperature anomalies (such as an active seep or aquifer) within the holes; however, the submersible's CTD sensor was about 3 m off the bottom. In fact, temperature, salinity, and oxygen measurements were very stable and consistent from the top to bottom of the holes. Also we did not see evidence of crevice openings in the bottom of the sinkholes but in general they appeared to be filled in with sand and cobble. Early researchers concluded that the Tertiary limestones of the Pourtalès Terrace were formed in shallow seas but that post-Miocene sea level lowering exposed the terrace allowing solution and collapse of underlying limestone (Jordan, 1954; Jordan et al., 1964). However, more recent studies suggest that these sinkholes were probably formed in the marine environment (Malloy and Hurley, 1970; Land et al., 1995; Land and Paull, 2000). Sea level lowstands were never great enough to expose the terrace; they were at the most 125 m below present levels during the late Pleistocene (Fairbanks, 1989) and prior to that the lowest stand was in the late Miocene (~10 Ma b.p.) when sea level was 75–125 m lower than present (Hallam, 1992). Also regional subsidence during Cenozoic was ~20 m Ma^{-1} (Freeman-Lynde et al., 1981). Land and Paull (2000) calculated that the combination of sea level lowstands and subsidence places the late Miocene shoreline at ~300 m below present. The depths of the top of both JS and MS are greater than that, at 366 and 461 m, respectively.

Formation of sinkholes in marine environments has been explained by the Kohout Convection Principle (Kohout, 1965; Kohout et al., 1988; Land and Paull, 2000), which postulates that cool seawater of the Straits of Florida seeps into the permeable limestone of the Tertiary Floridan Aquifer and flows inland. Geothermal heating causes this to migrate upward into the fresh ground water and the mixture discharges from submarine springs on the shelf edge. Kohout hypothesized that the submarine karst topography on the shelf and terraces are the result of the freshwater and saltwater mixing zone dissolution at sites of groundwater discharge (Land and Paull, 2000). Although the hydraulic head of the Floridan Aquifer in the Florida Keys is currently inadequate for submarine discharge, sea level lowstands in the Pleistocene may have resulted in sufficient hydraulic head to discharge at depths of 600 m (Land et al., 1995).

Bioherm Geomorphology.—Although the Pourtalès Terrace bioherms that were surveyed may be termed either bioherms or lithoherms, their development and internal structure are still unknown. Gomberg (1976) showed that the Pourtalès Terrace consisted of Tertiary limestones with some unconsolidated Miocene-Pliocene and Quaternary deposits on top. He concluded that high-relief pinnacles or knolls were karst topographic features formed from exposure to fresh water during the middle to late Miocene. However, he found no Tertiary rocks in his dredge samples from the knolls and suggested that the antecedent karst topography had been accentuated by accumulation of Quaternary material in that region. He also found skeletal debris of various colonial scleractinia including *Lophelia prolifera* [=*pertusa*] Linnaeus, 1758, *Madrepora exigua* [=*carolina*] (Pourtalès, 1871), and *Madrepora candida* [=*oculata*] Linnaeus, 1758, and stylasterid hydrocorals. He concluded that Quaternary deposition rates on the terrace were low and that accumulation rates were probably the highest in both the Pleistocene and Recent times on the high-relief knolls region but that the encrusting organisms were not abundant or productive enough to add significantly to the lithified Quaternary accumulation. Although we did not find evidence of *Lophelia* or *Madrepora* corals, we did find dense accumulations of living and dead stylasterid corals, tens of centimeters thick, on the tops and flanks of these mounds. Without coring the interior of these mounds, it is impossible to ascertain to what degree these mounds were formed by erosion and dissolution versus buildup by accumulation of biological skeletal materials.

The five Pourtalès Terrace bioherms are somewhat similar in morphology. The flanks generally consist of a series of terraces of limestone pavement, with vertical scarps on a slope of 20°–45°. The eastern flanks tend to be steeper and have more rock outcrops and terraces, whereas the west flanks appear to have more sediment and fewer ledge outcrops. Since the prevailing bottom currents appear to be from the southeast, the eastern flank is in the lee of the current. Strong downwelling currents and eddies form at the peaks and result in erosion under the edges of the limestone crusts on each limestone terrace. The peaks and terraces, however, are generally fairly smooth limestone pavement with little evidence of erosional features. The peaks are generally broad plateaus of fairly low relief limestone pavement, ranging from nearly a mile wide at A4 to a narrow rounded crest of only 15 m diameter at T2.

The Pourtalès Terrace bioherms are similar in morphology to the lithoherms described by Paull et al. (2000) at the base of the Florida-Hatteras slope off northern Florida and Georgia which are calcareous coral-capped mounds with relief of 40–150 m at depths of 440 to > 900 m. The individual mounds range from 100 to 1000 m long and 300 m wide. The mounds have steep (30°– 60°) slopes armored by outcropping crusts. In places the lithified crusts are eroded at the edges leaving exposed, undercut slabs, 20–30 cm thick, some of which are broken and slumped. Thickets of coral (*Lophelia pertusa* and *Enallopsammia profunda*), 1 m thick, cap the tops and southern flanks which face the prevailing currents. Except for the lack of *Lophelia* and dominance of stylasterid corals on the Pourtalès bioherms, the gross morphology of these two types of lithoherms is strikingly similar.

In contrast, the lithoherms on the eastern side of the Florida Straits, west of Little Bahama Bank, are mounds 50 m high and 300 m long at depths of 500–700 m, but are nearly completely lithified on the exterior (Neumann et al., 1977; Messing et al., 1990). They are composed of hardened concentric crusts of lithified muddy carbonate and appear to be constructed by subsea lithification of successive layers of trapped sediment and skeletal debris. They are capped by living *Lophelia pertusa* thickets and are also steep-sided: 20°–30° and up to 60° with some vertical scarps. Some flanks that are exposed by erosion show a series of overlapping concentric crusts, 10–30 cm thick. Neumann et al. (1977) concluded that the lithoherms on the eastern side of the Straits of Florida are more lithified than the western side due to hydrographical differences. They suggested that the ascending water on the east side of the Gulf Stream (Florida Current) results in reduced pressure and increased temperature which promotes increase of supersaturation of the CO^2 system and precipitation of cements.

It appears that the mounds on the Miami Terrace, Pourtalès Terrace and north Florida, all on the western side of the Florida Current, are intermediate in degree of lithification compared to those on the eastern side. In addition, mud mounds capped with thickets of live *Lophelia* coral occur at the base of the Florida-Hatteras slope off Miami (Neumann and Ball, 1970) and east of Cape Canaveral (Reed, 2004). These are the *Lophelia* banks of classic morphology, which show no signs of lithification but apparently are mounds of coral debris and mud, and capped with live coral (Teichert, 1958; Mullins et al., 1981). The *Oculina* banks along the east Florida shelf break are also primarily mud mounds capped with live coral (Reed, 1980).

Fish Communities.—In total, 31 fish taxa, of which 24 were identified to species level, were found to be associated with the deep-water sinkholes and high-relief bioherms on the south Florida shelf (Table 3). Few studies have directly documented deep-water fish associations with deep-water reef habitats in the western Atlantic. Most of the work in this region has concentrated on the Charleston Bump region of the Blake Plateau off Georgia and South Carolina (Sedberry, 2001). The following species were common to both the deep-water *Lophelia* reefs on the Blake Plateau off the Carolinas and those of this study: shortnose greeneye (*C. agassizi*), blackbelly rosefish (*H. dactylopterus*), roughies (*Hoplostethus* sp.), mora (*L. melanurum*), grenadiers (*Nezumia* spp.), and swordfish (*X. gladius*) (S. Ross, UNCW, pers. comm.).

Of the eight sites surveyed, six fish species were found exclusively on the west Florida shelf in association with the NS: speckled hind (*E. drummondhayi*), yellowedge grouper (*E. flavolimbatus*), green moray (*Gymnothorax* sp.), bigeye soldierfish (*O. trachypoma*), red porgy (*P. pagrus*), and blackbar drum (*P. iwamotoi*). This site is the shallowest of all the sites, and these species are also common on the shallower shelf-edge reefs in that region. Other species were exclusively found associated with the JS and MS; these included cusk eels (Ophidiidae), silky shark (*C. falciformis*), shortnose greeneye (*C. agassizi*), congrid eels (Congridae), marbled catshark (*G. arae*), big roughy (*Gephyroberyx darwinii*), and macrourid grenadiers (*Nezumia* spp.). Species most common to the high-relief bioherms included deepbody boarfish (*A. capros*), blueline tilefish (*C. microps*), snowy grouper (*E. niveatus*), and roughtongue bass (*P. martinicensis*). Some species were common at the sinkhole and bioherm sites and included snowy grouper (*E. niveatus*), blackbelly rosefish (*H. dactylopterus*), and mora (*L. melanurum*).

Although the video transects were not quantitative for fish counts, the Naples sinkhole appeared to have the greatest density and diversity of fishes. Twenty-six fish taxa were identified from all of the sinkhole sites and the Naples site had 14 species. In contrast, all five bioherm sites had a total of 16 taxa. Species of potential commercial importance included tilefish (*C. microps*), sharks (Carcharhinidae), speckled hind (*E. drummondhayi*), yellowedge grouper (*E. flavolimbatus*), Warsaw grouper (*E. nigritus*), snowy grouper (*E. niveatus*), blackbelly rosefish (*H. dactylopterus*), red porgy (*P. pagrus*), drum (*P. iwamotoi*), scorpionfish (Scorpaenidae), amberjack (*S. dumerili*), and phycid hakes (*Urophycis* sp.). However, the fish densities that we saw at any of the sites were insufficient to suggest commercial harvest. In fact, any of the features, both sinkholes and bioherms, could be overfished very easily since only a few individuals of the larger grouper species (*Epinephelus* spp.) were present at any one site.

BENTHIC COMMUNITIES.—The samples of macrobenthic organisms that were collected from the sinkholes and bioherms, although not quantitative, were representative of the community for the dominant, large (> 5 cm), sessile organisms that were directly associated with these features. Thinly encrusting organisms were not collected due to the difficulty of sampling these with the submersible's manipulator arm. This species list is by no means inclusive of the total benthic diversity of the region. The vast majority of knowledge of the diversity and taxonomy of marine organisms in the Straits of Florida comes from dredge collections and historical records (Pourtalès 1868, 1871; Cairns, 1979). However, dredge and trawl records cannot identify the exact location of the samples and most likely none were made on the steep, rocky walls of the sinkholes or from underneath the rock ledge overhangs of the bioherms as was possible with the submersibles. Also the submersibles allowed for direct measurements of benthic population densities and microhabitat associations of the individual species.

The deep-water Porifera found in association with the high-relief sinkholes and bioherms in this study was the most diverse group of all the macrobenthos. This taxonomically diverse group is also one of the least known and many of the taxa are in various stages of revision. As a result many of the sponge species could only be identified to higher taxa at this time. Those identified as "taxa(?)" are specimens that were similar to that taxa but some characteristics were incongruent. In total, 66 distinct sponge taxa were identified of which 33 were to genus or species level. Four were possible new species. Thirteen sponge taxa were found solely in the sinkholes and not on the bioherms and six of these were only associated with the NS. These included *Siphonodictyon* sp., *Pachastrella* sp., *Strongylophora* sp., Raspailliidae, and two Hadromerida. Possible new species of *Phakellia* sp. and Theonellidae were found exclusively on the bioherms. Although Gomberg (1976) reported at least six taxa of sponges in the dredge and sediment samples, he did not identify them to species. Messing et al. (1990) provided the most detailed of lithoherm-associated sponges in this region off Little Bahama Bank. They identified 18 taxa (of which seven were identified to genus level) that primarily dominated the crinoid-alcyonarian zone on the downcurrent side of the lithoherms. Sponges common to both these lithoherms and the Pourtalès Terrace sites included *Phakellia* sp., *Geodia* sp., *Corallistes* sp., and various Lithistida, Pachastrellidae, and Hexactinellida. They are also present on the lithoherms off north Florida and Blake Plateau (Reed, 2004).

Twenty-one taxa of Cnidaria were sampled or observed and 16 were identified to species level. These included three species of antipatharian black coral, five stylasterid hydrocorals, 11 octocorals with one possible new species, and one scleractinian

(*S. variabilis*). It is noteworthy that no Cnidaria were observed in association with the NS. Eight species were associated only with the Pourtalès Terrace sinkholes and not the bioherms; these included two species of antipatharians; the octocorals *P. placomus*, *P. pourtalesii*, *T. hirta*; and the scleractinian *S. variabilis*. Gomberg's (1976) geological samples on the Pourtalès Terrace listed six species of stylasterid corals and 18 species of scleractinian corals of which seven species of stylasterid and 15 species of Scleractinia were identified from the Pourtalès (1868, 1871) dredgings. Although Gomberg (1976) found evidence of skeletal remains of the colonial scleractinians *Lophelia* and *Madrepora* in sediment samples from the terrace, we did not observe any colonies at our dive sites. Both *Lophelia* and *Madrepora* occur on the mud mounds off the Miami Terrace at depths of 825 m (Neumann and Ball, 1970) whereas *Lophelia* and *Enallopsammia* are the dominant corals at the base of the Florida-Hatteras slope on the mud mounds off Cape Canaveral (Reed, 2004) and the lithoherms off north Florida at depths of 440 to > 990 m (Paull et al., 2000). On the eastern side of the Straits of Florida, *L. prolifera* (=*L. pertusa*) is the sole colonial coral on these lithoherms at depths of 600–700 m (Messing et al., 1990). Dead *Lophelia* rubble covers the entire upcurrent end of these lithoherms, and scattered live colonies cover the rampart of dead coral on the upcurrent crests. On the downcurrent side of these lithoherms, in the crinoid-alcyonarian zone, stylasterid hydrocorals are a dominant component along with the primnoid octocoral *P. pourtalesii*.

The densities of sponges, stylasterid hydrocorals, and octocorals were very high, especially on the plateaus and terraces of the bioherms on the Pourtalès Terrace. Maximum densities of sponges (> 5 cm) on the plateaus ranged from 1 to 80 col m^{-2}. Stylasterid coral densities ranged from 9 to 96 col m^{-2} and octocorals 16–48. Densities of sponges (1–2 col m^{-2}) and stylasterids (1–20) also dominated the terraces and slopes of the bioherm sites but generally in lower densities than the peak plateaus whereas the octocorals generally had higher densities on the flanks (1–80 col m^{-2}). The walls of the sinkholes were also densely encrusted with sponges, stylasterids, and octocorals, except for the NS, which lacked octocorals. Densities of demosponges on the sinkhole walls and upper rims ranged from 1 to 50 col m^{-2} and gorgonians were 1–25 col m^{-2}. Although stylasterids were present they were in much lower densities than found on the bioherms. The only other study to detail densities and biozonation of organisms on deep-water reefs in the West Atlantic is on the Bahamian lithoherms (Messing et al., 1990). They found maximum densities of small, unidentified lump and knob sponges ranging from 120 to 150 col m^{-2}, stylasterids 8–12 m^{-2}, and the primnoid octocoral *P. pourtalesii* 20 m^{-2}.

Crinoids, which are a dominant feature of the lithoherms in the eastern Straits of Florida (Messing et al., 1990), were absent from the Pourtalès Terrace sites, but were present at the NS. Crinoid skeletal debris was not listed by Gomberg (1976) from the Pourtalès Terrace sediments but he did report that several 30 cm stalked crinoids were dredged. Smaller comatulida crinoids, *Coccometra hagenii* (Pourtalès, 1867) and *Comatonia cristata* (Hartlaub, 1912), may also be locally abundant at locations along the inner and outer edges (Gomberg, 1976; C. Messing, Nova Southeastern Univ., pers. comm.). Messing et al. (1990) reported that the stalked crinoid-alcyonarian zone dominated the flanks and downcurrent crests of the Bahamian lithoherms. Stalked crinoids also appear to be missing or not a dominant component on other deep-water lithoherms on the west side of the Florida Current. They are not reported on the Miami Terrace (Neumann and Ball, 1979), the lithoherms of north Florida (Paull et al., 2000), or the *Lophelia* mud mounds off Cape Canaveral (Reed, 2004).

The major difference between the benthic communities of the Bahamian lithoherm site (Messing et al., 1990) and the Pourtalès Terrace bioherms is the relative lack of scleractinian corals; e.g., *Lophelia,* and stalked crinoids on the Pourtalès Terrace. The current conditions at both the eastern and western side of the Straits of Florida are similar and certainly conducive for these filter feeding crinoids and corals. Messing et al. (1990) reported that the mean current velocity in their study area was 10–20 cm s^{-1} to the north and at the crests of the lithoherms it occasionally exceeded 100 cm s^{-1} (2 kts). They considered that the currents played the dominant role in benthic zonation on these reefs. Currents on the Pourtalès bioherms also ranged from 0 to 60 cm s^{-1} near the bases, and often was 50–100 cm s^{-1} at the peaks.

Differences in current regimes and source of larvae may be other factors affecting the distribution of these benthic communities. The bottom currents on the eastern side of the Straits of Florida appear to be northerly (Neumann and Ball, 1979; Messing et al., 1990). However off Miami, on the Miami Terrace, dives with the BEN FRANKLIN submersible reported southerly currents of 8–10 cm s^{-1} on the west side of the terrace and a northerly current on top (Neumann and Ball, 1979). They concluded that this could be a counterclockwise gyre in the western Straits. Farther to the west of Pourtalès Terrace, in the Tortugas and Agassiz Valleys, ALVIN submersible dives also recorded a westerly flowing current of 9–23 cm s^{-1} at 430 m (Minter et al., 1975). They suggested that the morphological features of the bottom in these valleys indicated that the predominant flow had been to the east (in the direction of the Florida Current in this region) but apparently does reverse on occasion.

Perhaps these differences in currents on the eastern and western sides of the Straits of Florida affect larval distribution. Sources of *Lophelia* larvae occur upstream of these sites, in the Loop Current of the Gulf of Mexico. Live *Lophelia* thickets were reported from recent ROV dives on deep-water lithoherms at depths of 500 m off the west Florida shelf (Newton et al., 1987; Reed et al., 2004). It is not known how long larvae of deep-water *Lophelia* remain in the planktonic stage, although recent studies on deep-water *Oculina varicosa* Lesueur, 1821 coral reported that the planulae larvae may live at least 21 d before settlement (Brooke and Young, 2003). If *Lophelia* has a similar larval history, perhaps the gyres on the western side of the Straits of Florida prevent the larvae from reaching the Pourtalès Terrace. Cyclonic gyres off the Dry Tortugas may persist for several months before moving into the Straits and begin to decrease in size (Lee and Williams, 1999). It may be possible that these re-circulating gyres, which are on the Florida side of the Florida Current axis, may cause the retention of pelagic larvae and prevent them from immediately entering the Florida Current from the Loop Current (Fig. 1). Whereas larvae entering the Straits of Florida further seaward and in the main axis of the Florida Current may bypass these cyclonic gyres and move quickly upstream. Whether this is truly a factor affecting *Lophelia* larvae is only speculative until further data is compiled on the deep bottom currents and larval history.

Temperature may be another factor affecting the benthic communities on the western and eastern sides of the Straits of Florida. Messing et al. (1990) reported bottom temperatures of 10–12 °C on the Bahamian lithoherms, which is within the range of temperatures on the Pourtalès Terrace. However, cold water upwelling events are known to occur on the west side of the Straits of Florida along the east Florida shelf but are not known on the eastern side off the Bahamas. These episodic events are known to affect the deep-water *Oculina* reefs off central Florida (Reed, 1981, 1983) and also occur in the Florida Keys and Pourtalès Terrace (Smith, 1982; Lee and Williams, 1999; Leichter et al., 2003). Although our CTD records from the submersible dives recorded temperatures on top of the terrace ranging from 10 to 12.6 °C, bottom temperatures within the Marathon sinkhole were somewhat colder at 8.6 °C. Temperatures at the base of the Straits of Florida are 5–6 °C (Messing et al., 1990), so it may be possible that episodic upwelling events could affect organisms on the terrace. However, these temperatures should still be within the optimal range for *Lophelia*, which is 3–12 °C for the species and is known to occur at depths as shallow as 55 m in the Norwegian fjords (Teichert, 1958; Cairns, 1979; Roberts et al., 2003).

Although it is estimated that the Straits of Florida and Blake Plateau may have over 40,000 individual deep-water reefs or lithoherms covering an area of 400 km^2 (Paull et al., 2000), the great majority of this region has not been mapped adequately or explored visually by submersibles or ROVs. Certainly < 0.1% have ever been observed. Considerable differences exist among the various high-relief, hard-bottom sites: from *Lophelia* capped mud mounds and rocky lithoherms to stylasterid capped bioherms of the Pourtalès Terrace. The United Nations General Assembly recently reiterated its call for urgent consideration of ways to integrate and improve, on a scientific basis, the management of risks to the marine biodiversity of seamounts, cold-water coral reefs, and certain other underwater features (resolution 58/240 of 23 December 2003, paragraph 51). Recently over 1100 scientists from 69 countries have signed a consensus statement asking national and international governmental agencies to act urgently to protect these imperiled deep-sea ecosystems.

Acknowledgments

The crews of the R/V Edwin Link (Seward Johnson II), R/V Seward Johnson, and the Johnson-Sea-Link and Clelia submersibles are gratefully thanked for their logistical support, without which these surveys would not have been possible. Harbor Branch Oceanographic Institution (HBOI) provided funding for these cruises. We are especially grateful to all the personnel of the Division of Biomedical Marine Research at HBOI who are responsible for various aspects of research during these cruises. We thank additional taxonomic expertise provided by K. Reutzler and S. Cairns (National Museum of Natural History), C. Messing (Nova Southeastern University), M. Kelly (NIWA), G. Gilmore (ECOS), and R. Robbins (RSMAS). D. Domning (Howard University) kindly provided identification of the petrified dugong bones. P. Mikkelsen (American Museum of Natural History) identified molluscan fauna from sinkhole sediment samples. S. Ross (UNCW) provided fish identifications for deep-water *Lophelia* reefs on the Blake Plateau. J. Saint (HBOI) provided the line drawings. S. Reed (Smithsonian Marine Station), L. Land (New Mexico Bureau of Geology and Mineral Resources), and C. Messing are thanked for their comments and reviews on drafts of the manuscript. This is HBOI Contribution Number 1586.

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Date Submitted: 20 August, 2004. Date Accepted: 24 January, 2005.

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