BULLETIN OF MARINE SCIENCE, 84(1): 67–92, 2009 CORAL REEF PAPER

SHELF-EDGE AND UPPER-SLOPE REEF FISH ASSEMBLAGES IN THE SOUTH ATLANTIC BIGHT: HABITAT CHARACTERISTICS, SPATIAL VARIATION, AND REPRODUCTIVE BEHAVIOR

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ABSTRACT

Submersible video, supplemented with sonar surveys, was analyzed for habitat characteristics and variation of fish assemblages in shelf-edge and upper-slope reefs within proposed marine protected areas off the southeastern United States. Distinct fish assemblages were found between shelf-edge and upper-slope dive locations. Shelf-edge reefs were further categorized into morphology types, which were empirically defined based on rock shape and the amount of relief present. Variation in fish density was contrasted among the six reef morphology types observed: slab pavement, blocked boulders, buried blocked boulders, low-relief bioeroded rock, moderate-relief bioeroded rock, and high-relief bioeroded rock. High-relief bioeroded rock was the most densely populated reef morphology type when compared to all others. Four species had significantly varying densities on different reef morphology types, with three species having higher densities on structurally complex morphologies when compared to low-relief morphologies. Several other species also had significantly varying densities among different shelf-edge dive locations, with dive locations containing complex reef morphology types (high-relief bioeroded rock and blocked boulders) being more densely populated than dive locations containing low-relief morphology types. Reproductive behavior was incidentally observed for five commercially-important fish species at all dive locations. This study provides information on factors relevant to the placement of marine protected areas (MPAs), including reef morphology descriptions, areas of high fish density and diversity, and important spawning habitat locations. Our data also provide a habitat-specific baseline for monitoring the effects of MPAs on fish assemblages in the South Atlantic Bight (SAB).

The outer continental shelf and upper slope off the southeastern United States include a variety of bottom habitats and oceanographic features that influence the species composition, abundance, and life history of fishes throughout the region. The area known as the South Atlantic Bight (SAB) includes the coastal ocean region between Cape Hatteras, North Carolina, and Cape Canaveral, Florida. The SAB is bounded on the east by the Gulf Stream and is strongly influenced by this current and its interaction with seafloor topography and adjacent shelf waters (Schwartz, 1989; Lee et al., 1991; Bane et al., 2001). The Charleston Bump, a major topographic feature on the slope, deflects the Gulf Stream offshore, resulting in eddies, meanders, and cold water upwelling and intrusions shoreward across the shelf edge (Bane et al., 2001; Sedberry et al., 2001). Upwelling in eddies advects nutrients from the depths into euphotic zones, creating highly productive areas (Lee et al., 1991; Weaver and Sedberry, 2001). Combined with these areas of high productivity, complex bottom topography within the SAB provides habitats that support many ecologically and economically important reef fish species, such as snappers, groupers, and porgies (Koenig et al., 2000; Sedberry et al., 2001; Quattrini et al., 2004). Many of these species live and spawn on rocky reefs on the edge of the continental shelf and upper continental slope.

Many populations of economically valuable reef fishes in the South Atlantic Bight are considered overfished, undergoing overfishing, or have experienced decreased landings over time (Collins and Sedberry, 1991; Cuellar et al., 1996; Haedrich, 1998; McGovern et al., 1998; Parker and Mays, 1998; Sedberry et al., 1998; Wyanski et al., 2000; Harris et al., 2002). Since traditional management strategies have proven unable to reverse these declining trends, the South Atlantic Fishery Management Council (SAFMC) has proposed a series of marine protected areas (MPAs) throughout the SAB. Starting in 2001, public scoping meetings were held to gather information and knowledge of hard bottom areas off the south Atlantic coast in order to propose potential locations for MPAs. The Council then began working to determine which sites would best meet the management objective: to protect those habitats and locations that are essential to completing the life cycles of overfished species, mainly deepwater snapper and grouper species. The SAFMC siting process highlighted some significant gaps in knowledge of the characteristics of deep reef habitats, fish assemblages associated with these habitats, and spawning locations for commercially important fishes in the SAB. Knowledge of such habitats and fish assemblages will enable placement of MPA networks to maximize resource protection and surplus spillover into adjacent fished areas. The current study was one of many conducted to provide this needed information to fisheries managers, thereby enabling the most effective placement for MPAs in the SAB.

Potential locations for MPAs proposed by the SAFMC included continental shelf-edge and upper-slope reef habitats off the coasts of South Carolina, Georgia, and northern Florida (Fig. 1). These productive habitats have been described as live bottom areas or hard bottom habitats, and support large numbers of sessile invertebrates, including sponges, cnidarians, ascidians, and bryozoans (Struhsaker, 1969; Wenner et al., 1983), along with a wide variety of tropical and subtropical fish species (Struhsaker, 1969; Barans and Henry, 1984; Sedberry and Van Dolah, 1984). Shelf-edge habitats are located at depths between 45 and 90 m, and vary from smooth mud bottoms to rocky outcrops of high relief (Barans and Henry, 1984; Parker and Mays, 1998). These habitats range in lithology among sandy biomicrite (a limestone comprised of skeletal remains in a matrix of carbonate mud), algal limestone, quartz-rich calcarenite, and calcareous quartz sandstone (Barans and Henry, 1984). Reef sediments are both terrigenous (carbonate-cemented sands) and biogenic (organically-lithified carbonate) in origin (Benson et al., 1997). Relict calcareous carbonate sources contributing to these features may include, but are not limited to algae, corals, bryozoans, mollusks, and ooliths (Avent et al., 1977; Benson et al., 1997, Gardner et al., 2001). During the Pleistocene era, shelf-edge reefs were formed and shaped as depositional features at lower sea level stands (Avent et al., 1977; Benson et al., 1997; Thompson and Gilliland, 1980). Present day currents, however, probably still play an important role in shaping these features through erosional processes (Thompson and Gilliland, 1980). While most shelf-edge reefs are generally oriented parallel to the coast line (Avent et al., 1977), rock morphology comprising these reefs varies considerably among and within different locations. Morphologies seen in past studies included rounded outcrops, irregularly sized boulders and rubble, steep scarps, and flat ridge surfaces, with relief ranging from 0.5 to 15 m (Barans and Henry, 1984; Parker and Mays, 1998).

Upper continental slope habitats are located at depths between 175 and 250 m. These habitats have been previously described as “moderate relief capped mounds” of

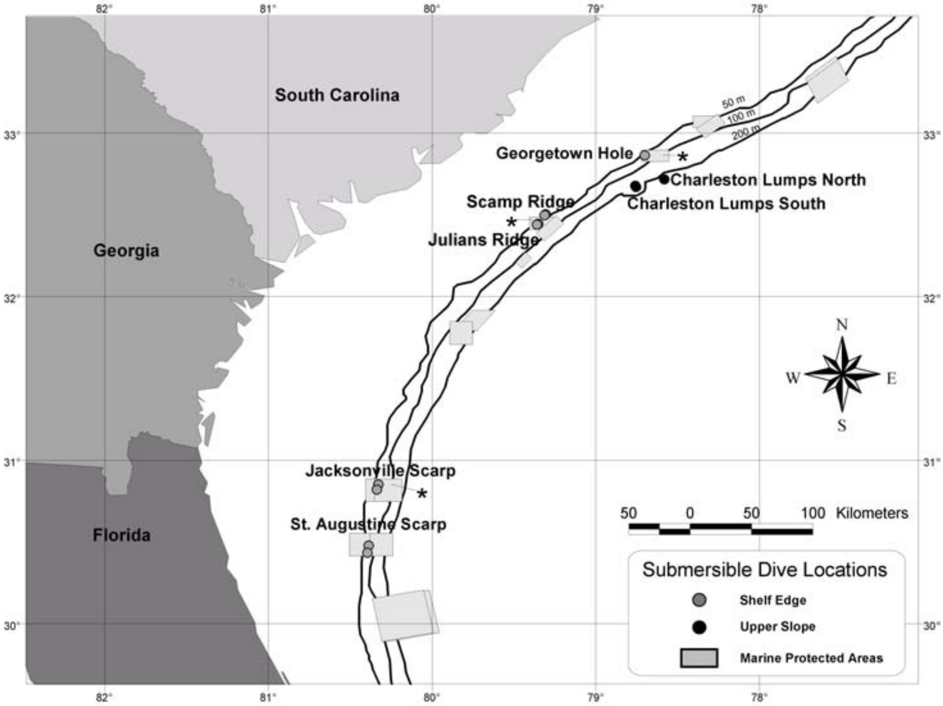

Figure 1. Locations for submersible dives and proposed marine protected areas. Gray symbols = shelf-edge dive locations, Black symbols = upper-slope dive locations, Striped polygons = proposed marine protected areas, * = marine protected areas approved by the SAFMC; awaiting final action by the U.S. Secretary of Commerce.

high local relief (~20 m) outcroppings (Wenner and Barans, 2001). Mounds are produced by the incomplete erosion of alternating substrates that comprise hard manganese phosphate pavement and soft strata. Resulting relief possesses large phosphorite slabs at the top of the mound, boulders forming the sides, and smaller boulder rubble at the base. Sand and smooth mud-clay bottoms surround areas of irregular rocky-relief (Russell et al., 1988; Wenner and Barans, 2001).

Many past studies have described the distribution and abundance of fish assemblages associated with deep reef habitats in the SAB (Struhsaker, 1969; Grimes et al., 1982; Chester et al., 1984; Sedberry and Van Dolah, 1984; McGovern et al., 1998), but the traditional gears used to sample fishes, including trawls, traps, and longlines, do not provide information on specific habitat use and fish behavior (Uzmann et al., 1977; Cailliet et al., 1999). Also, traditional gears may not effectively sample fish diversity and abundance in continental shelf-edge and upper-slope habitats, due to the complex bottom types and reef morphology (Uzmann et al., 1977; Barans and Henry, 1984; Parker et al., 1994; Starr et al., 1995). Visual observations of fish assemblages within these complex habitats may be more effective than traditional gears for sampling distribution and abundance, and may provide information on specific habitat use and behavior.

We utilized submersible video to better characterize fish assemblages inhabiting shelf-edge and upper-slope habitats off the southeast coast. The objectives of this study were sixfold: (1) to describe fish assemblages associated with deep reef habitats along the shelf edge and upper continental slope; (2) to determine variation in fish density among reef morphology types within shelf-edge habitats; (3) to determine spatial variation in fish assemblages among shelf-edge dive locations; (4) to document and describe important fish behaviors observed, especially those associated with reproduction; (5) to provide information on factors relevant to the placement of marine protected areas, including reef morphology descriptions, areas of high fish density and diversity, and important spawning habitat locations; and (6) to provide baseline data for future monitoring of MPAs in the SAB.

METHODS

FIELD METHODS.—Twelve submersible dives were conducted in the JOHNSON-SEA-LINK II (JSL-2) at seven locations along continental shelf-edge and upper-slope reef habitats on 28 July–4 August 2002 (Fig. 1). Dive locations between St. Augustine, Florida, and Charleston, South Carolina, were determined from the South Carolina Department of Natural Resources (SCDNR) historical database of suspected or known important reef fish aggregations and spawning activity (Sedberry et al., 2006). All shelf-edge dives were conducted within, or directly adjacent to the boundaries of potential MPAs proposed by the SAFMC (SAFMC, 2007). Dive locations varied by habitat type and depth (Table 1). The submersible transected study habitats at an average speed of 1 knot at four minute intervals. Submersible speed varied due to currents and bottom topography, but never exceeded 2.2 m s^{-1} (Partyka et al., 2007). A video camera attached to the submersible was held at a constant tilt angle (45° from the bottom), and zoomed out (maximum wide angle) for a panoramic view, while videotaping fishes and associated reef habitats. Camera altitude was held constant between 2 and 3 m off the bottom. The submersible was equipped with Harbor Branch-developed xenon arc lights, which illuminated bottom habitats and fishes in "true color," resembling daylight conditions. Dives were recorded on mini digital videocassettes (mini-DVs).

Subsequent to dive operations, some dive sites were surveyed (in 2006 and 2007) with multibeam and side scan sonar to further characterize the sites and to place them within the context of the local shelf-edge and upper-slope reefs (Fig. 2).

VIDEO ANALYSIS.—Video transects were viewed continuously with a Sony DV recorder and 14 inch flat screen color monitor to determine fish species seen and abundance per cubic meter (density). Fish counts were determined using a "tally" system. Freeze frames were used to identify and count fish when multiple species were present and in areas with high fish abundance. Individual fish were identified to the genus and species level, but if confident identifications could not be made, or if the fish was too far in the distance, individuals were identified to the lowest possible taxonomic level or labeled as "unknown." Counts for large schools of fish were estimated. Attempts were made to avoid or minimize recounting fish by noting unique color patterns, body markings, and attraction behaviors (i.e., greater amberjack schooling around the sub).

Transect volume (measured in cubic kilometers) was determined by multiplying transect length by the two-dimensional area viewed by the camera. Two laser beams (separated by a known distance of 25 cm) mounted on the submersible camera were used to estimate the two-dimensional area viewed by the camera (or transect height and width). Transect length was determined by plotting (GIS Software-Arcview 3.2) and measuring distances between best estimates of latitude and longitude coordinates for transect start and stop positions along each dive track. These dive track coordinates were obtained from the support vessel, R/V SEWARD JOHNSON, which tracked the underwater location of the submersible using an ORE Trackpoint II system. When reliable coordinates were not available for transect positions, an average transect length was used, based on the mean transect length of all transects conducted during that dive (Table 1).

DESCRIPTION OF REEF MORPHOLOGY.—Shelf-edge reef morphology types were empirically defined based on rock shape and the amount of relief present, as observed from the

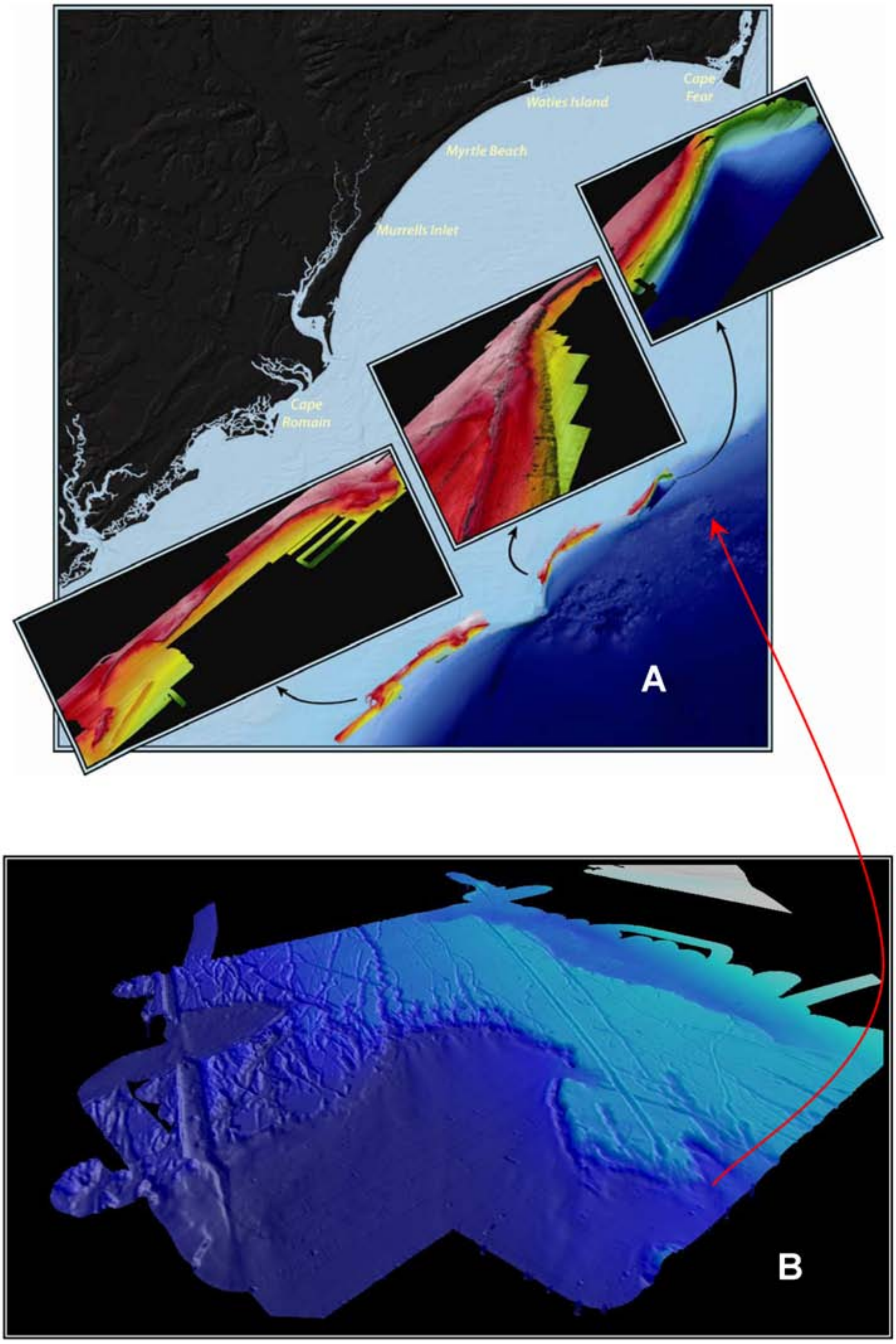

Figure 2. Multibeam and side scan sonar imagery of shelf-edge (A) and upper-slope reefs (B) off of South Carolina.

Table 1. Submersible dives (JSL-2) with corresponding location name, date, latitude and longitude coordinates (in decimal degrees), habitat type (SE = shelf edge, US = upper slope), mean depth (D), temperature (T), and salinity (S), total transect volume (km^3), # of transects, and mean transect length (km^3 ± SD). Coordinates, depth, temperature, and salinity are from the "on bottom" location for each dive.

Dive #	Location	Date mo-d-yr	Latitude	Longitude	Habitat	D (m)	T (°C)	S	Total Tran. Vol.	# Tran.	Mean tran. length
3289	St. Augustine Scarp	07-28-2002	29.9914	–80.2768	SE	55	20.0	36.5	1.76	6	0.076 (± 0.004)
3290	St. Augustine Scarp	07-28-2002	29.9393	–80.2846	SE	55	20.0	36.5	3.34	16	0.075 (± 0.022)
3291	Jacksonville Scarp	07-30-2002	30.4397	–80.2049	SE	54	18.6	36.4	2.04	7	0.063 (± 0.018)
3292	Jacksonville Scarp	07-30-2002	30.4009	-80.2162	SE	51	19.0	36.5	2.97	6	0.104 (± 0.059)
3293	Julians Ridge	08-01-2002	32.3481	–79.0357	SE	50	--	--	4.80	16	0.075 (± 0.034)
3294	Julians Ridge	08-01-2002	32.3428	–79.0452	SE	55	21.0	36.6	4.44	14	0.076 (± 0.025)
3295	Scamp Ridge	08-02-2002	32.4196	–78.9813	SE	47	22.1	36.6	6.94	16	0.091 (± 0.028)
3296	Scamp Ridge	08-02-2002	32.4112	–78.9883	SE	48	21.1	36.6	5.95	12	0.106 (± 0.021)
3297	Charleston Lumps S.	08-03-2002	32.6277	–78.3238	US	190	13.0	35.7	4.78	13	0.080 (± 0.031)
3298	Charleston Lumps S.	08-03-2002	32.6193	–78.3186	US	192	13.2	35.7	5.92	10	0.115 (± 0.041)
3299	Charleston Lumps N.	08-04-2002	32.7308	–78.1121	US	177	13.1	35.7	3.45	12	0.068 (± 0.039)
3300	Georgetown Hole	08-04-2002	32.8505	–78.2551	SE	51	20.8	36.5	2.32	15	0.038 (± 0.018)

submersible. Transects were categorized by the dominant reef morphology type observed. Most transects followed a single ridge feature and consisted of only one reef morphology type. Those transects that were conducted along more than one reef morphology type were not used in further analyses to prevent inaccurate density assessments of fishes in relation to specific bottom types. The overall reef orientation and topography were described from multibeam and side scan sonar mapping (Fig. 2).

Analysis of Fish Counts.—To compare fish assemblages observed among different dive locations and reef morphology types, density estimates were determined for each fish species by dividing the total abundance seen during each transect by the total volume viewed. Density data were not normally distributed, so non-parametric statistics (Mann-Whitney U and Kruskal Wallis tests) were employed.

To determine variation in fish density among reef morphology types within shelf-edge dive locations, median fish densities were calculated for each species within each reef morphology type at each shelf-edge dive location. Dive locations with only one reef morphology type surveyed (St. Augustine Scarp and Georgetown Hole) were not used to determine variation in fish density among different reef morphology types. Diversity parameters [number of species present (S), Margalef's index of species richness (D), Pielou's evenness index (J′), Shannon index (H′ ($\log_e$))] and the Bray-Curtis similarity coefficient were determined from mean fish densities that were calculated for each species from pooled transects for each reef morphology type. Species assemblages were elucidated using the Bray-Curtis similarity coefficient to compare pairs of reef morphology types based on species composition and density. Density data used for similarity calculations were pretreated using the fourth root transformation. This transformation down-weighs the dominance of highly abundant species, allowing not only the mid-range but also the rarer species to exert some influence on the calculation of similarity (Clarke and Warwick, 2001). Species that occurred as "singletons" were not used in similarity calculations since no match between reef morphology types would be possible. A cluster analysis was performed on the Bray-Curtis similarity matrix using PRIMER v5 (Plymouth Routines In Multivariate Ecological Research) software (Clark and Warwick, 2001). Only fish identified to the species level were used in diversity and similarity analyses.

To determine spatial variation in fish assemblages, median fish densities were calculated for each species at each shelf-edge dive location. Kruskal Wallis tests were employed to determine significant variation in fish densities among dive locations. Previously mentioned diversity parameters and the Bray-Curtis similarity coefficient were determined from mean fish densities that were calculated for each species from pooled transects at each shelf-edge dive location. Spatial variation data used in similarity calculations were also pretreated using the fourth root transformation, and species that occurred as "singletons" were removed.

Results

Submersible Dives.—One hundred and eight transects with a total volume of 34.568 km^3 were conducted during nine submersible dives along shelf-edge reefs. Shelf-edge dives had an average depth of 51.8 m (± 3.1 m), temperature of 20.3 °C (± 1.2 °C), and salinity of 36.5 (± 0.1) (Table 1). Thirty-five transects with a total volume of 14.154 km^3 were conducted during three upper slope dives, and had an average depth of 186.3 m (± 1.0 m), temperature of 13.1 °C (± 0.1 °C), and salinity of 35.7 (± 0.0).

Side Scan and Multibeam Sonar Imagery.—Sonar surveys of the shelf-edge reef off South Carolina indicated a nearly continuous scarp-like feature that somewhat parallels the present-day cuspate shoreline of the Carolinas. Dominant features included a sheer ridge and scarp feature (Fig. 2) at the shelf break, with about 10 m (from 44 to 54 m depth) of near-vertical relief. The ridge on top of the scarp was from

100 to 1500 m wide and rose from 2 to 5 m above the seafloor on the shoreward side of the shelf break. Offshore, the scarp was nearly vertical, and sloped toward relatively level sandy bottom at about 55 m. Other locations consisted of a lower eroded ridge about 3 m high (at 50 m, then dropping down to 53 m), with rough eroded bottom extending down to 60 m. The ridge at the shelf break in those locations was about 100 m wide. Other locations had a double-ridge system, with 4–9 m high ridges at depths around 46 and 58 m.

The slope reef consisted of a plateau at about 170 m depth that was elevated 10–20 m above the bottom. There were numerous kilometer-scale furrows on the plateau at 170–220 m water depth. The furrows were 10–100 m wide and < 10 m deep, with some larger furrows up to 400 m wide and 20 m deep. Many of the furrows were flanked by lateral berms and rock piles several meters high. Analysis of sonar and submersible observations indicate that the bottom in this area has been scoured by icebergs during Quaternary glaciations (Hill et al., 2008).

FISH ASSEMBLAGES.—Twelve total dives produced 143 transects encompassing 48.722 km^3 of water. Video analysis scored a total of 24,306 specimens. Of these, 20,965 were successfully identified to family and 19,801 to species. A total of 23,636 specimens, 25 families, and 54 species was seen during nine shelf-edge dives (108 transects). Three upper-slope dives (35 transects) yielded 706 specimens, seven families, and seven species (Appendix 1).

Distinct fish assemblages were found at shelf-edge versus upper-slope dive locations; no common species were observed between these two habitat types. In shelf-edge habitats tomtate, *Haemulon aurolineatum* Cuvier, 1830; vermilion snapper, *Rhomboplites aurorubens* (Cuvier, 1829); and yellowtail reeffish, *Chromis enchrysura* Jordan and Gilbert, 1882 made up over 70% of the total percent abundance (Appendix 1). Other fishes seen in shelf-edge habitats included unidentified damselfishes (Pomacentridae); cubbyu, *Pareques umbrosus* Jordan and Eigenmann, 1889; reef butterflyfish, *Chaetodon sedentarius* Poey, 1860; sunshinefish, *Chromis insolata* (Cuvier, 1830); squirrelfish, *Holocentrus adscensionis* Osbeck, 1765; tattler, *Serranus phoebe* Poey, 1851; sharpnose puffer, *Canthigaster rostrata* (Bloch, 1786); spotfin hogfish, *Bodianus pulchellus* (Poey, 1860); and wrasses (Labridae). In upper-slope habitats yellowfin bass, *Anthias nicholsi* Firth, 1933 and blackbelly rosefish, *Helicolenus dactylopterus* (Delaroche, 1809) made up over 86% of the total percent abundance (Appendix 1). Other species found along deeper slope habitats included smallscale mora, *Laemonema barbatulum* Goode and Bean, 1883; big roughy, *Gephyroberyx darwinii* (Johnson, 1866); snowy grouper, *Epinephelus niveatus* (Valenciennes, 1828); and blueline tilefish, *Caulolatilus microps* Goode and Bean, 1878.

SHELF-EDGE REEF MORPHOLOGY VARIATION.—Reef morphology types seen during shelf-edge dives varied among dive sites (Table 2). Six reef morphology types were empirically defined from transects conducted in shelf-edge habitats: slab pavement, blocked boulders, buried blocked boulders, low-relief bioeroded rock, moderate-relief bioeroded rock, and high-relief bioeroded rock (Fig. 3). Dive locations carried out at southern shelf-edge reefs (St. Augustine Scarp and Jacksonville Scarp) were composed of three reef morphology types: slab pavement, blocked boulders, and buried blocked boulders. Slab pavement was a thin, flat layer of rock that made up the surface of the reef. These slabs were often separated by fissures and cracks filled with sediment (Fig. 3A). Blocked boulders made up the offshore, steep-sloping face of the ridge. These squared-off rocks were nearly a rectangular prism in shape and

Table 2. Six reef morphology categories are listed by shelf-edge dive location. "X" denotes presence of reef morphology at dive location. SAS = St. Augustine Scarp, JS = Jacksonville Scarp, JR = Julians Ridge, SR = Scamp Ridge, GH = Georgetown Hole. SAS and JS are southern reefs. JR, SR, and GH are northern reefs.

Reef morphology	SAS	JS	JR	SR	GH
Slab pavement	X	X			
Blocked boulders	X	X			
Buried blocked boulders		X			
Low-relief bioeroded rock			X	X	X
Moderate-relief bioeroded rock			X	X	
High-relief bioeroded rock			X	X	

about 1 m in height (Fig. 3B). Buried blocked boulders were the same shape and size as blocked boulders; however, those rocks were less exposed than blocked boulders due to accumulated layers of sediment surrounding them (Fig. 3C). Dive locations conducted at northern shelf-edge reefs (Julians Ridge, Scamp Ridge, and Georgetown Hole) were composed completely of bioeroded rock (Table 2). This morphology type was divided into three categories based on the amount of relief present: low (< 1 m), moderate (1–2 m), and high relief (> 2 m). Low-relief bioeroded rock was pitted with small depressions, which were filled with sediment. Those rocks had relatively flat surfaces overall (Fig. 3D). Moderate-relief bioeroded rock had larger depressions (still filled with sediment) and more surface relief (small ledges and overhangs) than low-relief bioeroded rock (Fig. 3E). High-relief bioeroded rock was much more irregular in shape, had the most surface relief overall, and larger ledges, overhangs and crevices were seen when compared to low- and moderate-relief bioeroded rocks. Also, high-relief rocks had eroded so much in some areas that fish were seen swimming through holes in the rocks (Fig. 3F).

The number of transects conducted and total area viewed varied within each reef morphology type and within each dive location (Table 3). Mean fish densities from each reef morphology type revealed that high-relief bioeroded rock was the most densely populated reef morphology with a total density of 2013 (± 716) individuals

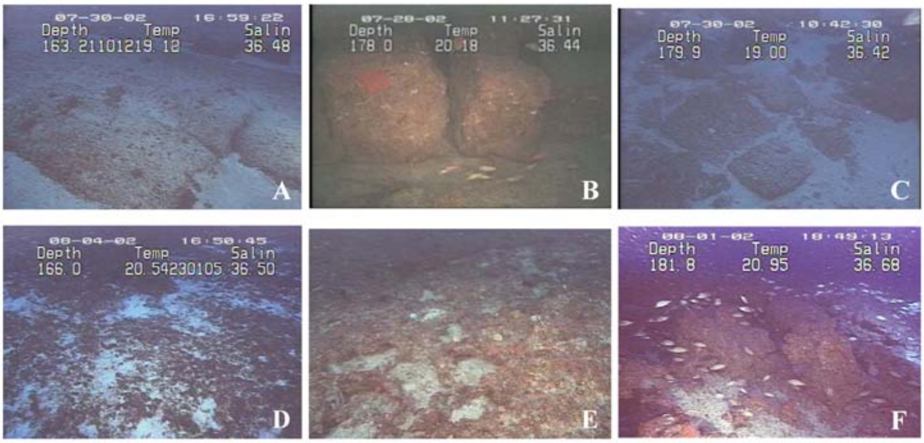

Figure 3. Six reef morphology types seen during shelf-edge dives. A = slab pavement, B = blocked boulders, C = buried blocked boulders, D = low-relief bioeroded rock, E = moderate-relief bioeroded rock, F = high-relief bioeroded rock.

Table 3. Total transect volume (m^3) conducted entirely within each reef morphology type is listed by dive location. SAS = St. Augustine Scarp, JS = Jacksonville Scarp, JR = Julians Ridge, SR = Scamp Ridge, GH = Georgetown Hole. Number in parentheses denotes the number of transects conducted within each category at that dive location.

Reef morphology	SAS	JS	JR	SR	GH
Slab pavement		1,284 (3)			
Blocked boulders	3,988 (17)				
Buried blocked boulders		1,900 (7)			
Low-relief bioeroded rock			3,821 (12)		2,319 (15)
Moderate-relief bioeroded rock			1,895 (4)	4,992 (11)	
High-relief bioeroded rock			1,715 (7)	2,068 (4)	

km^{-3}, followed by blocked boulders (933 km^{-3} ± 544), moderate-relief bioeroded rock (535 km^{-3} ± 405), buried blocked boulders (445 km^{-3} ± 423), low-relief bioeroded rock (313 km^{-3} ± 338), and slab pavement (50 km^{-3} ± 5). Three dive locations had transects conducted in more than one reef morphology type: Jacksonville Scarp, Julians Ridge, and Scamp Ridge. Mann-Whitney U tests (Jacksonville Scarp and Scamp Ridge) and Kruskal Wallis tests (Julians Ridge) revealed four species with median densities that varied significantly ($\alpha = 0.05$) among different reef morphology types (Figs. 4–6). Three of these species had higher densities on complex reef morphology types than on low-relief rocks; while one species had higher densities on low- or moderate-relief reef morphology types when compared to high-relief rocks. At Jacksonville Scarp, tomtate had statistically higher densities ($P = 0.04$) on buried blocked boulders (BBB) than on slab pavement (SP, median = 0, Fig. 4). At Julians Ridge, tomtate and scamp, *Mycteroperca phenax* Jordan and Swain, 1884, had statistically higher median densities on high-relief bioeroded rock (HB, $P = 0.006$ and 0.025 respectively) than on low- and moderate-relief bioeroded rock (LB and MB, tomtate median = 0). Tattler had statistically lower densities ($P = 0.001$) on high-relief bioeroded rock (HB, median = 0) than low and moderate-relief bioeroded rocks (LB and MB) at Julians Ridge (Fig. 5). At Scamp Ridge, vermilion snapper had statistically higher densities ($P = 0.013$)

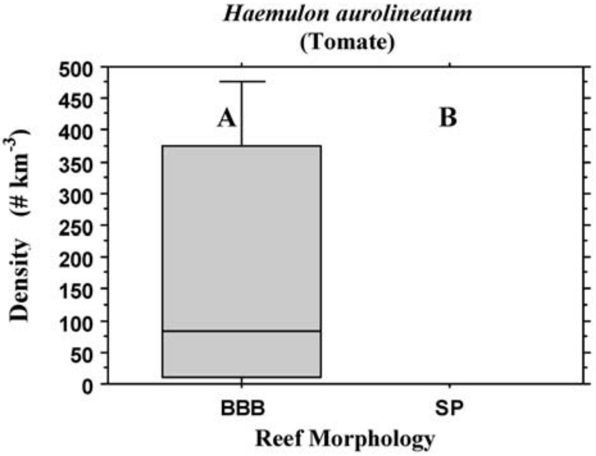

Figure 4. Box plot showing significant differences in median densities for tomtate (*Haemulon aurolineatum*) between different reef morphology types found at Jacksonville Scarp (BBB = buried blocked boulders, SP = slab pavement). Midline through box represents median density (50th percentile), box edges represent 25th and 75th percentiles, bars represent 10th and 90th percentiles. Different letters denote significant differences in median densities between reef morphology types.

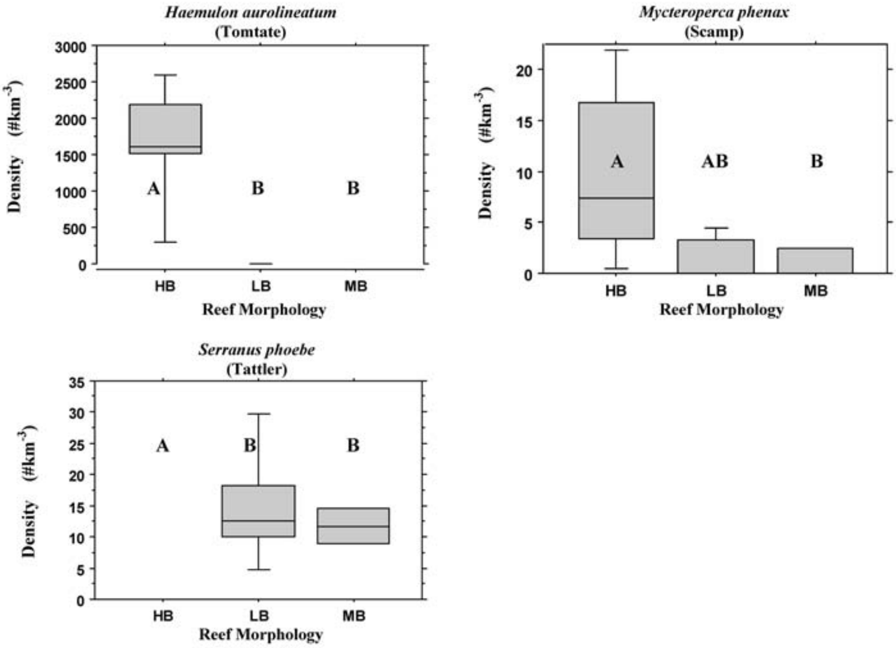

Figure 5. Box plots showing significant differences in median fish densities among different reef morphology types found at Julians Ridge (LB = low-relief bioeroded rock, MB = moderate-relief bioeroded rock, HB = high-relief bioeroded rock). Midline through box represents median density (50th percentile), box edges represent 25th and 75th percentiles, bars represent 10th and 90th percentiles. Different letters denote significant differences in median densities among reef morphology types.

on high-relief bioeroded rock (HB) than on moderate-relief bioeroded rock (MB, Fig. 6).

The mean number of fish species per transect (S) for different reef morphology types ranged from 11 to 36. Moderate-relief bioeroded rock had the highest number of species, while slab pavement had the fewest (Table 4). Species richness (D) ranged from 2.53 to 5.39, with slab pavement having the lowest species richness, and moderate-relief bioeroded rock having the highest value. Slab pavement had the greatest species evenness (0.91), while high-relief bioeroded rock had the least (0.41). H′ diversity varied among reef morphology types, with high-relief morphology types (high-relief bioeroded rock and blocked boulders) having the lowest values, and low- to moderate-relief morphology types having the highest H′ values.

Bray-Curtis similarity values for shelf-edge reef morphology types ranged from 40.43 to 71.60 (Table 5). Two main groups of morphology types fell out in the cluster analysis (Fig. 7). Bioeroded rock types and block boulder types formed one group with relatively high similarity (> 59%). Slab pavement was separated from all other reef morphology types at a lower similarity level (< 43%).

Spatial Variation.—Ten species had densities that varied significantly among shelf-edge dive locations, including the spotfin hogfish, knobbed porgy, *Calamus nodosus* Randall and Caldwell, 1966, sharpnose puffer, spotfin butterflyfish, *Chaetodon ocellatus* Bloch, 1787, yellowtail reeffish, sunshinefish, tomtate, bigeye, *Priacanthus arenatus* Cuvier, 1829, vermilion snapper, and tattler (Fig. 8). No clear trend was seen

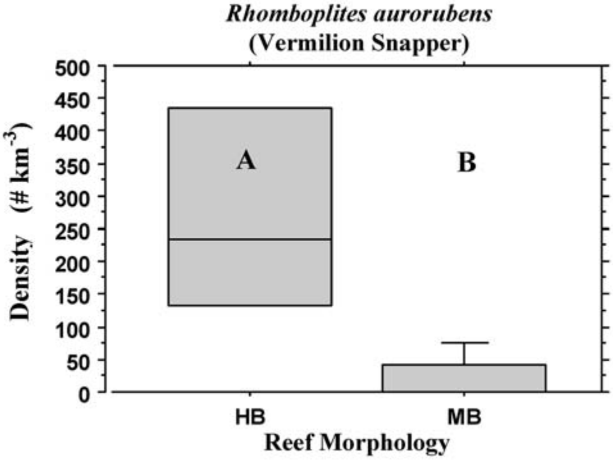

Figure 6. Box plot showing significant differences in median densities of vermilion snapper (*Rhomboplites aurorubens*) between reef morphology types found at Scamp Ridge (MB = moderate-relief bioeroded rock, HB = high-relief bioeroded rock). Midline through box represents median density (50th percentile), box edges represent 25th and 75th percentiles, bars represent 10th and 90th percentiles. Different letters denote significant differences in median densities between reef morphology types.

with respect to species density and latitude distribution for any one species. Also, no clear trends were observed in fish densities for individual species between northern (Julians Ridge, Scamp Ridge, Georgetown Hole) and southern (St. Augustine Scarp, Jacksonville Scarp) shelf-edge reefs. Mean total fish density did not vary significantly among dive locations (St. Augustine Scarp: 892 individuals km^{-3} ± 546, Julians Ridge: 950 km^{-3} ± 1181, Scamp Ridge: 919 km^{-3} ± 813, Georgetown Hole: 344 km^{-3} ± 396, Jacksonville Scarp: 300 km^{-3} ± 352).

Mean number of species seen at dive locations ranged from 18 to 37, with Georgetown Hole having the fewest species and Scamp Ridge having the most (Table 6). A similar pattern was seen with species richness, with Georgetown Hole having the lowest value (2.47) and Scamp Ridge having the highest (5.24). Georgetown Hole, however, had the highest species evenness (0.76) of all shelf-edge dive locations. H′ diversity varied among dive locations, but no trend was seen among diversity parameters and latitude.

Bray-Curtis similarity values for shelf-edge dive locations were not highly variable (based on species composition and abundance), with coefficients ranging from 55.59 to 71.90 (Table 7). The cluster analysis revealed that similarity increased with decreasing dive-site latitude (Fig. 9).

Table 4. Diversity parameters are listed for reef morphology types seen during shelf-edge dives. S = Mean number of species, N = Total mean density per km^3 of water, D = Margalef's index of species richness, J′ = Pielou's evenness index, H′ = Shannon index.

Reef morphology	S	N	D	J′	H′ ($\log_e$)
Slab pavement	11	52	2.53	0.91	2.18
Blocked boulders	26	1,075	3.58	0.49	1.50
Buried blocked boulders	19	637	2.79	0.70	2.06
Low-relief bioeroded rock	27	978	3.78	0.69	2.29
Moderate-relief bioeroded rock	36	665	5.39	0.60	2.13
High-relief bioeroded rock	23	2,271	2.85	0.41	1.27

Table 5. Bray-Curtis similarity coefficients for shelf-edge reef morphology types. SP = slab pavement, BB = blocked boulders, BBB = buried blocked boulders, LB = low-relief bioeroded rock, MB = moderate-relief bioeroded rock, HB = high-relief bioeroded rock.

	BB	BBB	HB	LB	MB	SP
BB						
BBB	71.60					
HB	63.01	67.08				
LB	61.41	64.20	62.27			
MB	65.97	65.49	68.73	67.58		
SP	40.43	53.27	40.35	40.74	38.91	

Reproductive Behavior and Uncommon Species.—Although actual spawning was not observed during submersible dives, reproductive behaviors, including courtship and parental care, were observed for five species: scamp, hogfish, *Lachnolaimus maximus* (Walbaum, 1792), speckled hind, *Epinephelus drummondhayi* Goode and Bean, 1878, red snapper, *Lutjanus campechanus* (Poey, 1860), and gray triggerfish, *Balistes capriscus* Gmelin, 1789.

Scamp were observed displaying the "gray-head" courtship phase previously described by Gilmore and Jones (1992) at all dive locations except Georgetown Hole. Displays occurred at depths of 48–65 m, temperatures of 19.3–20.0 °C, and salinity of 36.6. This reproductive behavior was seen in late July and early August, between 1000 EDT and 1923 EDT. The cat paw color phase, an apparent secondary signature of dominance, was video-documented at the same shelf-edge dive locations, but much more frequently than the gray-head color phase (40 occurrences, sometimes with multiple scamp displaying) between 0916 EDT and 1930 EDT.

Hogfish were also observed displaying courtship behavior. On two separate instances, a brightly-colored male displayed to one or two drab-colored females. During courtship displays the male flared the spines in his first dorsal fin, while

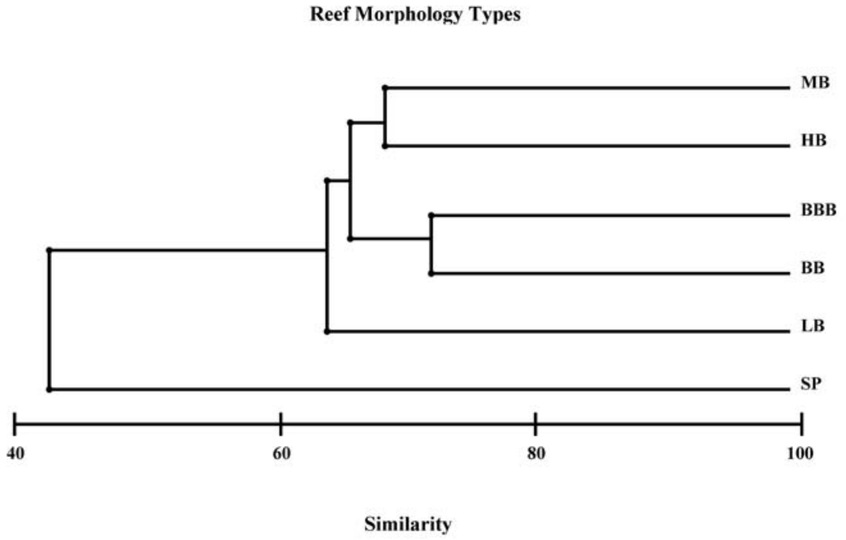

Figure 7. Normal cluster analysis of species by shelf-edge reef morphology type. Dendrogram was constructed from a cluster analysis of Bray-Curtis similarity coefficients. SP = slab pavement, LB = low-relief bioeroded rock, BB = blocked boulders, BBB = buried blocked boulders, MB = moderate-relief bioeroded rock, HB = high-relief bioeroded rock.

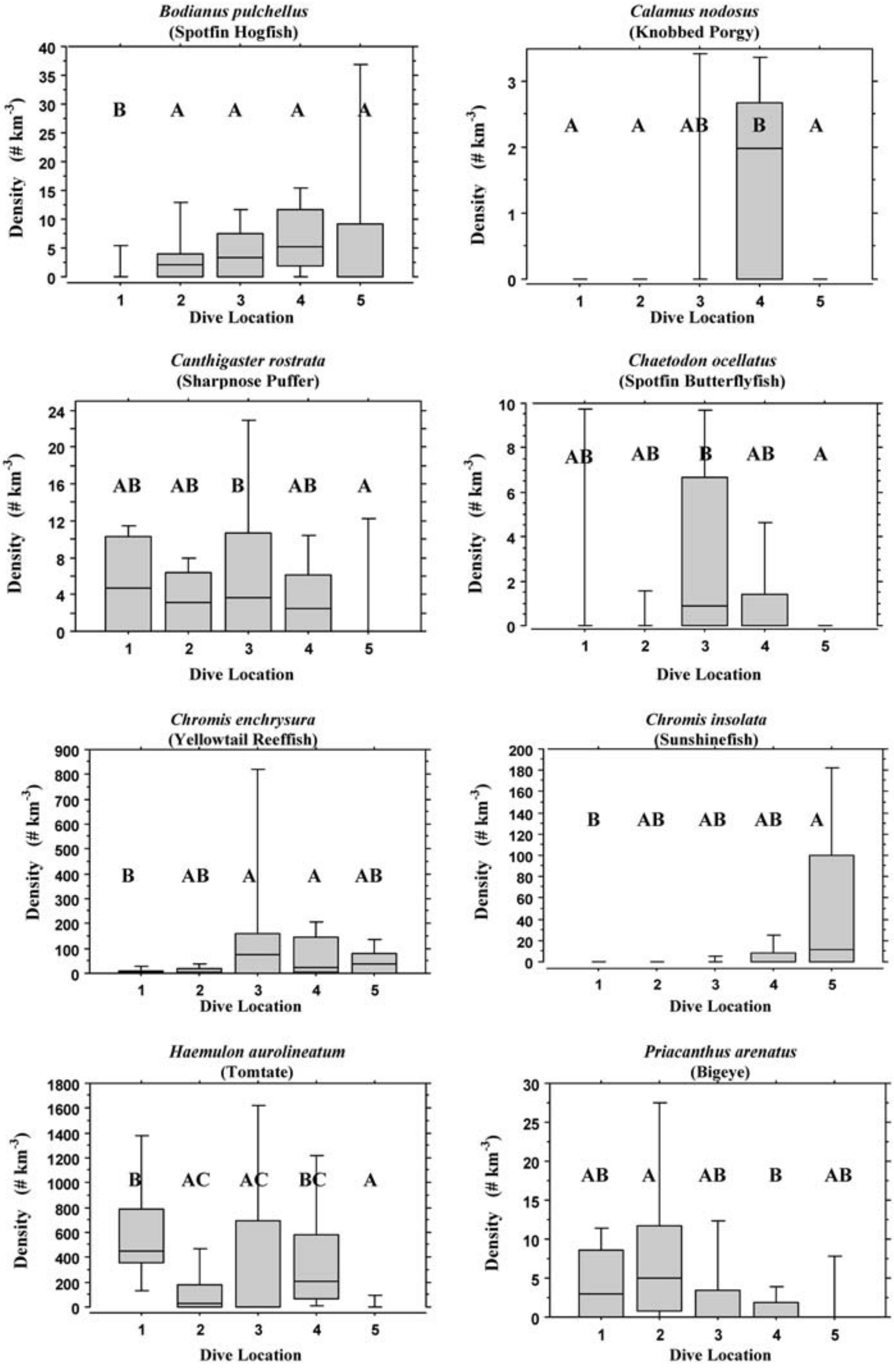

Figure 8. *(see also opposite page)* Box plots showing significant differences in median densities among shelf-edge dive locations for 10 fish species. Midline through box represents median density (50th percentile), box edges represent 25th and 75th percentiles, bars represent 10th and 90th percentiles. Dive location numbers 1–5 are in order of increasing latitude. 1 = St. Augustine Scarp, 2 = Jacksonville Scarp, 3 = Julians Ridge, 4 = Scamp Ridge, 5 = Georgetown Hole. Medians with the same letter are not significantly different.

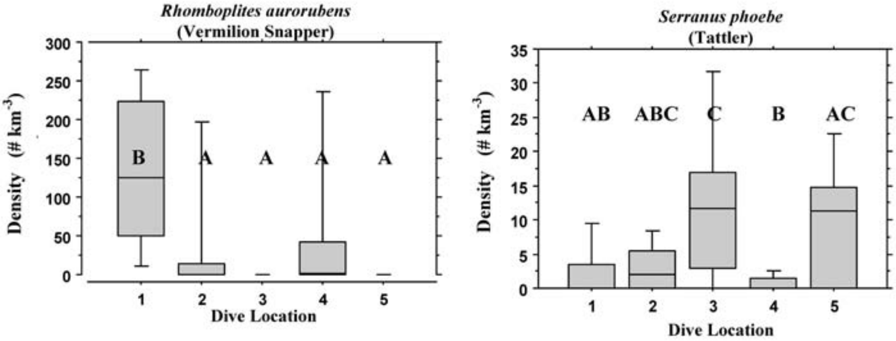

Figure 8. *(see previous page for legend).*

swimming quickly toward the female with rapid quivering oscillations (Colin, 1982; Parker, 2000). Displays were observed at Jacksonville Scarp on July 30, 2002, at 1852 and 1927 EDT, at an average depth of 52 m, temperature of 18.6 °C, and salinity of 36.5.

Other reproductive behavior was observed in red snapper. A large school of at least 20–30 individuals, which appeared to be a spawning aggregation, was observed at Scamp Ridge at 1929 EDT on August 2, 2002. This school was seen at 53 m, with a bottom temperature of 20.9 °C, and salinity of 36.5.

During submersible dives at Jacksonville Scarp, one speckled hind was observed on July 30, 2002, with an obviously distended abdomen, apparently full of ripe eggs. This gravid female was observed at 1745 EDT, in 51 m of water, with a bottom temperature of 20.9 °C and a salinity of 36.5.

Reproductive behavior was observed in gray triggerfish on August 4, 2002 at 1647 EDT. During a dive at Georgetown Hole, a large triggerfish was observed guarding a nest with an apparent egg mass. The individual seen guarding the nest was presumably a male (since this sex tends to the nest after it is constructed by the female), but no definite determination of sex could be made (Barlow, 1981; Murdy et al., 1997). The nest was located in 50 m of water at a bottom temperature of 20.6 °C and salinity of 36.5. Another unguarded nest structure was observed on August 1, 2002 at 1748 EDT during a dive on Julians Ridge. This empty nest was located in 59 m of water at a bottom temperature of 20.7 °C and salinity of 36.6.

Two species that are not commonly observed off South Carolina, the cherubfish, *Centropyge argi,* Woods and Kanazawa, 1951 and the longsnout butterflyfish, *Prognathodes aculeatus,* (Poey, 1860), were seen during shelf-edge submersible dives. One

Table 6. Diversity parameters are listed for shelf-edge dive locations. S = Mean number of species, N = Total mean density per km^3 of water, D = Margalef's index of species richness, J′= Pielou's evenness index, H′ = Shannon index.

Dive location	S	N	D	J′	H′(log$_e$)
Georgetown Hole	18	974	2.47	0.76	2.20
Scamp Ridge	37	969	5.24	0.58	2.08
Julians Ridge	31	2,066	3.93	0.43	1.49
Jacksonville Scarp	25	610	3.74	0.65	2.09
St. Augustine Scarp	28	1,057	3.88	0.50	1.68

Table 7. Bray-Curtis similarity coefficients for shelf-edge dive locations. GH = Georgetown Hole, JS = Jacksonville Scarp, JR = Julians Ridge, SR = Scamp Ridge, SAS = St. Augustine Scarp.

	GH	JS	JR	SR	SAS
GH					
JS	60.09				
JR	65.37	69.02			
SR	55.59	60.65	66.87		
SAS	57.38	71.90	67.26	62.98	

cherubfish was observed swimming in 59 m of water (temperature = 20.8 °C, salinity = 36.5) among heavily encrusted rocky relief at Georgetown Hole. Additionally, two longsnout butterflyfish were observed on separate dives. The first was documented at 1107 EDT at Scamp Ridge, in 52 m of water (temperature = 22 °C, salinity = 36.6). The second individual was observed at 1729 EDT at Georgetown Hole, in 59 m of water (temperature = 20.7 °C, salinity = 36.5).

Discussion

Reef Morphology Variation.—Reef morphology types varied greatly among dive locations seen in this study, and this variation is most probably due to large-scale geological, biological, and oceanographic processes, as well as local variation in sedimentation and bioerosion rates (MacIntyre and Milliman, 1970; Wilkinson, 1983; Riggs et al., 1998). Most morphology types seen have been described previously by Barans and Henry (1984), who also observed flat ridge tops (“slab pavement”) and blocky rock outcrops, separated by cracks filled with sand (“buried blocked boulders”). An additional morphology found in this study, which was not described previously, was “blocked boulders.” These large rocks, typically a rectangular prism in shape, were found off the coast of northern Florida, and most probably resulted from

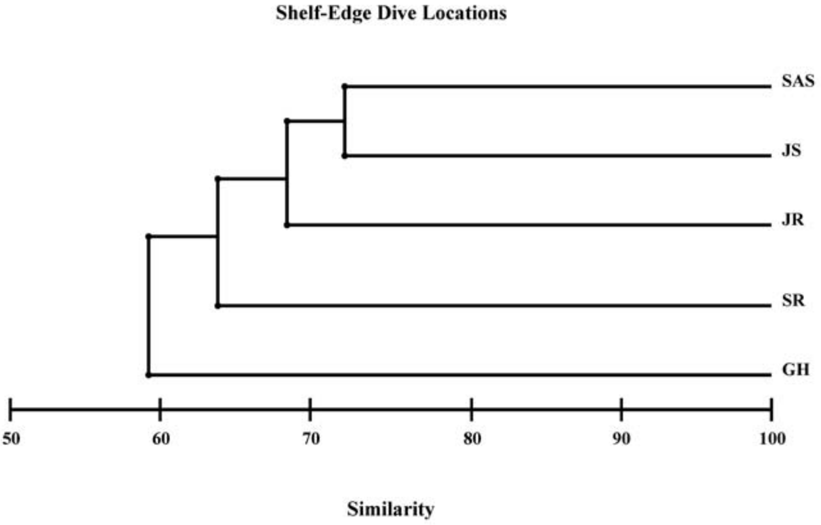

Figure 9. Normal cluster analysis of species by shelf-edge dive location. Dendrogram was constructed from a cluster analysis of Bray-Curtis similarity coefficients. JS = Jacksonville Scarp, SR = Scamp Ridge, SAS = St. Augustine Scarp, GH = Georgetown Hole, JR = Julians Ridge.

faulting processes (L. Sautter, Geology Department, College of Charleston, pers. comm.). We observed irregular rocky rubble also reported by Barans and Henry (1984), but in the current study this morphology type was further divided based on the amount of relief present due to bioerosional processes. Bioerosion is a term used to describe the activities of a broad array of marine organisms, which erode calcium carbonate substrates through a number of mechanisms, including chemical dissolution, mechanical abrasion, and muscle-like excavation (Wilkinson, 1983). Bioerosion may be responsible for the differences in reef morphology types seen in the current study. Shelf-edge rocks at all dive locations in this study were heavily encrusted with invertebrate growth, and these encrusting organisms, such as algae, sponges, and corals, along with other individuals (polychaetes, mollusks, and echinoderms) play an important role in shaping and modifying the hard substrates on which they live (Riggs et al., 1998). Rocks composing different reef morphology types can consist of different mineral compositions (Riggs et al., 1998) and/or supported different bioeroding organisms (Fraser and Sedberry, 2008), and thus be modified at different rates.

Several species (scamp, tomtate, and vermilion snapper) in the current study had higher densities on more complex bottom types (high-relief bioeroded rock and blocked boulders) than on low-relief or flat-ridge top habitats. Two other studies conducted in the SAB (Barans and Henry, 1984; Sedberry and Van Dolah, 1984) also observed (remotely operated underwater camera) higher densities of fishes in complex habitats. Barans and Henry (1984) found higher fish densities associated with irregular-rubble bottom types (9.7 fish 100 m^{-2}) when compared to regular, flat habitats (0.4 fish 100 m^{-2}), while Sedberry and Van Dolah (1984) observed greater numbers of several species, including bank seabass, *Centropristis ocyurus* (Jordan and Evermann, 1887), yellowtail reeffish, large groupers, red porgy, *Pagrus pagrus* (Linnaeus, 1758), and *Equetus* sp., in high-relief outer shelf stations when compared to low relief inner and middle shelf stations. Higher density of fishes in complex bottom types is a common trend seen in many studies conducted in a wide variety of habitats (Parker and Ross, 1986; Koenig et al., 2000; Sluka et al., 2001), and is most likely attributed to increased protection from predators found in structurally complex habitats (Jordan et al., 1996; Ohman and Rajasuriya, 1998).

Diversity parameter results (species number, H′-diversity, species evenness) measured during this study were variable. Bioeroded rock and block boulder morphology types had the highest species number and species richness, while slab pavement had the lowest. Sample size, however, was very low in the slab pavement morphology type, and species richness is dependent on sampling effort (Clarke and Warwick, 2001). Further sampling effort in slab pavement morphology types may reveal similar species number and richness to other shelf-edge morphology types. H′-diversity was lower in complex habitats than in low-relief bottom types. Decreased species evenness due to the overwhelming dominance of a few species (tomtate and vermilion snapper) within high-relief and blocked boulder habitats may have contributed to low H′ values (Sedberry and Van Dolah, 1984).

Continued investigation of deepwater habitats is needed to further define fish and habitat associations. Although only four species (vermilion snapper, tomate, scamp, tattler) had significantly different densities among habitats, additional research using visual sampling techniques may reveal other habitat-specific relationships, especially for uncommon species. Uncommon species are usually encountered too rarely to detect statistically significant relationships between habitat and density (O'Connell and Carlile, 1993; Felley and Vecchione, 1995).

Spatial Variation.—Many factors can influence the spatial variation of reef fish populations, including recruitment (Tolimieri, 1995; Mora and Sale, 2002), habitat quality and availability (Sale et al., 1984; Tolimieri, 1995; Choat et al., 1998), predation (Hixon, 1986; Hixon and Beets, 1993; Juncker et al., 2005), water temperature (Miller and Richards, 1980; Sedberry and Van Dolah, 1984; Francis, 1993; Sedberry et al., 2001), food availability (Lee et al., 1991; Verity et al., 1993), and fishing pressure (Russ and Alcala, 1989; Haedrich, 1998; McGovern et al., 1998; Koenig et al., 2000). Habitat type varied spatially among shelf-edge dive locations in the current study, and several fish species may have settled non-randomly in certain areas in response to habitat choice. For example, tattler had significantly higher abundances at Georgetown Hole and Julians Ridge when compared to other shelf-edge dive locations (Kruskal Wallis, $P < 0.05$), and these dive locations were either predominantly or completely composed of low- and moderate-relief bioeroded rock. Also, tomtate and vermilion snapper were most prevalent at dive locations with high-relief bioeroded rock and blocked boulders (St. Augustine Scarp and Scamp Ridge).

Habitat type may also play an important role in structuring fish assemblages by mediating predator-prey interactions after settlement. The amount of relief and refuge provided by structurally complex habitats varied among dive locations in this study. Some species with higher densities at dive locations with structurally complex habitats (such as vermilion snapper and tomtate) than in other locations with low-lying habitats may have resulted from decreased predation and mortality found in complex habitats (Hixon, 1986; Hixon and Beets, 1993; Jordan et al., 1996; Juncker et al., 2005).

Diversity parameters (species number, evenness, and H′-diversity) also varied spatially among shelf-edge dive locations, and this may be explained by fish-habitat interactions. Dive locations with the highest number of species (31 and 37) contained complex reef morphologies (moderate- to high-relief bioeroded rock); conversely, Georgetown Hole, which contained mostly low-relief bioeroded rock, had the lowest number of species (18). Dive locations with mostly complex bottom types (St. Augustine Scarp and Julians Ridge), however, had the lowest H′-diversity values (1.68 and 1.49). Low H′-diversity in these dive locations was linked to low species evenness, which resulted from a few dominant schooling species (mostly tomtate and vermilion snapper). Habitat quality, however, is just one of many possible factors that may have influenced spatial variation in reef fish assemblages observed in this study.

Reproductive Behavior.—Reproductive behaviors or conditions, including distended females, large aggregations, courtship and nest guarding, were video-documented for five commercially important species (scamp, hogfish, red snapper, speckled hind, and gray triggerfish) at all shelf-edge dive locations, and coincided with peak spawning seasons and locations (Gilmore and Jones, 1992; Murdy et al., 1997; Parker et al., 2000; White and Palmer, 2004; Sedberry et al., 2006). At southern shelf-edge reefs, reproductive behaviors were observed for more species at Jacksonville Scarp (courting hogfish, gravid speckled hind, and courting scamp) than at St. Augustine Scarp (courting scamp). At northern shelf-edge reefs, reproductive behaviors were observed more frequently (for nest-guarding triggerfish, large aggregations of red snapper, and courting scamp) at Julians Ridge and Scamp Ridge locations than at Georgetown Hole (only nest-guarding triggerfish). Differences observed in reproductive behavior may be the result of different reef morphology types found at different dive locations. For example, Julians Ridge and Scamp Ridge were mostly composed of moderate- and high-relief bioeroded rock, whereas Georgetown Hole was composed of low-relief bioeroded rock.

Many species, in addition to the five observed, may also spawn within these habitats even though their reproductive behaviors were not observed during this study (Sedberry et al., 2006). Many reef fish species spawn at dusk or at night when the submersible was not deployed. Also, lights from submersibles and other underwater sampling gear may alter the natural behavior of many species (Barans and Henry, 1984; Barans, 1986; Gutherz et al., 1994), and could prevent normal spawning activities. Finally, many species may spawn during different times of the year, or too infrequently to be observed by submersible divers. Further investigation of shelf-edge habitats using visual gear (e.g., submersibles, AUVs, ROVs) and/or passive acoustic techniques should help elucidate exactly which species utilize these habitats for reproductive purposes, and the important characteristics associated with productive shelf-edge reefs.

Two other species not commonly observed off South Carolina, the cherubfish and the longsnout butterflyfish, were seen during submersible dives conducted in 2002. Both species have recently been documented off of North Carolina in 2001 by submersible divers (Quattrini et al., 2004). The specimens observed off of South Carolina during this study are additional sightings of two species uncommon to the northern region of the SAB. Recent sightings are most likely the result of more sophisticated sampling techniques (e.g., submersibles and ROVs) and increased effort in complex habitats that have previously been poorly surveyed (Quattrini et al., 2004).

Proposed Marine Protected Areas.—The SAFMC has proposed the establishment of MPAs in the SAB to help protect the populations and habitats of slow growing, long-lived deepwater snapper/grouper species from directed fishing pressure, and to achieve a more natural sex ratio, age, and size structure within the proposed MPAs, while minimizing adverse social and economic impacts (SAFMC, 2007). Eight MPAs have been approved by the SAFMC (one off southern North Carolina, three off South Carolina, one off Georgia, and three off Florida) and are awaiting final action by the U.S. Secretary of Commerce (Fig. 1). These MPAs are proposed as “Type 2,” in which no person may fish for or possess a South Atlantic snapper/grouper complex species.

All shelf-edge submersible dives from the current study were conducted within, or directly adjacent to proposed MPAs (SAFMC, 2007). Dives conducted at Jacksonville Scarp, Scamp/Julians Ridge, and Georgetown Hole fell within three of the SAFMC-approved MPAs (Fig. 1). Thus, this study provides baseline fish counts prior to MPA implementation, and allows comparisons between SAFMC-approved MPA sites and other proposed MPA sites that will remain open to bottom fishing.

Acknowledgments

Most of this study was conducted while the first author was a student at the College of Charleston, SC/Grice Marine Laboratory. We thank C. A. Barans, P. C. Jutte, and G. Sancho and two anonymous reviewers for comments on earlier drafts. J. Stephen helped with database development. J. Hill (Coastal Carolina University) produced sonar imagery from

NOAA-OE cruise data. Funding and other support for this project was provided by the South Carolina Department of Natural Resources, the College of Charleston, and by grants to the South Carolina Department of Natural Resources from the NOAA Office of Ocean Exploration (Grants NA16RP2697, NA04OAR4600055 and NA06OAR4600095 to G. R. Sedberry) and from NOAA Fisheries (Grants NA03NMF4720321 and MARFIN-NA17FF2874 to G. R. Sedberry). This is Contribution Number 334 from the Grice Marine Lab.

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Date Submitted: 11 January, 2008.
Date Accepted: 27 October, 2008.
Available Online: 19 November, 2008.

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Appendix 1. Species seen during submersible dives are listed with corresponding habitats, abundance, % total abundance, and density (per km^3). Species are listed by decreasing abundance. (Authorities not indicated in table appear in text).

Habitat	Species	Family	Abundance	% total abundance	Density
Shelf edge	*Haemulon aurolineatum*	Haemulidae	12,325	52.15	379.40
Shelf edge	Unknown juvenile swarm		3,155	13.35	111.55
Shelf edge	*Chromis enchrysura*	Pomacentridae	2,491	10.54	87.63
Shelf edge	*Rhomboplites aurorubens*	Lutjanidae	2,051	8.68	58.73
Shelf edge	Pomacentridae	Pomacentridae	595	2.52	17.67
Shelf edge	*Chaetodon sedentarius*	Chaetodontidae	337	1.43	11.25
Shelf edge	Labridae	Labridae	319	1.35	13.27
Shelf edge	*Pareques umbrosus*	Sciaenidae	235	0.99	6.97
Shelf edge	Serranidae	Serranidae	219	0.93	6.08
Shelf edge	*Chromis insolata*	Pomacentridae	210	0.89	13.15
Shelf edge	*Holocentrus adscensionis*	Holocentridae	187	0.79	7.01
Shelf edge	*Serranus phoebe*	Serranidae	159	0.67	5.88
Shelf edge	*Canthigaster rostrata*	Tetraodontidae	154	0.65	5.18
Shelf edge	*Bodianus pulchellus*	Labridae	154	0.65	5.42
Shelf edge	Unknown		135	0.57	4.49
Shelf edge	*Holacanthus bermudensis* Goode, 1876	Pomacanthidae	130	0.55	5.31
Shelf edge	*Mycteroperca phenax*	Serranidae	120	0.51	5.34
Shelf edge	*Prognathodes aya* (Jordan, 1886)	Chaetodontidae	119	0.50	4.19
Shelf edge	*Priacanthus arenatus*	Priacanthidae	95	0.40	3.49
Shelf edge	*Chaetodon ocellatus*	Chaetodontidae	56	0.24	1.74
Shelf edge	*Lutjanus buccanella* (Cuvier, 1828)	Lutjanidae	40	0.17	1.42
Shelf edge	*Seriola dumerili* (Risso, 1810)	Carangidae	36	0.15	1.78
Shelf edge	*Stegastes partitus* (Poey, 1868)	Pomacentridae	31	0.13	0.68
Shelf edge	*Sargocentron bullisi* (Woods, 1955)	Holocentridae	27	0.11	2.20
Shelf edge	*Calamus nodosus*	Sparidae	26	0.11	0.65
Shelf edge	*Pseudupeneus maculatus* (Bloch, 1793)	Mullidae	23	0.10	0.57
Shelf edge	*Ocyurus chrysurus* (Bloch, 1791)	Lutjanidae	22	0.09	0.76

Appendix 1. Continued.

Habitat	Species	Family	Abundance	% total abundance	Density
Shelf edge	*Lutjanus campechanus*	Lutjanidae	17	0.07	0.70
Shelf edge	*Myripristis jacobus* Cuvier, 1829	Holocentridae	16	0.07	0.33
Shelf edge	*Acanthostracion quadricornis* (Linnaeus, 1758)	Ostraciidae	13	0.06	0.51
Shelf edge	*Chromis scotti* Emery, 1968	Pomacentridae	12	0.05	0.57
Shelf edge	*Centropristis ocyurus*	Serranidae	8	0.03	0.25
Shelf edge	*Liopropoma eukrines* (Starck and Courtenay, 1962)	Serranidae	8	0.03	0.39
Shelf edge	*Chaetodipterus faber* (Broussonet, 1782)	Ephippidae	8	0.03	0.24
Shelf edge	*Acanthurus* spp.	Acanthuridae	8	0.03	0.16
Shelf edge	*Holacanthus tricolor* (Bloch, 1795)	Pomacanthidae	7	0.03	0.35
Shelf edge	*Cephalopholis cruentata* (Lacépède, 1802)	Serranidae	5	0.02	0.15
Shelf edge	*Mycteroperca microlepis* (Goode and Bean, 1879)	Serranidae	5	0.02	0.15
Shelf edge	*Lachnolaimus maximus*	Labridae	5	0.02	0.17
Shelf edge	*Seriola rivoliana* Valenciennes, 1833	Carangidae	5	0.02	0.24
Shelf edge	*Synodus* spp.	Synodontidae	4	0.02	0.12
Shelf edge	*Pagrus pagrus*	Sparidae	4	0.02	0.17
Shelf edge	*Rypticus* spp.	Serranidae	4	0.02	0.23
Shelf edge	*Pterois volitans* (Linnaeus, 1758)	Scorpaenidae	4	0.02	0.09
Shelf edge	*Halichoeres bivittatus* (Bloch, 1791)	Labridae	4	0.02	0.04
Shelf edge	*Epinephelus drummondhayi*	Serranidae	3	0.01	0.19
Shelf edge	*Pomacanthus arcuatus* (Linnaeus, 1758)	Pomacanthidae	3	0.01	0.17
Shelf edge	Muraenidae	Muraenidae	3	0.01	0.20
Shelf edge	*Mulloidichthys martinicus* (Cuvier, 1829)	Mullidae	3	0.01	0.06
Shelf edge	*Lutjanus griseus* (Linnaeus, 1758)	Lutjanidae	3	0.01	0.12
Shelf edge	Unknown Labridae 3	Labridae	3	0.01	0.18
Shelf edge	*Haemulon striatum* (Linnaeus, 1758)	Haemulidae	3	0.01	0.14
Shelf edge	*Balistes capriscus*	Balistidae	3	0.01	0.08
Shelf edge	*Balistes vetula* Linnaeus, 1758	Balistidae	3	0.01	0.07

Appendix 1. Continued.

Habitat	Species	Family	Abundance	% total abundance	Density
Shelf edge	*Diplodus holbrookii* (Bean, 1878)	Sparidae	2	0.01	0.06
Shelf edge	Scorpaenidae	Scorpaenidae	2	0.01	0.07
Shelf edge	*Centropyge argi*	Pomacanthidae	2	0.01	0.23
Shelf edge	*Prognathodes aculeatus*	Chaetodontidae	2	0.01	0.13
Shelf edge	*Sphyraena barracuda* (Edwards, 1771)	Sphyraenidae	1	0.00	0.03
Shelf edge	*Cephalopholis fulva* (Linnaeus, 1758)	Serranidae	1	0.00	0.04
Shelf edge	*Epinephelus morio* (Valenciennes, 1828)	Serranidae	1	0.00	0.04
Shelf edge	*Pareques* spp.	Sciaenidae	1	0.00	0.10
Shelf edge	*Aluterus scriptus* (Osbeck, 1765)	Monacanthidae	1	0.00	0.02
Shelf edge	*Stephanolepis hispida* (Linnaeus, 1766)	Monacanthidae	1	0.00	0.02
Shelf edge	Unknown Labridae 1	Labridae	1	0.00	0.10
Shelf edge	Unknown Labridae 2	Labridae	1	0.00	0.10
Shelf edge	Holocentridae	Holocentridae	1	0.00	0.03
Shelf edge	*Fistularia* spp.	Fistulariidae	1	0.00	0.05
Shelf edge	*Dactylopterus volitans* (Linnaeus, 1758)	Dactylopteridae	1	0.00	0.03
Shelf edge	*Balistes* spp.	Balistidae	1	0.00	0.03
Shelf edge	*Aulostomus maculatus* Valenciennes, 1837	Aulostomidae	1	0.00	0.09
Total			**23,636**		**769.04**
Upper slope	*Anthias nicholsi*	Serranidae	520	73.65	44.78
Upper slope	*Helicolenus dactylopterus*	Scorpaenidae	92	13.03	8.82
Upper slope	Unknown		45	6.37	10.95
Upper slope	*Epinephelus niveatus*	Serranidae	16	2.27	2.50
Upper slope	*Gephyroberyx darwinii*	Trachichthyidae	14	1.98	1.85
Upper slope	*Caulolatilus microps*	Malacanthidae	6	0.85	0.34
Upper slope	*Laemonema barbatulum*	Moridae	4	0.57	0.16
Upper slope	Unknown A		4	0.57	0.28
Upper slope	*Scyliorhinus retifer* (Garman, 1881)	Scyliorhinidae	2	0.28	0.13
Upper slope	Unknown B		2	0.28	0.16
Upper slope	*Synodus* spp.	Synodontidae	1	0.14	0.08
Total			**706**		**70.05**