SUBMERSIBLE OBSERVATIONS OF SOUTHEASTERN U.S. DEEP REEF FISH ASSEMBLAGES: HABITAT CHARACTERISTICS, SPATIAL AND TEMPORAL VARIATION, AND REPRODUCTIVE BEHAVIOR

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Abstract

Submersible videos were analyzed for habitat characteristics, and spatial and temporal variation and reproductive behavior in assemblages of fishes in shelf-edge and upper-slope reefs of the South Atlantic Bight. Shelf-edge habitats were categorized by reef morphology, and variation in fish density was determined among habitat type. Six shelf-edge habitat types were described from dives conducted in 2002: 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 when compared to all others. Four species had significantly varying densities on different reef morphologies, and most of these species had higher densities on structurally complex morphologies when compared to low-relief morphologies. Several species also had significantly varying densities among different shelf-edge dive locations, however, no clear trend was observed with respect to species density and location. Dive locations with complex reef morphologies (high-relief bioeroded rock and blocked boulders) were more densely populated than dive locations with low-relief morphologies. Significant variation was detected in densities of ten species between 1985 and 2002 dives. Overall, most species had significantly decreased densities between years. Reproductive behaviors were observed for five commercially important fish species, and at all 2002 dive locations. This project provides information on areas containing complex reef morphologies, high fish densities and diversity, and important spawning habitats that should be considered when determining the placement of marine protected areas.

INTRODUCTION

The outer continental shelf and upper slope off the southeastern U.S. include a variety of bottom habitats and oceanographic features that influence the species composition, abundance, and life history of fishes throughout the region. This region, called the South Atlantic Bight (SAB), includes the coastal ocean area between Cape Hatteras, North Carolina and Cape Canaveral, Florida. The SAB is bounded on the east by the Gulf Stream and 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, deflects the Gulf Stream offshore, resulting in eddies, meanders, and cold water intrusions (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 at the edge of the continental shelf and on the upper continental slope.

The ecology and life history characteristics of many reef fish species (slow growth to late maturity, long life, large body size, and complex reproductive behavior) make them highly vulnerable to overfishing (PDT, 1990). Complex reproductive

behaviors include spawning aggregations that are predictable in time and space and sex changes (Thresher, 1984; Gilmore and Jones, 1992; Koenig *et al.*, 2000). Many fish species found within the SAB 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; Harris *et al.*, 2002; Wyanski *et al.*, 2000; NMFS, 2005). Traditional management strategies, including bag and size limits, quotas, seasonal and/or area closures, and bycatch reduction, are not always able to reverse these trends (Bohnsack and Ault, 1996; Garcia-Charton *et al.*, 2000; Koenig *et al.*, 2000; Rodwell *et al.*, 2003; NMFS, 2005). These strategies are commonly single-species oriented, and do not address the issue that reef species have complex interactions with each other and with their biotic and abiotic environment (Koenig *et al*., 2000).

Ecosystem-oriented management strategies, which target the preservation of overall biodiversity and essential fish habitat, may prove more effective at reversing decreasing population trends. Ecosystem strategies are being considered more, especially since 1996, when the Sustainable Fisheries Act amended the Magnuson-Stevens Fishery Conservation Act. This amendment included an essential fish habitat mandate, which requires fisheries managers to identify and protect waters and substrates necessary to fish for spawning, feeding, and reproduction (Schmitten, 1999).

One ecosystem-based management strategy being proposed to the South Atlantic Fisheries Management Council (SAFMC) is the establishment of Marine Protected Areas (MPAs) that would prohibit bottom fishing; these types of reserves have proven to be effective for restoring stocks of reef fish (PDT, 1990; Sedberry *et al*., 1999; Carter and

Sedberry, 1997; McGovern *et al*., 1998; Koenig *et al.*, 2000; SAFMC, 2004). MPAs proposed by the SAFMC will include areas of the sea completely protected from all bottom fishing. Marine reserves that prohibit bottom fishing have been shown to restore or conserve biodiversity (Bohnsack and Ault, 1996; McClahahan and Arthur, 2001; Roberts *et al*., 2001), protect essential fish habitat from destructive fishing practices (Freese *et al.*, 1999; Kaiser *et al.*, 2002), and possibly enhance fisheries stocks through spillover effects (PDT, 1990; McClanahan and Mangi, 2000). Other beneficial characteristics of marine reserves include protection of intraspecific genetic diversity, maintenance of population age structure, and insurance against recruitment failure due to environmental variability (PDT, 1990; Bohnsack and Ault, 1996).

Although no-take MPAs have produced positive results in elevating fish biomass, abundance and mean size (Bohnsack and Ault, 1996; Sedberry *et al.*, 1999; McClanahan and Arthur, 2001; Roberts *et al.*, 2001), they are considered by some to be a drastic management strategy (Shipp, 2003). In order to maximize effectiveness, no-take MPAs should be located in habitats that are known to be essential to exploited species, including fish spawning grounds (Koenig *et al.*, 2000; Lindeman *et al.*, 2000). Potential locations for MPAs proposed by the SAFMC include 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). In order to determine the most effective placement for

MPAs, more information is needed on the fish assemblages inhabiting shelf-edge and upper slope habitats within the SAB, including density estimates, diversity measurements, spawning locations, and specific habitat use.

Many past studies have described the distribution and abundance of fish assemblages associated with deep reef habitats (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 samples 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).

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 from 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 include, but are not limited to, algae, corals, bryozoans, mollusks, and ooliths (Avent *et al.*, 1977; Benson *et al.*, 1997). During the Pleistocene era, shelf-edge reefs were formed and shaped as depositional features at lower sea level stands (Avent *et al.*, 1977; Thompson and Gilliland, 1980; Benson *et al.*, 1997). 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 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).

Visual observations of fish assemblages within these complex habitats may prove to be more effective than traditional gears for sampling distribution and abundance, and would provide information on specific habitat use and behavior. SCUBA observations would be useful; however, many important habitats are located at depths deeper than this equipment can safely operate. Submersibles, on the other hand, can operate at deep depths (up to 10,000 m), and sample for long periods of time (several hours). Also, video cameras used in conjunction with submersibles provide permanent video-documentation without destroying fauna and habitat (Parker *et al.*, 1994). Disadvantages associated with

video analysis include the avoidance or attraction of some species to the submersible (Uzmann *et al*., 1977; Barans, 1986), misidentification of organisms (Parker *et al*., 1994), inaccurate representation of small and cryptic species (Brock, 1982). Limitations of video cameras, however, can be estimated, and judgment made concerning potential bias. While the best assessments of faunal abundance and distribution are probably achieved through a combination of gear types (Uzmann *et al.*, 1977; Starr *et al*., 1995), the overall advantages achieved from submersible visual assessments cannot be surpassed by other techniques used separately in complex deep habitats (Uzmann *et a*l., 1977; Parker and Ross, 1986). In spite of some limitations, submersibles observations are a valuable method of study for fish assemblages inhabiting shelf-edge and upper slope reefs within the SAB.

For this study, in order to better characterize fish assemblages inhabiting shelf-edge and upper slope habitats off the southeast coast, I utilized video footage recorded during submersible dives. The objectives of this study were fourfold. I first wanted to learn about species-specific habitat use by determining how fish assemblages varied among different reef morphologies within shelf-edge reefs surveyed in 2002. Secondly, I wanted to determine how fish assemblages varied among different dive locations within shelf-edge habitats (2002). I then wanted to use observations from two different research cruises, the first conducted in 1985 and the second in 2002, to determine how fish assemblages may have changed over time within shelf-edge and upper slope habitats. Finally, I wanted to document and describe important fish behaviors seen, especially those associated with reproduction. The overall goal of this study was to provide important information – including changes in relative fish abundance over time, species

specific habitat use, and potential fish spawning ground locations – that can be incorporated into multi-species and ecosystem based management models (*Ecopath* and *Ecosim*) (Pauly *et al.*, 2000; Latour *et al.*, 2003). This information may also aid fisheries managers in the future when determining the most effective placement of marine protected areas.

METHODS

Field Methods

In 1985, six submersible dives in the *Johnson Sea Link I* were carried out at five locations along continental shelf-edge and upper-slope reef habitats on 14-19 July. Dive locations off the coast of South Carolina (Fig. 1) were chosen from historical exploratory fishing and fishery survey data (Strushsaker, 1969; Barans and Henry, 1984; Russell *et al.*, 1988; Collins and Sedberry, 1991). Dive locations varied by habitat type and depth (Table 1). The submersible transected these habitats at slow speed for 91.4-m (100-yd.) intervals. A video camera attached to the submersible was held at a constant angle (45° from the bottom), and zoomed out (wide angle) for a panoramic view, while videotaping fishes and associated reef habitats. Transect observations were recorded on beta broadcast videocassettes, which were later copied to VHS cassettes. Dives resulted in a total of 5 h of videotape.

In 2002, 12 additional submersible dives in the *Johnson Sea Link II* were carried out at seven locations along continental shelf-edge and upper slope reef habitats on 28 July - 4 August. Dive locations between St. Augustine, Florida and Charleston, South Carolina were determined from the SCDNR (South Carolina Department of Natural Resources) historical database of suspected or known important reef fish aggregations and spawning activity (Sedberry *et al.*, in press). All shelf-edge dives were conducted within the boundaries of proposed marine protected areas (Fig. 1). Dive locations varied

by habitat type and depth (Table 1). The same general videotaping procedure used during the 1985 cruise was used during the 2002 cruise; however, in 2002 timed transects (4-min) were recorded on mini digital videocassettes (DVs). Dives in 2002 resulted in 34 h of digital videotape.

Video Analyses

Distance (100-yd) transects recorded in 1985 were viewed on a Sanyo 4-Head Hi-Fi VCR a minimum of four times to determine fish species seen and abundance per cubic meter (density). Videos were reviewed, paused, and played in slow motion until identifications and counts were established for each fish. Fish coloration, pattern markings, shape, and swimming behaviors were used to identify individuals to genus and species level using field guides (Robins *et al.*, 1986; Carpenter, 2002). If confident species identifications could not be made, fishes were identified to the lowest possible taxonomic level, or labeled as "unknown." Counts for large schools of fish were estimated.

Transect volume (m^3) was determined by multiplying transect length by transect height and width. Measurements for transect width and height were estimated from two laser beams mounted on the submersible camera. Videos from the 2002 submersibles dives were viewed following the same protocol, except these digital videos were played on a Sony mini digital videocassette recorder (model # GV-D900 NTSC). Also, timed transects (4 min) from 2002 dives varied in length (unlike 1985 dives which had transects of 91.4 m in length). Therefore, 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 *Johnson* in 1985; R/V *Seward Johnson* in 2002), which tracked the underwater location of the submersible. 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. Transect volume (m^3) was determined similarly to transects from 1985 dives (transect length multiplied by transect height and width).

Description of Reef Morphology

Reef morphology data, based on rock size and shape, were collected from the 2002 dives (shelf-edge habitats only). Descriptions of slope reefs followed those of Wenner and Barans (2001); however analysis of fish distribution by habitat type was limited to the morphologically diverse shelf-edge reefs. Shelf-edge reef morphologies were classified into broad categories. Each transect was characterized by the dominant reef morphology that occurred along the transect. Most transects followed a single ridge feature and consisted of only one reef morphology. Those transects that were conducted along more than one reef morphology were not used in further analyses to prevent inaccurate density assessments related to specific bottom types.

Analysis of Fish Counts

In order to compare fish assemblages seen between different years, and among different dive locations, and reef morphologies, 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 (Shapiro-Wilk test), so non-parametric statistics, which report significant variation among median values, rather than means, were used.

To examine changes in fish assemblages among different shelf-edge reef morphologies, or rock size and shape categories, fish density estimates were determined for each fish species within each type of reef morphology. Nonparametric tests (Mann-Whitney U, and Kruskal Wallis) were used to determine if fish density varied significantly ($p<0.05$) among different rock shapes within each dive location. A Mann-Whitney U test was used when dive locations contained only two reef morphologies (Jacksonville Scarp and Scamp Ridge). A Kruskal-Wallis test was used when dive locations contained more than two reef morphologies (Julians Ridge). A multiple comparisons Dunn test was performed to determine which pair(s) of median values varied significantly between one another (Zar, 1999). Dive locations with only one reef morphology sampled (St. Augustine Scarp and Georgetown Hole) were not used in statistical analyses. Species with median densities $<1/km^3$ were considered rare and dropped from statistical analyses.

Diversity parameters [number of species present (S), Margalef's index of species richness (D), Pielou's evenness index (J'), and Simpson index (H')] were calculated for each reef morphology at pooled 2002 shelf-edge dives based on median fish densities. Only fish identified to the species level were used in diversity analyses. Species assemblages were elucidated using Bray-Curtis similarity coefficients to compare pairs of reef morphologies based on species composition and density. A cluster analysis was performed on a similarity matrix generated using PRIMER (Plymouth Routines In

Multivariate Ecological Research) software. Species that contributed to less than 0.03 % of the total fish density (a combined total of less than 0.05 %) were defined as rare and dropped from analyses, since the chance observation of rare species provides little information on dominant patterns and community structure. Densities were transformed (log (x + 1)) to down-weigh the dominance of highly abundant species, so that similarities depended not only on the co-occurrence of very abundant species, but also on those of less common ("mid-range") species. Due to different sample sizes, densities were also standardized to give the percentage of total abundance (over all species) that is accounted for by each species (Clark and Warwick, 2001).

To examine spatial changes in fish assemblages, density estimates were determined for each fish species at all 2002 shelf-edge dive locations (St. Augustine Scarp, Jacksonville Scarp, Julians Ridge, Scamp Ridge, and Georgetown Hole). A Kruskal Wallis test ($p<0.05$) was used to determine if median values for species density varied significantly among dive locations, and a multiple comparisons Dunn test was used to determine which median values were significant from one another. Species with median densities of $<1/km^3$ were considered rare and dropped from statistical analyses. Diversity parameters (S, D, H', J') were also calculated for each shelf-edge dive location (2002) based on median fish densities for spatial comparison. Bray-Curtis similarity coefficients were calculated for quantitative species similarity between each pair of dive locations based on species composition and log (x+1) transformed median density data. A cluster analysis was performed on these similarity coefficients to elucidate species assemblages associated with each dive location.

In addition to spatial comparisons of fish assemblages, temporal changes in assemblages among shelf-edge and upper slope dive locations that were sampled in 1985 and 2002 were analyzed. Density estimates were determined for each fish species at dive locations located off the coast of South Carolina (excluding Georgetown Hole). A Mann-Whitney U test ($p<0.05$) was used to determine significant variation between median values for fish species density at pooled shelf-edge sites in 1985 (M1, M2, M3) and 2002 (Scamp Ridge and Julians Ridge), and between pooled upper slope sites in 1985 (D1 and D3) and 2002 (Charleston Lumps North and Charleston Lumps South). Species with median densities < $1/km^3$ were considered rare and dropped from statistical analyses. Species that had significantly varying densities over time, and that were considered important fishery species were further investigated by comparing trends in commercial landings and fishery-independent surveys. Commercial landings data obtained from the National Oceanographic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) database (http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html) were plotted (pers. comm., NMFS, Fisheries Statistics Division) and compared to data obtained from a fishery-independent survey conducted by the South Carolina Department of Natural Resources (SCDNR) Marine Resources Monitoring, Assessment and Prediction (MARMAP) program. The NMFS database includes fishes caught in the south Atlantic region from North Carolina to Key West. SCDNR MARMAP collections were made between Cape Fear, North Carolina and Cape Canaveral, Florida with occasional samples from north and south of this area.

Diversity parameters (S, D, J', H') were also compared temporally based on median fish densities. Values were calculated for pooled shelf-edge and pooled upper

slope dive locations during 1985 and 2002. Comparisons were made between 1985 and 2002 dive locations conducted within similar habitats (shelf-edge or upper slope).

Reproductive Behavior and Uncommon Species

Reproductive behaviors seen during videos were described and documented. Geographic locations of these behaviors were determined and mapped using ArcView GIS 3.2. Additional observations made of species uncommon to this study site or outside of their normal ranges were also documented and described.

RESULTS

Submersible Dives

Submersible dives conducted in 1985 along shelf-edge habitats had an average depth of 51.8 m (± 1.6 m), and an average temperature of 19.4°C (± 0.4°C), while dives conducted along upper slope habitats had an average depth of 202 m (± 7.8 m), and an average temperature of 13.3°C (± 0.6°C). Submersible dives conducted in 2002 along shelf-edge reefs had an average depth, temperature, and salinity of 51.8 m (± 3.1 m), 20.3°C (± 1.2°C), and 36.5 psu (± 0.1 psu), respectively. Upper slope dives in 2002 had an average depth, temperature, and salinity of 186.3 m (± 1.0 m), 13.1°C (± 0.1°C), and 35.7 psu (± 0.0 psu) in 2002. Dives conducted in 1985 and 2002 varied in transect number, transect volume, and total area viewed (Table 1).

Fish Assemblages

In 1985, 48 transects encompassing 7110 m^3 of water contained a total of 8812 specimens. Of these, 8723 were successfully identified to family, and of those, 8374 to species. A total of 8421 specimens, 16 families, and 28 species were seen during shelf-edge dives. Upper slope dives had far fewer individuals: 391 specimens, four families, and four species (Appendix 1). Dives in 2002 produced 143 transects encompassing 48,722 m^3 of water. These transects contained 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 were seen during shelf-edge dives. Similar to

1985 dives, upper slope dives had far fewer individuals: 706 specimens, seven families, and seven species (Appendix 1).

Distinct fish assemblages were found at shelf-edge versus upper slope dive locations. During both years, shelf-edge habitats were dominated by tomtate (*Haemulon aurolineatum*), vermilion snapper (*Rhomboplites aurorubens*), and yellowtail reeffish (*Chromis enchrysura*) (Appendix 1). Vermilion snapper was the most abundant species seen during 1985, whereas tomtate was the must abundant in 2002. Other common fishes seen in 1985 were bank sea bass (*Centropristis ocyurus*), unidentified damselfishes (Pomacentridae), cubbyu (*Equetus umbrosus*), juvenile yellowfin bass (*Anthias nicholsi*), reef butterflyfish (*Chaetodon sedentarius*), and wrasses (Labridae). Similar species were seen in 2002 shelf-edge habitats, except bank sea bass and juvenile yellowfin bass were less common or absent, and sunshinefish (*Chromis insolata*), squirrelfish (*Holocentrus adscensionis*), tattler (*Serranus phoebe*), sharpnose puffer (*Canthigaster rostrata*), and spotfin hogfish (*Bodianus pulchellus*) were more common. Upper slope habitats were dominated by adult yellowfin bass and blackbelly rosefish (*Helicolenus dactylopterus*) during both years (Appendix 1). The smallscale mora (*Laemonema barbatulum*) was the third most abundant species during 1985 dives on the upper slope, while big roughy (*Gephyroberyx darwinii*) was more prevalent in 2002 dives.

Reef Morphology Variation

Reef morphology seen during 2002 shelf-edge dives varied among dive sites (Table 2). Six reef morphology categories were designated for 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. 2). Dive locations carried out at southern shelf-edge reefs (St. Augustine Scarp and Jacksonville Scarp) were composed of three reef morphology categories: 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. 2 A). Blocked boulders made up the offshore, steep-sloping face of the ridge. These squared-off rocks were about one meter in height, and almost perfectly cubed in shape (Fig. 2 B). 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. 2 C). Dive locations conducted at northern shelf-edge reefs (Julians Ridge, Scamp Ridge, and Georgetown Hole) were composed completely of the bioeroded rock reef morphology (Table 2). This morphology was divided into three categories based on the amount of relief present: low, moderate, and high relief. Low-relief bioeroded rock was pitted with small depressions, which were filled with sediment. Those rocks had relatively flat surfaces overall (Fig. 2 D). 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. 2 E). 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. 2 F).

The number of transects conducted and total area viewed varied within each reef morphology category and within each dive location (Table 3). Average fish densities from each reef morphology revealed that high-relief bioeroded rock was the most densely populated reef morphology with a total density of 2,012 individuals/ km^3, followed by blocked boulders (933/ km^3), moderate-relief bioeroded rock (534/ km^3), buried blocked boulders (444/ km^3), low-relief bioeroded rock (313/ km^3), and slab pavement (50/ km^3). Three dive locations had transects conducted in more than one reef morphology: Jacksonville Scarp, Julians Ridge, and Scamp Ridge. Mann-Whitney U (Jacksonville Scarp and Scamp Ridge) and Kruskal Wallis (Julians Ridge) tests revealed four species with densities that varied significantly among different reef morphologies (Figs. 4-6). Three of these species [tomtate, scamp (*Mycteroperca phenax*), and vermilion snapper] had higher densities on complex reef morphologies, including buried blocked boulders and high-relief bioeroded rock, than on slab pavement and low-relief rocks. The fourth species, tattler, had highest densities on low- or moderate-relief reef morphologies that were often covered in thick layers of sediment. At Jacksonville Scarp, tomtate had higher densities on buried blocked boulders than slab pavement (Fig. 3). At Julians Ridge, tomtate and scamp had higher median densities on high-relief bioeroded rock than low- and moderate-relief. Tattler, unlike the other three species, had lower densities on high-relief bioeroded rock than low and moderate-relief rocks (Fig. 4). At Scamp Ridge, vermilion snapper had higher densities on high-relief bioeroded rock than moderate-relief (Fig. 5).

The median number of fish species (S) for different reef morphologies ranged from 3 to 11. Buried blocked boulders had the highest number of species, closely

followed by high-relief bioeroded rock, blocked boulders, and moderate-relief bioeroded rock (Table 4). Slab pavement and low-relief had far fewer species, 5 and 3, respectively. Species richness (D) ranged from 0.45 to 2.00, with low-relief bioeroded rock having the lowest, and buried blocked boulders having the highest value. Slab pavement had the greatest species evenness, while high-relief bioeroded rock had the least. Overall diversity (H') was highly variable among reef morphologies (Table 4). Buried blocked boulders contained the greatest diversity of fish species, followed by slab pavement, moderate relief, low relief, blocked boulders, and high relief.

Bray-Curtis similarity values were highly variable, ranging from 13.81 to 72.99 (Table 5). Two major groups of morphologies fell out in the cluster analysis (Fig. 6). Slab pavement and low-relief bioeroded rock formed one site group based on similar fish species composition, while the other group was composed of blocked boulders, buried blocked boulders, and moderate and high-relief bioeroded rock.

Spatial Variation

Ten species had densities that varied significantly among 2002 shelf-edge dive locations, including the spotfin hogfish (*Bodianus puchellus*), knobbed porgy (*Calamus nodosus*), sharpnose puffer, spotfin butterflyfish (*Chaetodon ocellatus*), yellowtail reeffish, sunshinefish, tomtate, bigeye (*Priacanthus arenatus*), vermilion snapper, and tattler (Fig. 7). No clear trend was seen 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. Overall, St.

Augustine Scarp was the most densely populated dive site with a total density of 892 individuals/ km^3 of water, followed by Julians Ridge (768/ km^3), Scamp Ridge (704/ km^3), Georgetown Hole (346/ km^3), and Jacksonville Scarp (264/ km^3).

Median number of species seen at dive locations varied from 4 to 10, with Georgetown Hole having the fewest species and Scamp Ridge and St. Augustine Scarp having the most. Georgetown Hole also had the lowest species richness, but this dive location had the highest species evenness (Table 6). H' diversity varied among dive locations, but no trend was seen among diversity parameters and latitude.

Dive locations had relatively high similarity (based on species composition and abundance) with coefficients ranging from 40.54 to 66.64 (Table 7). The cluster analysis revealed that the most closely related dive sites were Scamp Ridge, St. Augustine Scarp and Jacksonville Scarp, while Georgetown Hole and Julians Ridge formed a separate group (Fig. 8). Again, no trend was seen between dive site similarity and latitude.

Temporal Variation

Significant variation between 1985 and 2002 was detected in densities of eight of the 14 shelf-edge fish species tested (Table 8). Two species, the squirrelfish and the sharpnose puffer, had significantly increased median densities between years. Six species, including the knobbed porgy, bank sea bass, spotfin butterflyfish, bigeye, bank butterflyfish (*Prognathodes aya*), and vermilion snapper had significantly decreased median densities from 1985 to 2002. Significant differences in fish density between 1985 and 2002 were detected in two upper slope species (Table 8). Both of these species, the blackbelly rosefish and smallscale mora (*Laemonema barbatulum*), had significantly

decreased median densities between years. Overall, habitats surveyed during 1985 were more densely populated (shelf-edge: 1,760 fish/ km^3; upper slope: 335 fish/ km^3) than those in 2002 (shelf-edge: 769 fish/ km^3; upper slope: 70 fish/ km^3).

Data obtained from the MARMAP fishery-independent survey documented decreased catch per unit effort over time in vermilion snapper and blackbelly rosefish (Figs. 9 & 10); while commercial landings data showed increased landings in metric tons for these species during the same time period (Figs. 9 & 10). Another species that had decreased densities over time and is commercially important was the knobbed porgy. While knobbed porgy does not make up a large percentage of commercial catches, landings have substantially increased since the NMFS began monitoring annual landings for this species in the "south Atlantic" region (Fig. 11). No clear trend was seen in MARMAP fishery-independent survey data for CPUE in knobbed porgy (Fig. 11), as this species was rare in MARMAP catches.

Diversity parameters (S, D, H', J') calculated from median fish densities were compared between 1985 and 2002 shelf-edge and upper slope habitats (Table 9). Median number of species (S), species richness (D) and H' diversity decreased in both habitats over time. Upper slope habitats had decreased species evenness (Pielou's index) in 2002 compared to 1985, whereas shelf-edge habitats remained the same. Overall, decreased diversity parameters were more pronounced in upper slope habitats over time than in shelf-edge habitats. During both years, shelf-edge habitats were more species rich and diverse than upper slope habitats.

Reproductive Behavior

Although actual spawning was not observed during submersibles dives, reproductive behaviors, including courtship and parental care, were observed for five species (Fig. 12). These species included scamp, hogfish, speckled hind (*Epinephelus drummondhayi*), red snapper (*Lutjanus campechanus*), and gray triggerfish (*Balistes capriscus*).

Scamp were observed displaying three different color morphologies, which have been previously described by Gilmore and Jones (1992) in relation to a complex social hierarchy. The most common color phase seen was a light to dark brown body pigmentation (Fig. 12 A). The second most common color morph observed was the "cat paw" phase. Individuals with this color morph had lightened, pale body coloration with clusters of dark brown pigment in the shape of a cat's paw (Fig. 12 B). The third color morph observed was the gray-head phase. In this color morph, the posterior section of the body had dark gray pigmentation with white spots along the belly, and light gray pigmentation anteriorly with interspersed dark gray striations and spots (Fig. 12 C). Scamp displaying the "gray-head" morphology were the largest individuals in the area, and would exhibit courtship behavior by displaying the gray-head color morph, along with rapid, jerky, lateral head movements towards smaller scamp with dark/light brown and cat paw color morphs (Fig. 12 D). Gray-head scamp would display for several seconds, and then change to the cat paw color morph, and finally resume the dark/light gray pigmentation. Gray-head courtship displays were video-documented six times throughout all 2002 shelf-edge dive locations, excluding Georgetown Hole (Fig. 13). These displays occurred at depths from 48-65 m, temperatures between 19.3 and 20.0°C,

and salinities of 36.6 psu. 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 while displaying courtship behavior. On two separate instances, a brightly-colored male [white body with red-brown coloration along head, dorsal surface, and base of caudal fin, and yellow pectoral fins, (Fig. 12 E)] displayed to one or two drab-colored females [brown-pink body, with intricate swirled pattern on head, (Fig. 12 F)]. During courtship displays the male flared the spines in his first dorsal fin (Fig. 12 G, H), while swimming quickly toward the female with rapid quivering oscillations (Colin, 1982; Parker, 2000). Displays were observed at Jacksonville Scarp on July 30, 2002 (Fig. 13), at 1852 and 1927 EDT, at an average depth of 52 m, temperature of 18.6°C, and salinity of 36.5 psu.

Other reproductive related behavior was observed in red snapper. A large school of at least 20-30 individuals (Fig. 12 I), which appeared to be a spawning aggregation, was observed at Scamp Ridge at 1929 EDT on August 2, 2002 (Fig. 13). This school was seen at 53 m, with a bottom temperature of 20.9°C, and salinity of 36.5 psu.

During submersible dives at Jacksonville Scarp (Fig. 13), one speckled hind was observed on July 30, 2002 with an obviously distended abdomen, apparently full of ripe eggs (Fig. 12 J). 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 psu.

Reproductive behavior was observed in gray triggerfish on August 4, 2002 at 1647 EDT. During a dive at Georgetown Hole (Fig. 13), a large triggerfish was observed guarding a nest with an apparent egg mass (Fig. 12 K). 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 psu. Another unguarded nest structure was observed on August 1, 2002 at 1748 EDT during a dive on Julians Ridge (Fig. 12 L). This empty nest was located in 59 m of water, at a bottom temperature of 20.7°C, and salinity of 36.6 psu.

Range Extensions and Uncommon Species

One species, the red lionfish (*Pterois volitans*), was observed during submersible dives outside of its known documented range. A total of four red lionfish (Fig. 14) were observed during 2002 shelf-edge submersible dives at Julians Ridge, Scamp Ridge, and Georgetown Hole. This invasive species was found singularly, and in pairs, sitting on moderate- and high-relief bioeroded rock. Several other species, including speckled hind, blue angelfish, and yellowtail reeffish, were observed in the immediate vicinity, and appeared unaffected by the presence of the lionfish.

Two species that are not commonly observed off South Carolina, the cherubfish (*Centropyge argi*) and the longsnout butterflyfish (*Prognathodes aculeatus*), were seen during submersible dives conducted in 2002. One cherubfish was observed swimming in 59 m of water (temperature=20.8°C, salinity=36.5 psu) among heavily encrusted rocky relief at Georgetown Hole. No individuals of this species were collected, but

identification was made from video footage in which striking color and pattern characteristics were observed (deep blue-purple coloration on body, with yellow-orange coloration on head and chest). 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 psu). The second individual was observed at 1729 EDT at Georgetown Hole, in 59 m of water (temperature=20.7 °C, salinity=36.5 psu). Unlike other butterflyfish species seen, longsnout butterflyfish were not observed swimming in pairs.

DISCUSSION

Reef Morphology Variation

Reef morphology varied greatly among dive locations seen in this study, and this variation is most probably due to large-scale geological, biological, and oceanographic processes (MacIntyre and Milliman, 1970; Wilkinson, 1983; Snyder *et al.*, 1995; Riggs, 1998). Most morphologies seen have been described previously by Barans and Henry (1984). Both studies 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, almost perfectly cubed in shape, were found off the coast of St. Augustine, Florida, and most probably resulted from faulting processes (pers. comm., Leslie Sautter, Geology Department, College of Charleston). Both studies also observed irregular rocky rubble, but in the current study this morphology 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 seen in reef morphology between northern and southern shelf-edge reefs. Northern shelf edge reefs appeared to have high levels of bioerosion, while southern reefs were composed of regular, minimally-modified

rocks (blocked boulders and slab pavement). 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 (Snyder *et al.*, 1995). Although most rocks had invertebrate growth, rocks at northern and southern reefs may have consisted of different mineral compositions and/or supported different bioeroding organisms, and thus were modified at different rates (Riggs, 1998). Another possibility for reef morphology variation is that rocks at northern shelf edge reefs were exposed to physical (Gulf Stream erosion) and biological (bioerosion) activities earlier, and for longer periods of time, when compared to southern reefs. Further investigation is needed to determine why reef morphology varied among dive locations.

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 higher densities of fishes in complex habitats with visual sampling methods (submersibles and remotely operated underwater television). 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*), yellowtail reeffish, large groupers, red porgy (*Pagrus pagrus*), 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 (Carpenter *et al.*, 1981; Parker and Ross, 1986; Felley *et al.*, 1989; Gilmore and Jones, 1992; Murie *et al.*, 1994; 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; Lindholm *et al.*, 2000).

Unlike other species, tattler were more abundant in low-relief habitats often covered in sediment than in high-relief bioeroded rock. Tattler may have been more abundant in sandy habitats because of its ability to camouflage itself well over light-colored substrates. Tattlers have pale whitish bodies with a prominent broad brown bar that is vertically positioned under the dorsal fin rays. Fish were able to change back and fourth between dark (white with dark bar) and light (all white) color morphs by fading this broad bar and other smaller bars along the body. Fish traveling over sandy bottoms displayed the light color morph, whereas individuals swimming in habitats with rocky relief and invertebrate cover displayed the dark color morph. Cryptic behavior may allow tattler to avoid predator attacks while exploiting additional sandy habitats for food resources adjacent to the main rocky reef feature.

Diversity parameters (species number, H'-diversity, species evenness) measured during this study were variable. I found higher species number in complex habitats (an average of 10) than in low-relief, flat habitats (an average of four), as has been noted by other investigators (Parker and Ross, 1986; Ohman and Rajasuriya, 1998; Koenig *et al.*, 2000; Garcia-Charton and Perez-Ruzafa, 2001). H'-diversity, however, was unexpectedly 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 than at present. 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). Other species observed in the current study possibly have biologically significant habitat interactions, but these species may not have been observed from the submersible often enough to determine statistically significant relationships.

Additional habitat research will also benefit future management planning when stock assessment information is insufficient. Advanced technologies, including high-resolution multibeam sonar imagery, GIS techniques, and submersibles, can be used to determine and characterize the distribution of habitat types, and indirectly produce estimates of stock abundance from habitat-specific density estimates (O'Connell and Carlile, 1993; McRea *et al.*, 1999; Yoklavich *et al.*, 2000; Nasby-Lucas *et al.*, 2002). Future management strategies may also benefit from the reverse scenario: the use of fish-distribution data collected from non-visual survey methods (*e.g.* trawls) as a proxy for bottom type and habitat distributions (Auster *et al.*, 2001).

Spatial and Temporal Variation

Many factors can influence the spatial and temporal dynamics 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; Booth, 1992; Wellington, 1992), predation (Hixon, 1986; Hixon and Beets, 1993; Carr and Hixon, 1995; Juncker *et al.*, 2005), water temperature (Huntsman and Manooch, 1978; Miller and Richards, 1980; Sedberry and Van Dolah, 1984; Bohling *et al.*, 1991; 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; Claro, 1991; Koenig *et al.*, 2000). Several fish species densities varied both spatially and temporally in this study, and one could speculate on the causes behind this variation. Further research is needed to determine exactly which factors play a dominant role in structuring fish populations on shelf-edge reefs in the SAB.

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, and interestingly, 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). Several studies have documented varying distribution and abundance of reef fish recruits due to habitat choice during settlement (Sale *et al.*, 1984; Tolimieri, 1995; Choat *et al.*, 1998; Booth, 1992; Wellington, 1992).

For example, threespot damselfish (*Stegastes planifrons*) has been found to settle in higher abundances on a large boulder-building coral, *Monastrea*, than in other habitat types (Tolimieri, 1995). As *Monastrea* coral heads increase in size, it develops many crevices which may function as shelter from predation. Like threespot damselfish, species in the current study with varying densities among different dive locations possibly used reef morphology or habitat type as a settling cue.

Habitat type may also play an important role in structuring fish assemblages by mediating predator-prey interactions after settlement. The amount of relief and refugia 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).

Another factor that may explain spatial and temporal variation in fish species density includes changes and/or variation in water temperature and food availability. Water temperature and food availability have been shown to influence year class strength (Bohling *et al.*, 1991; Francis, 1993; Sedberry *et al.*, 2001) and distribution of many fish species (Huntsman and Manooch, 1978; Miller and Richards, 1980; Sedberry and Van Dolah, 1984). Upwelling events, induced by Gulf Stream meanders and frontal eddies, are the most important processes affecting water temperature and temporal and spatial variability of phytoplankton productivity and biomass at the shelf edge (Lee *et al.*, 1991; Verity *et al.*, 1993). Phytoplankton variability, in turn, influences the growth and survival of zooplankton, larval fish and adult planktivorous fish (Verity *et al.*, 1993).

Bottom temperatures were similar at all submersible dive locations throughout this study (Table 1); however, upwelling events that could drastically affect surface and midwater temperatures, phytoplankton blooms, and species distribution, occur quickly (days to weeks) and regularly along continental shelf-edge habitats (Mathews and Pashuk, 1984; Mathews and Pashuk, 1986; Lee *et al.*, 1991). Upwelling events and variations in sea surface temperature (SST) are regularly documented with NOAA's Geostationary Operational Environmental Satellites (GOES). Imagery from these GOES satellites shows that sea surface temperatures varied among different dive locations, and also among similar dive locations over time, during this study (Fig. 15). Although upwelling events and the varying oceanic parameters (SST and chlorophyll concentrations) that result from such events were not measured in the current study, these variables probably played a continuous role in species recruitment, distribution, and abundance, and may have contributed to fish species spatial and temporal variation seen among dive locations.

One final factor that may have influenced species density over time and among dive locations was fishing pressure. The demand for fishes by the United States has increased dramatically over the past several decades, and many species of reef fish off the Southeast Atlantic coast are overfished or undergoing overfishing, including red porgy (*Pagrus pagrus*), black sea bass (*Centropristis striata*), gag (*Mycteroperca microlepis*), snowy grouper, red grouper (*Epinephelus morio*), black grouper (*M. bonaci*), goliath grouper (*E. itajara*), warsaw grouper (*E. nigritus*), Nassau grouper (*E. striatus*), speckled hind, red snapper, vermilion snapper, and tilefish (*Lopholatilus chamaeleonticeps*) (NMFS, 2005). The change in density of some species seen over time in the current study may directly result from the removal of individuals from a population through

fishing efforts, or indirectly result from ecosystem overfishing. Ecosystem overfishing causes shifts in community structure and changes in relative abundance, as fishing efforts remove top predators and commercially valuable species from the population (McGovern *et al.*, 1998). Shifts in community structure caused by overfishing have been observed along Philippine corals reefs (Russ and Alcala, 1989), the Cuban shelf (Claro, 1991), the continental shelf of the southeastern United States (McGovern *et al.*, 1998), and shelf-edge reefs off western Florida (Koenig *et al.*, 2000). In those studies, shifts in relative abundance of fishes occurred as commercially important species decreased over time, while economically unimportant species increased over time. The current study shows similar trends in vermilion snapper and tomtate populations. In 1985, the vermilion snapper, a recreationally and commercially important species, was most abundant, while tomtate, a commercially unimportant species, was second most abundant. In 2002, however, tomtate was the most abundant species, followed by yellowtail reeffish and then vermilion snapper. Also, a significant decrease in density of vermilion snapper was observed from 1985 to 2002. Similar shifts in relative abundance of vermilion snapper and tomtate in fishery-independent trap surveys were also observed during the same time period (1983-1996) by McGovern *et al.* (1998). While definitive conclusions cannot be made from the current study alone, dramatic increases in commercial landings over time, correlated with decreases in catch per unit effort determined by independent fisheries surveys and reduced numbers observed from submersible, suggest that increased fishing pressure may have caused declines in densities in species like vermilion snapper.

Fishing pressure may have also caused decreased densities in other species seen during this study, such as blackbelly rosefish and knobbed porgy. Blackbelly rosefish are

found within upper slope habitats and are captured incidentally by the bottom longline fishery that targets snowy grouper (White *et al.*, 1998). The fishery directed at rosefish is relatively new and small, but landings for this species have increased greatly since 1989 (up to 147,000 lbs/yr), when the National Marine Fishery Service first began monitoring commercial landings. Landings have also increased for knobbed porgy. Although knobbed porgy does not make up a large percentage of commercial catches, up to 75,000 lb/yr have been landed since 1985. Further monitoring is needed to determine if fishing pressure is significantly affecting densities of these commercially important fish, and other species within the assemblage.

Factors affecting spatial and temporal variation in densities of fish species may have also influenced spatial and temporal variation in community diversity. Similar to other studies (Barans and Henry, 1984; Sedberry and Van Dolah, 1984; Russell *et al.*, 1998), H'-diversity and number of species were much higher in shelf-edge habitats (an average of 1.5 and 11, respectively) than in upper-slope habitats (an average of 0.79 and 3, respectively). Low H'-values in upper slope habitats may be explained by decreased habitat variability and potentially limited food resources with depth (Dennis and Bright, 1988; Lee *et al.*, 1991; Verity *et al.*, 1993; Sedberry *et al.*, 2001; Weaver and Sedberry, 2001; Wenner and Barans, 2001). Diversity parameters (species number, evenness, and H'-diversity) also varied spatially among dive locations, and this may be explained by fish-habitat interactions. Dive locations with the highest number of species (10) contained complex reef morphologies (moderate- to high-relief, and blocked boulders); conversely, Georgetown Hole, which contained mostly low-relief bioeroded rock, had the lowest number of species (4). Unexpectedly, dive locations with mostly complex bottom

types (St. Augustine Scarp and Scamp Ridge) had the lowest H'-diversity values (0.83). Low H'-diversity in these dive locations was linked to low species evenness, which resulted from of a few dominating schooling species (mostly tomtate and vermilion snapper). Temporal variation in diversity parameters (H'-diversity and species number) observed within shelf-edge and upper slope habitats is not easily explained. Similarly to temporal variation seen in fish species density, one possible cause for decreased H'-diversity and species number over time was increased fishing pressure. While it is unlikely that increased fishing results in the removal of an entire species from a community, it is possible that populations of some species were greatly reduced, and thus less likely to be observed during submersible transects. Additionally, ecosystem overfishing may have occurred, which would have caused shifts in relative abundance and dominance of fish species. Since H'-diversity is a measure of not only total number of species, but also species evenness, such shifts in relative abundance may reduce species evenness, and thus lower overall H'-diversity over time.

Reproductive Behavior

Although no actual spawning events were observed during submersible dives, several associated behaviors suggested that spawning for many species occurs within all of the 2002 dive locations. Reproductive behaviors for five commercially important species (scamp, hogfish, red snapper, speckled hind, and triggerfish) were video-documented, and coincided with peak spawning seasons and locations (Matheson *et al.*, 1986; Brule *et al.*, 2000; White and Palmer, 2004; Parker *et al.*, 2000; Murdy *et al.*, 1997; Sedberry *et al.*, in press). At southern shelf-edge reefs, reproductive behaviors were

observed for more species at Jacksonville Scarp (hogfish, speckled hind, scamp) than at St. Augustine Scarp (scamp). At northern shelf-edge reefs, reproductive behaviors were observed more frequently (for triggerfish, red snapper, and scamp) at Julians Ridge and Scamp Ridge locations than at Georgetown Hole (only triggerfish). Differences observed in reproductive behavior may be the result of different habitat types found at different dive locaitons. 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. More fish species may utilize the higher relief habitats at Julians/Scamp Ridge for spawning because structurally complex bottom habitats may provide increased food and shelter availability for spawning fishes compared to low-relief areas such as those observed at Georgetown Hole (Ohman and Rajasuriya, 1998; Lindeman *et al.*, 2000; Lindholm *et al.*, 2000).

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.*, in press). 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; Shipp *et al.*, 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.

Range Extensions and Uncommon Species

One of the three uncommon species observed during submersible dives, the red lionfish, was the result of a human introduction. The normal range for the red lionfish is throughout the Indo-Pacific (Smith, 1969). Recently, however, lionfish have been spotted by SCUBA divers and submersibles in several locations along the western Atlantic coast, including Florida, Georgia, South Carolina, North Carolina, New York, and Bermuda (Whitfield *et al.*, 2002; Meister *et al.*, 2005). It has been speculated that this species was introduced via hurricane damage to mariculture ponds for the aquarium trade. It is unknown what the impacts of this invasive species will be on the naturally occurring ecosystem, but the recent documentation of over ninety specimens, including juveniles, along Atlantic coastal waters suggests that this species is successfully reproducing and becoming established on the western Atlantic coast.

Two other species not commonly observed off South Carolina are the cherubfish and the longsnout butterflyfish, both normally found in southern Florida, Bermuda, the Bahamas, and the Gulf of Mexico along the Caribbean Island arc to the northern coast of South America (Burgess, 2002a; Burgess, 2002b). 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). Continued investigation with submersibles and ROVs may reveal even more species that were thought to be absent or uncommon to deep reef habitats.

Proposed Marine Protected Areas:

In order to maximize the effectiveness of MPAs, designated areas should include essential fish habitats (EFH), defined as waters and substrates that are necessary not only for feeding and growth of fishes, but also for spawning (Bohnsack and Ault, 1996; Schmitten, 1999; Coleman *et al.*, 2000; Koenig *et al.*, 2000; Lindeman *et al.*, 2000; Rodwell *et al.*, 2003). Many recreationally and commercially important fish species are thought to utilize shelf-edge habitats as principle spawning locations (Gilmore and Jones, 1992; Koenig *et al.*, 2000; Sedberry *et al.*, in press), and thus MPAs that would prohibit bottom fishing have been proposed along these habitats. In order to establish effective reserves, it is important to document spawning events and the associated habitat characteristics within proposed locations.

All shelf-edge submersible dives conducted in 2002 were done within proposed MPAs (SAFMC, 2004). Although all proposed locations for MPAs surveyed contained essential fish habitats and reproductive behavior, some proposed MPAs had higher diversity values (H'-diversity, species number) and more species utilizing habitats for reproductive purposes. Results from the current study provide useful information to fisheries managers on potential MPA locations. More research is needed, however, especially in proposed areas not surveyed, to determine exactly which proposed locations should be designated as MPAs in the SAB.

Two potential locations have been proposed for one MPA site off the coast of northern Florida: St. Augustine Scarp dives were inside one potential MPA location, while dives at Jacksonville Scarp were inside the other. Submersible dives conducted at potential locations documented similar habitats (blocked boulders and slab pavement) and fish species composition. H'-diversity values and reproductive behaviors documented within proposed locations, however, differed between sites. H'-diversity was higher at Jacksonville Scarp (1.68) than at St. Augustine Scarp (0.78). Also, more species with reproductive behavior were observed at Jacksonville Scarp (hogfish, speckled hind, scamp) than at St. Augustine Scarp (scamp). Results from the current study suggest that Jacksonville Scarp may contain higher fish assemblage diversity and preferred spawning habitats for more fish species. Another study (Sedberry *et al.*, in press) found vermilion snapper and red porgy spawning in the Jacksonville Scarp site, and gray triggerfish and vermilion snapper spawning in the St. Augustine site. Additional observations are needed to determine which potential location would act as a more effective MPA off the coast of northern Florida.

Two potential locations have been proposed for one MPA site off the coast of central South Carolina, and three optional locations have been proposed for another site off the coast of northern South Carolina. Submersible dives were conducted inside one central and one northern potential location. Recommendations cannot be made from the current study alone concerning which potential locations would make the most effective central and northern MPAs, because dives were conducted inside only one of the two potential locations off central South Carolina, and one of the three potential locations off the coast of northern South Carolina. Preliminary comparisons can be made, however,

between central (Julians Ridge/Scamp Ridge) and northern (Georgetown Hole) locations. Dives conducted inside northern and central locations revealed very different habitat types, species densities, and reproductive behaviors. Julians Ridge and Scamp Ridge had more complex reef morphologies (moderate- and high-relief bioeroded rock), higher fish densities (an average of 736 fish/ km^3), and a greater number of species with reproductive behaviors (three) than Georgetown Hole (low-relief bioeroded rock; 346 fish/ km^3; 1, respectively). Sedberry *et al.* (in press) also found many species spawning at, or near, Julians Ridge and Scamp Ridge (proposed MPA Site B, option 1, off coast of central South Carolina), including gray triggerfish, knobbed porgy, blueline tilefish, bank sea bass, red grouper, red snapper, gag, scamp, red porgy and vermilion snapper. Results from both studies suggest that sites near Julians Ridge and Scamp Ridge may act as more productive locations for future MPAs than areas near Georgetown Hole; however, more research should be conducted to determine the characteristics of other proposed optional locations off of South Carolina not observed during the current study.

SUMMARY AND CONCLUSIONS

Video footage recorded during submersible dives documented variation in the habitat characteristics, spatial and temporal distribution of fishes, and fish reproductive activity in shelf-edge and upper slope reef habitats in the SAB. Shelf-edge habitats were composed of six reef morphologies, with southern reefs consisting of less modified shapes (blocked boulders, buried blocked boulders, slab pavement) and northern reefs consisting of more bioeroded shapes (low-, moderate-, high-relief bioeroded rock). Several species (tomtate, scamp, vermilion snapper) had higher densities on structurally complex reef morphologies (blocked boulders, moderate-, high-relief bioeroded rock) than on low-relief rocks. Tattler was the only species found with higher densities on low-relief rock than on more complex habitats. Several species also had significantly varying densities among different shelf-edge dive locations; however, no clear trend was observed between species density and location. Dive locations with structurally complex habitats (Julians/Scamp Ridge, St. Augustine Scarp) had higher fish densities than those composed of low-relief habitats (Georgetown Hole). Ten species had significantly varying densities between 1985 and 2002, with eight species having decreased densities over time. Some commercially valuable species, such as vermilion snapper, may be experiencing decreased densities due to increases in fishing pressure over time. Reproductive behaviors were observed for five commercially important species (scamp, hogfish, red snapper, speckled hind, triggerfish). At southern reefs, Jacksonville Scarp had three species (scamp, hogfish, speckled hind) with reproductive behaviors, whereas

St. Augustine Scarp only had one (scamp). At northern reefs, more species were observed with reproductive behaviors at Julians Ridge and Scamp Ridge than at Georgetwon Hole. Certain dive locations observed during the current study, such as Jacksonville Scarp, Julians Ridge and Scamp Ridge, contained higher fish species densities and diversity, and may contain preferable spawning habitats for more species.

The overall goal of the current project was to make information on fishes and associated reef habitats available to fisheries managers to aid in the process of identifying the most effective placement for marine protected areas within the SAB. Areas containing complex reef morphologies, high fish densities and diversity, and important spawning habitats should be considered for MPA status as an alternative management strategy for sustainable fisheries. Continued research should be conducted, however, to assess the effects of MPAs on reef fish populations, and to determine if MPAs act as a successful management tool that ensures the persistence of healthy fish stocks in the South Atlantic Bight.

LITERATURE CITED

Auster, P. J., K. Joy and P. C. Valentine. 2001. Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (northwest Atlantic, Gulf of Maine). Environ. Biol. Fish. 60: 331-346.

Avent, R. M., M. E. King and R. H. Gore. 1977. Topographic and faunal studies of shelf-edge prominences off the central eastern Florida coast. Int. Revue ges. Hydrobiol. 62 (2): 185-208.

Bane, Jr., J. M., L. P. Atkinson and D. A. Brooks. 2001. Gulf Stream physical oceanography at the Charleston Bump: deflection, meanders, and upwelling. Am. Fish. Soc. Symp. 25: 25-36.

Barans, C. A. and V. J. Henry. 1984. A description of the shelf edge groundfish habitat along the southeastern United States. Northeast Gulf Sci. 7 (1): 77-96.

Barans, C. A.. 1986. Submersible avoidance by yellowfin bass, *Anthias nicholsi*. Northeast Gulf Sci. 8 (1): 91-95.

Barlow, G. W.. 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. Environ. Biol. Fish. 6 (1): 65-85.

Benson, D. J., W. W. Schroeder and A. W. Shultz. 1997. Sandstone hardbottoms along the western rim of DeSoto Canyon, northeast Gulf of Mexico. Gulf Coast Assoc. Geol. Soc. Trans. XLVII: 43-48.

Bohling, P., R. Hudd, H. Lehtonen, P. Karas, E. Neuman and G. Thoresson. 1991. Variations in year-class strength of different perch (*Perca fluviatilis*) populations

in the Baltic Sea with special reference to temperature and pollution. Can. J. Fish. Aquat. Sci. 48: 1181-1187.

Bohnsack, J.A. and J. S. Ault. 1996. Management strategies to conserve marine biodiversity. Oceanography 9 (1): 73-82.

Booth, D. J.. 1992. Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. J. Exp. Mar. Biol. Ecol. 155: 85-104.

Brock, R. E.. 1982. A critique of the visual census method for assessing coral reef fish population. Bull. Mar. Sci. 32: 269-276.

Brule, T., T. Colas-Marrufo, A. Tuz-Sulub and C. Deniel. 2000. Evidence for protogynous hermaphroditism in the serranid fish *Epinephelus drummondhayi* (Perciformes: Serranidae) from the Campeche Bank in the southern Gulf of Mexico. Bull. Mar. Sci. 66: 513-521.

Burgess, W.E. 2002a. Pomacanthidae. In: K.E. Carpenter (ed.). The living marine resources of the Western Central Atlantic. Vol. 3. Bony fishes part 2 (Opistognathidae to Molidae). *FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologist Special Publication* No. 5. Rome, FAO, pp. 1673-1683.

Burgess, W.E. 2002b. Chaetodontidae. In: K.E. Carpenter (ed.). The living marine resources of the Western Central Atlantic. Vol. 3. Bony fishes part 2 (Opistognathidae to Molidae). *FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologist Special Publication* No. 5. Rome, FAO, pp. 1663-1672.

Cailliet, G. M., A. H. Andrews, W. W. Wakefield, G. Moreno and K. L. Rhodes. 1999. Fish faunal and habitat analyses using trawls, camera sleds and submersibles in benthic deep-sea habitats off central California. Oceanologica Acta 22 (6): 579-592.

Carpenter, K. E., R. I. Miclat, V. D. Albaladejo and V. T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. Proc. Fourth Int. Coral Reef Symp., Manila. 2: 497-502.

Carpenter, K. E. (ed.). 2002. The living marine resources of the Western Central Atlantic. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. Vols. 1-3. Rome, FAO, 2127 pp.

Carr, M. H. and M. A. Hixon. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. Mar. Eco. Prog. Ser. 124 (1): 31-42.

Carter, J. and G. R. Sedberry. 1997. The design, function and use of marine fishery reserves as tools for the management and conservation of the Belize Reef. Proc. 8th Int. Coral Reef Symp. 2: 1911-1916.

Choat, J. H., A. M. Ayling and D. R. Schiel. 1998. Temporal and spatial variation in an island fish fauna. J. Exp. Mar. Biol. Ecol. 121: 91-111.

Chester, A. J., G. R. Huntsman, P. A. Tester and C. S. Manooch, III. 1984. South Atlantic Bight reef fish communities as represented in hook-and-line catches. Bull. Mar. Sci. 34: 267-279.

Clark, K. R. and R. M. Warwick. 2001. Change in Marine Communities: An approach to statistical analysis and interpretation. 2nd edition. PRIMER-E Ltd. Plymouth Marine Laboratory, UK.

Claro, R.. 1991. Changes in fish assemblages structure by the effect of intense fisheries activity. Trop. Ecol. 32 (1): 36-46.

Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, R. W. Chapman, G. R. Sedberry and C. B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. Fisheries 25 (3): 14-21.

Colin, P. L.. 1982. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae). Fish. Bull. 80 (4): 853-862.

Collins, M. R. and G. R. Sedberry. 1991. Status of vermilion snapper and red porgy stocks off South Carolina. Trans. Am. Fish. Soc. 120:116-120.

Cuellar, N., G. R. Sedberry, D. J. Machowski and M. R. Collins. 1996. Species composition, distribution and trends in abundance of snappers of the southeastern USA, based on fishery-independent sampling. In: Arreguin-Sanchez, F., J. L. Munro, M. C. Balgos, and D. Pauly (eds.). *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, pp. 59-73.

Dennis, G. D. and T. J. Bright. 1988. Reef fish assemblages on hard banks in the northwestern Gulf of Mexico. Bull. Mar. Sci. 43: 280-307.

Felley, J. D., M. Vecchione, G. R. Gaston and S. M. Felley. 1989. Habitat selection by demersal nekton: analyses of videotape data. Northeast Gulf Sci. 10(2): 69-84.

Felley, J. and M. Vecchione. 1995. Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles. Fish. Bull. 93: 262-273.

Francis, M. P.. 1993. Does water temperature determine year class strength in New Zealand snapper (*Pagrus auratus*, Sparidae)? Fish. Oceanog. 2(2): 65-72.

Freese, L., P. J. Auster, J. Heifetz and B. L. Wing. 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar. Ecol. Prog. Ser. 182: 119-126.

Garcia-Charton, J. A.G., I. D. Williams, A. R. Ruzafa, M. Milazzo, R. Chemello, C. Marcos, M. S. Kitsos, A. Koukouras and S. Riggio. 2000. Evaluating the ecological effects of Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems. Env. Cons. 27(2):159-178.

Garcia-Charton, J. A. and A. Perez-Ruzafa. 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar. Biol. 138: 917-934.

Gilmore, R. G. and R. S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. Mar. Sci. 5:83-103.

Grimes, C. B., C. S. Manooch and G. R. Huntsman. 1982. Reef and rock outcropping fishes of the outer continental shelf of North Carolina and South Carolina, and ecological notes on the red porgy and vermilion snapper. Bull. Mar. Sci. 32: 277-289.

Gutherz, E. J.,W. R. Nelson, R. S. Jones, C. A. Barans, C. A. Wenner, G. M. Russell and A. K. Shah. 1994. Population estimates of deep-water finfish species based on submersible observations and intensive fishing efforts off Charleston, S. C.. In: Bohnsack, J. A. and A. Woodhead (eds.). *Proc. 1987 SEAMAP Passive Gear Assessment Workshop Mayaguez, Puerto Rico*. NMFS-SEFSC-365, pp. 103-123.

Haedrich, R. L.. 1998. Overfishing and the biogeography of a continental shelf fish community. Int. Conf. Pelagic Bio. Netherlands. IOC Workshop Report No. 142: 143-147.

Harris, P. J., D. M. Wyanski, D. B. White and J. L. Moore. 2002. Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern north Atlantic, 1979-1997. Bull. Mar. Sci. 70:113-132.

Hixon, M. A.. 1986. Fish predation and local prey diversity. Gutshop ’84. Workshop on fish food habits, Pacific, Grove, CA. Dec. 2-6.

Hixon, M. A. and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63 (1): 77-101.

Huntsman, G. R. and C. S. Manooch, III. 1978. Coastal pelagic and reef fishes in the South Atlantic Bight. Marine Recreational Fisheries, No. 3. Proc. 2nd Ann. Mar. Rec. Fish. Symp., Norfolk, Va.

Jordan, F., M. Bartolini, C. Nelson, P. E. Patterson and H. L. Soulen. 1996. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Lennaeus). J. Exp. Mar. Biol. Ecol. 208: 45-56.

Juncker, M., L. Wantiez, D. Lecchini and R. Galzin. 2005. Effects of habitat on the behaviour and mortality of juveniles of *Chromis viridis* (Pomacentridae). Cybium 29 (1): 3-12.

Kaiser, M. J., J. S. Collie, S. L. Hall, S. Jennings and I. R. Poiner. 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish and Fisheries 3:114-136.

Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperature reef-fish fisheries of shelf-edge reefs of Florida. Bull. Mar. Sci. 66: 593-616.

Latour, R. J., M. J. Brush and C. F. Bonzek. 2003. Toward ecosystem-bases fisheries management: strategies for multispecies modeling and associated data requirements. Fisheries 28(9):10-22.

Lee, T. N., J. A. Yoder and L. P. Atkinson. 1991. Gulf Stream frontal eddy influence on productivity of the southeast U.S. continental shelf. J. Geo. Res. 96 (C12): 22,191-22,205.

Lindeman, K. C., R. Pugliese, G. T. Waugh and J. S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bull. Mar. Sci. 66: 929-956.

Lindholm, J. B., P. J. Auster, M. Ruth and L. Kaufman. 2000. Modeling the effects of fishing and implications for the design of marine protected areas: juvenile fish responses to variations in seafloor habitat. Cons. Biol. 15(2): 424-437.

MacIntyre, I. G. and J. D. Milliman. 1970. Physiographic features on the outer continental shelf and upper slope, Atlantic continental margin, southeastern United States. Geo. Soc. Am. Bull. 81: 2577-2598.

Matheson, III, R. H., G. R. Huntsman and C. S. Manooch, III. 1986. Age, growth, mortality, food, and reproduction of the scamp, *Myteroperca phenax*, collected off North Carolina and South Carolina. Bull. Mar. Sci. 38: 300-312.

Mathews, T. D. and O. Pashuk. 1984. Shelfwater response to the cold winters of 1977 and 1978 in the South Atlantic Bight (SAB). Litoralia 1(1): 41-58.

Meister, H. S., D. M. Wyanski, J. K. Loefer, S. W. Ross, A. M. Quattrini and K. J. Sulak. 2005. Further evidence for the invasion and establishment of *Pterios Volitans* (Teleostei: Scorpaenidae) along the Atlantic coast of the United States. Southeast. Nat. 4 (2): 193-206.

McClanahan, T. R. and R. Arthur. 2001. The effect of marine reserves and habitat on populations of east African coral reef fishes. Ecol. Appl. 11: 559-569.

McClanahan, T. R. and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecol. Appl. 10: 1792-1805.

McGovern, J. C., G. R. Sedberry and P. J. Harris. 1998. The status of reef fish stocks off the southeast United States, 1983-1996. Proc. Gulf Caribb. Fish. Inst. 50: 870-895.

McRea, Jr., J. E., H. G. Greene, V. M. O'Connell and W. W. Wakefield. 1999. Mapping marine habitats with high resolution sidescan sonar. Oceanolgica Acta. 22(6): 679-686.

Miller, G. C. and W. J. Richards. 1980. Reef fish habitat, faunal assemblages and factors determining distributions in the South Atlantic Bight. Proc. Gulf Caribb. Fish. Inst. 32: 114-130.

Mora, C. and P. F. Sale. 2002. Are populations of coral reef fish open or closed? Trends in Ecol. and Evo. 17 (9): 422-428.

Murdy, E. O., R. S. Birdsong and J. A. Musick. 1997. Fishes of the Chesapeake Bay. Smithsonian Institution Press, Washington, 324 pp.

Murie, D. J., D. C. Parkyn, B. G. Clapp and G. G. Krause. 1994. Observations on the distribution and activities of rockfish, *Sebastes* spp., in Saanich Inlet, British Columbia, from the *Pisces IV* submersible. Fish. Bull. 92: 313-323.

Nasby-Lucas, N. M., B. W. Embley, M. A. Hixon, S. G. Merle, B. N. Tissot and D. J. Wright. 2002. Integration of submersible transect data and high-resolution multibeam sonar imagery for a habitat-based groundfish assessment of Heceta Bank, Oregon. Fish. Bull. 100: 739-751.

NMFS. 2005. Annual report to Congress on the status of U.S. Fisheries - 2004. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, MD. 20 pp.

O'Connell, V. M. and D. W. Carlile. 1993. Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska. Fish. Bull. 91: 304-309.

Ohman, M. C. and A. Rajasuriya. 1998. Relationships between habitat structure and fish communities on coral and sandstone reefs. Env. Biol. Fish. 53: 19-31.

Parker, Jr., R. O. and S. W. Ross. 1986. Observing reef fishes from submersibles off North Carolina. Northeast Gulf Sci. 8(1): 31-49.

Parker, Jr., R. O., A. J. Chester and N. S. Russell. 1994. A video transect method for estimating reef fish abundance composition, and habitat utilization at Gray's Reef National Marine Sanctuary, Georgia. Fish. Bull. 92: 787-799.

Parker, Jr., R. O. and R. W. Mays. 1998. Southeastern U. S. deepwater reef fish assemblages, habitat characteristics, catches, and life history summaries. NOAA Technical Report NMFS 138, 41 pp.

Parker, Jr., R. O.. 2000. Courtship in hogfish, *Lachnolaimus maximus*, and other behavior of reef fishes off Beaufort, North Carolina. J. Elisha Mitchell Sci. Soc. 116 (3): 260-261.

Pauly, D., V. Christensen and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. J. Mar. Sci. 57: 1-10.

PDT (Plan Development Team). 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA Tech. Mem. NMFS-SEFC-216, Miami, FL, pp. 1-40.

Quattrini, A. M., S. W. Ross, K. J. Sulak, A. M. Necaise, T. L. Casazza and G. Dennis. 2004. Marine fishes new to continental United States waters, North Carolina, and the Gulf of Mexico. Southeastern Naturalist 3 (1): 155-172.

Riggs, S. R., M. A. Garcia del Cura and J. Soria. 1998. Development of hardbottoms and associated sediment facies on sediment-starved continental margins. International Sedimentological Congress, Alicante, Spain, pp. 663-664.

Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Sci. 294: 1920-1923.

Robins, C. R. and G. C. Ray. 1986. Peterson field guide: Atlantic coast fishes. Houghton Mifflin Co., Boston, 354 pp.

Rodwell, L. D., E. B. Barbier, C. M. Roberts and T. R. McClanahan. 2003. The importance of habitat quality for marine reserve-fishery linkages. Can. J. Fish. Aquat. Sci. 60: 171-181.

Russ, G. R. and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Mar. Ecol. Prog. Ser. 56: 13-27.

Russell, G. M., E. J. Gutherz and C. A. Barans. 1988. Evaluation of demersal longline gear off South Carolina and Puerto Rico with emphasis on deep-water reef fish stocks. Mar. Fish. Rev. 50 (1): 26-31.

SAFMC. 2004. Informational public hearing document on marine protected areas to be included in Amendment 14 to the fishery management plan for the snapper grouper fishery of the South Atlantic region. South Atlantic Fishery Management Council, Charleston, South Carolina, 48 pp. Unpubl. MS.

Sale, P. F., Douglas, W. A., and P. J. Doherty. 1984. Choice of microhabitats by coral reef fishes as settlement. Coral Reefs. 3: 91-99.

Schmitten, R. A.. 1999. Essential fish habitat: opportunities and challenges for the next millennium. In: L. R. Benaka, (ed.). *Fish habitat: essential fish habitat and rehabilitation.* American Fisheries Society, Symposium 23, Bethesda, Maryland, pp. 3-10.

Schwartz, F. J.. 1989. Zoogeography and ecology of fishes inhabiting North Carolina's marine waters to depths of 600 meters. In: George, R. Y., and A. W. Hulbert (eds.). *North Carolina coastal oceanography symposium*, pp. 335-374.

Sedberry, G. R. and R. F. VanDolah. 1984. Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. Env. Biol. Fish. 11 (4): 241-258.

Sedberry, G. R., J. C. McGovern and C. A. Barans. 1998. A comparison of fish populations in Gray's Reef National Marine Sanctuary to similar habitats off the

southeastern U.S.: Implications for reef fish and sanctuary management. Proc. Gulf Caribb. Fish. Inst. 50: 452-481.

Sedberry, G. R., H. J. Carter and P. A. Barrick. 1999. A comparison of fish communities between protected and unprotected areas of the Belize reef ecosystem: implications for conservation and management. Proc. Gulf Caribb. Fish. Inst. 45: 95-127.

Sedberry, G. R., J. C. McGovern and O. Pashuk. 2001. The Charleston Bump: An island of essential fish habitat in the Gulf Stream. Am. Fish. Soc. Symp. 25: 2-24.

Sedberry, G. R., O. Pashuk, D. M. Wyanski, J. A. Stephen and P. Weinbach. (In press). Spawning locations for Atlantic reef fishes off the southeastern United States. Proc. Gulf Caribb. Fish. Inst 57.

Shipp, R. L., W. A. Tyler, III and R. S. Jones. 1986. Point count censusing from a submersible to estimate reef fish abundance over large areas. Northeast Gulf Sci. 8: 83-89.

Shipp, R. L.. 2003. A perspective on marine reserves as a fishery management tool. Fisheries. 23 (12): 10-21.

Sluka, R. D., M. Chiappone and K. M. Sullivan-Sealey. 2001. Influence of habitat on grouper abundance in the Florida Keys, U.S.A.. J. Fish Bio. 58: 682-700.

Smith, J. L. B.. 1969. Fishes of Inhaca. In: Macnae, W. and M. Kalk (eds.). *A natural history of Inhaca Island, Moçambique*. Witwatersrand University Press, Johannesburg, pp. 131-136.

Snyder, S. W., S. R. Riggs, K. A. Schmid and W. G. Ambrose. 1995. Sediment production/dynamics on a sediment-starved continental margin. SEPM Congress on Sedimentary Geology, Saint Petersburg, FL.

Starr, R. M., D. S. Fox, M. A. Hixon, B. N. Tissot, G. E. Johnson and W. H. Barss. 1995. Comparison of submersible-survey and hydroacoustic-survey estimates of fish density on a rocky bank. Fish. Bull. 94: 113-123.

Struhsaker, P.. 1969. Demersal fish resources: composition, distribution, and commercial potential of the continental shelf stocks off southeastern United States. Fish. Ind. Res. 4: 261-300.

Thresher, R. E.. 1984. Reproduction in reef fishes. T.F.H. Publications, Inc. Ltd.. Neptune City, NJ, 399 pp.

Thompson, M. J. and L. E. Gilliland. 1980. Topographic mapping of shelf edge prominences off southeastern Florida. Southeastern Geology. 21: 155-164.

Tolimieri, N.. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia 102: 52-63.

Uzmann, J. R., R. A. Cooper, R. B. Theroux and R. L. Wigley. 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible vs camera sled vs otter trawl. Mar. Fish. Rev. 39 (12): 11-19.

Verity, P. G., T. N. Lee, J. A. Yoder, G. A. Paffenhofer, J. O. Blanton and C. R. Alexander. 1993. Outer shelf processes. In: Menzel, D. W. (ed.). *Ocean processes: U.S. southeast continental shelf*. U. S. Department of Energy. Oak Ridge, TN, pp. 45-74.

Weaver, D. C. and G. R. Sedberry. 2001. Trophic subsidies at the Charleston Bump: Food web structure of reef fishes on the continental slope of the southeastern United States. Am. Fish. Soc. Symp. 25: 137-152.

Wellington, G. M.. 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. Oecologia. 90: 500-508.

Wenner, E. L., D. M. Knott, R. F. Van Dolah and V. G. Burrel, Jr.. 1983. Invertebrate communities associated with hard bottom habitats in the South Atlantic Bight. Estuarine Coastal Shelf Sci. 17: 143-158.

Wenner, E. L. and C. A. Barans. 2001. Benthic habitats and associated fauna of the upper- and middle-continental slope near the Charleston Bump. Am. Fish. Soc. Symp. 25: 161-175.

White, D. B., D. M. Wyanski and G. R. Sedberry. 1998. Age, growth, and reproductive biology of the blackbelly rosefish from the Carolinas, U.S.A.. J. Fish Biol. 53: 1274-1291.

White, D. B. and S. M. Palmer. 2004. Age, growth, and reproduction of the red snapper, *Lutjanis campechanus*, from the Atlantic waters of the southeastern U.S.. Bull. Mar. Sci. 75: 335-360.

Whitfield, P. E., T. Gardner, S. P. Vives, M. R. Gilligan, W. R. Courtenay, Jr., C. Ray and J. A. Hare. 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. Mar. Ecol. Prog. Ser. 235: 289-297.

Wilkinson, C. R.. 1983. Role of sponges in coral reef structural processes. In: Barnes, D. J.. *Perspective on coral reefs*. Brian Clouston Publisher, Manuka, Australia, pp. 263-274.

Wyanski, D. M., D. B. White and C. A. Barans. 2000. Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. Fish. Bull. 98: 199-218.

Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea and M. S. Love. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. Fish. Bull. 98: 625-641.

Zar, J. H.. 1999. Biostatistical Analysis. Prentice-Hall, New Jersey. 663 pp.

Figure 1. Locations for submersible dives and proposed marine protected areas. Triangles=Dives conducted in 1985, Circles=Dives conducted in 2002, Gray symbols=Shelf-edge dive locations, Black symbols=Upper-slope dive locations, Striped polygons=Proposed marine protected areas.

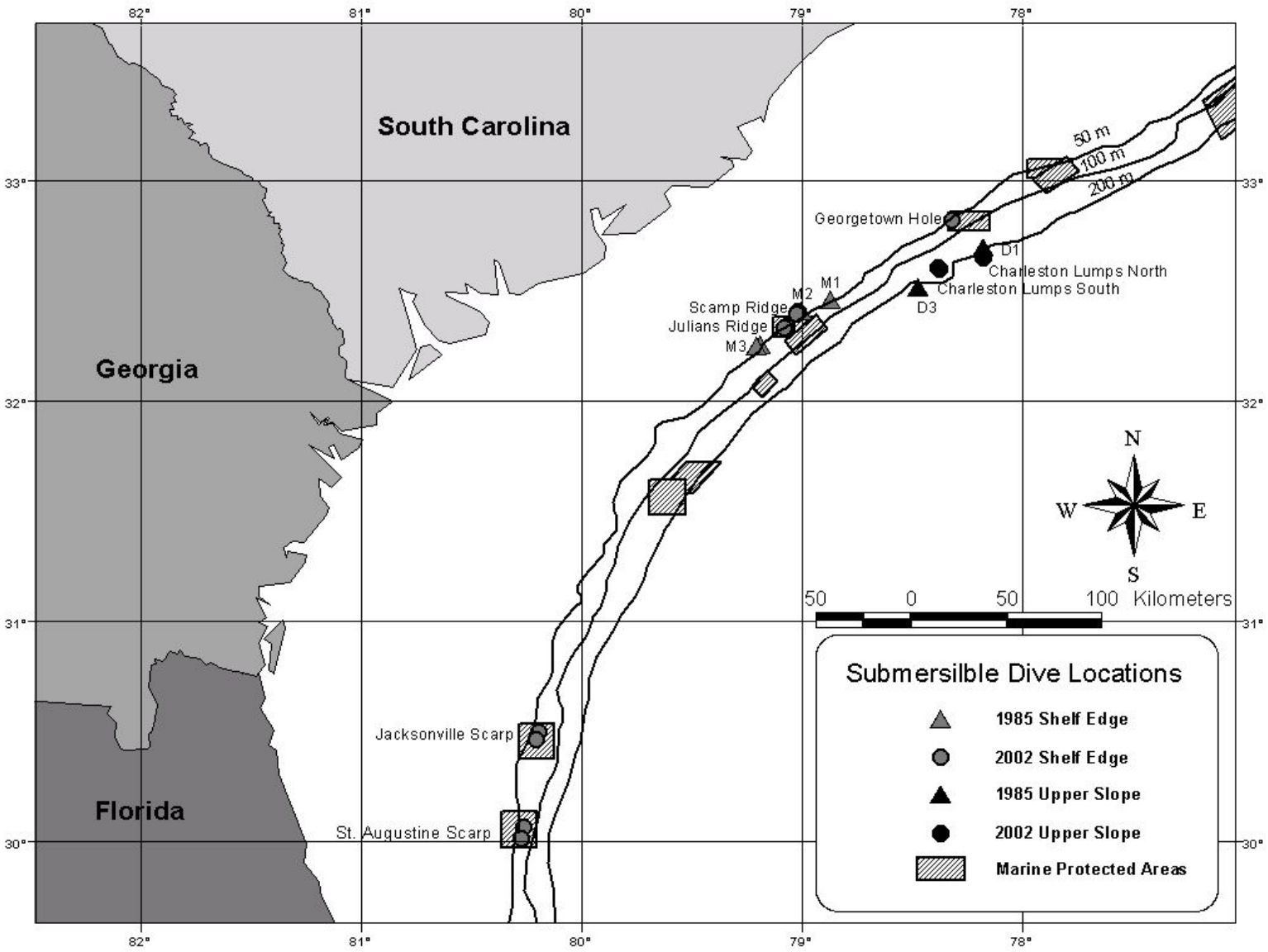
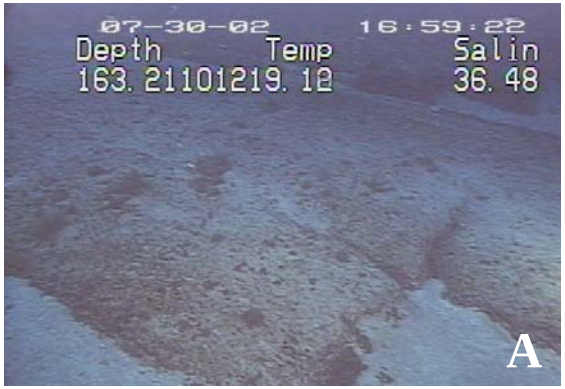

South Carolina
Georgia
Florida
82°
81°
80°
79°
78°
33°
32°
31°
30°
50 m
100 m
200 m
Georgetown Hole
D1
Charleston Lumps North
Charleston Lumps South
D3
M1
M2
Scamp Ridge
Julians Ridge
M3
Jacksonville Scarp
St. Augustine Scarp
N
W
E
S
50
0
50
100 Kilometers
Submersilble Dive Locations
1985 Shelf Edge
2002 Shelf Edge
1985 Upper Slope
2002 Upper Slope
Marine Protected Areas

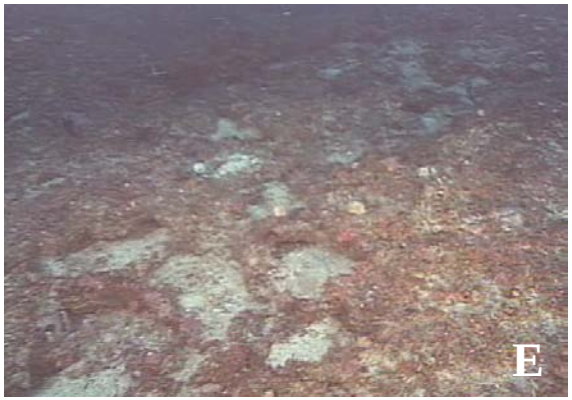
Figure 2. Six reef morphology categories seen during 2002 shelf-edge dives. A=Slab Pavement, B=Blocked Boulders, C=Buried Blocked Boulders, D=Low-relief Bioeroded, E=Moderate-relief Bioeroded, F=High-relief Bioeroded.


07-30-02 16:59:22
Depth Temp Salin
163.21101219.12 36.48
A

07-28-02 11:27:31
Depth Temp Salin
178.0 20.18 36.44
B

07-30-02 10:42:30
Depth Temp Salin
179.9 19.00 36.42
C

08-04-02 16:50:45
Depth Temp Salin
166.0 20.54230105.36.50
D


E

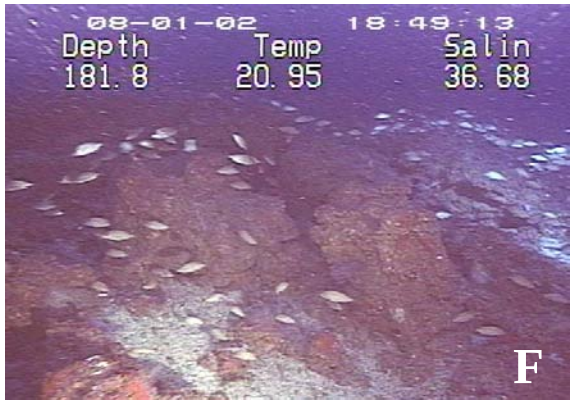

08-01-02 18:49:13
Depth Temp Salin
181.8 20.95 36.68
F

Figure 3. Box plot showing significant differences in median densities for tomtate (*Haemulon aurolineatum*) between different reef morphologies 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 morphologies.

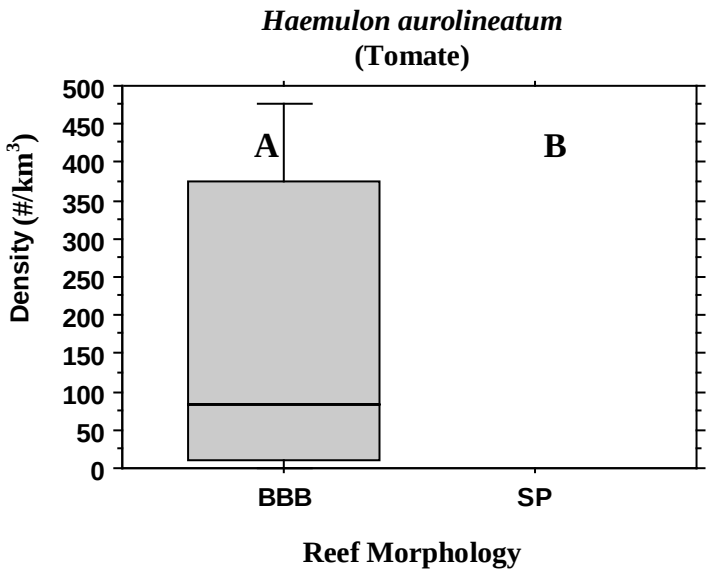
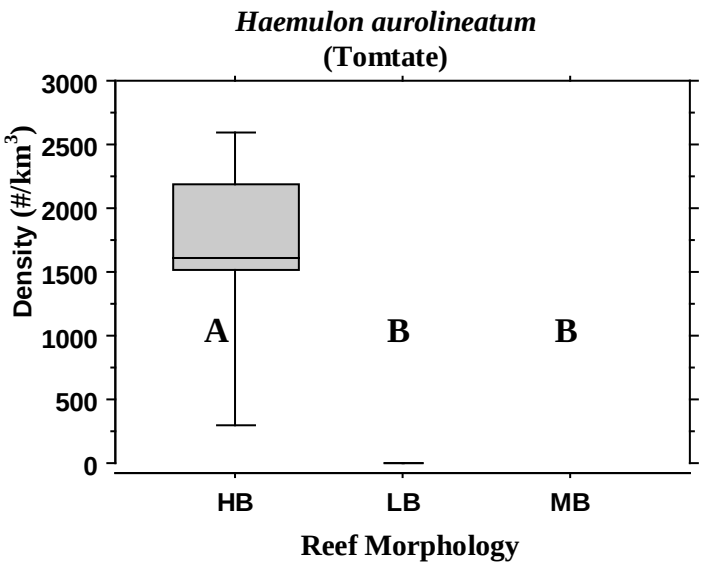
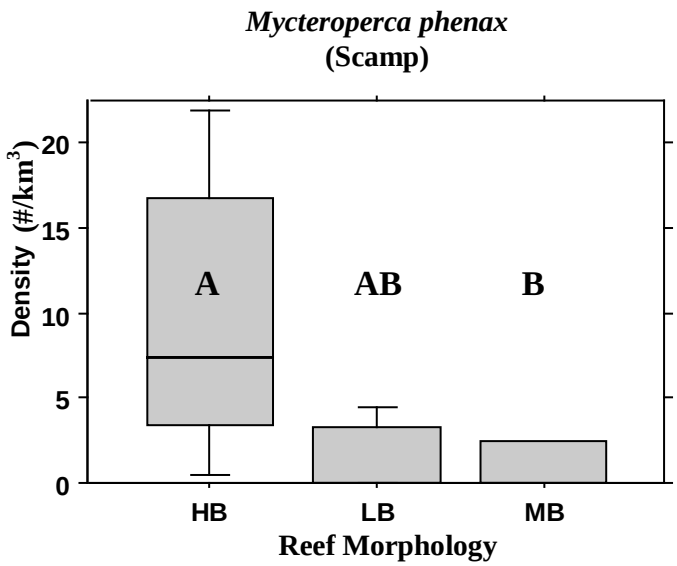

Haemulon aurolineatum
(Tomate)
Density (#/km^3)
500
450
400
350
300
250
200
150
100
50
0
A
B
BBB
SP
Reef Morphology

Figure 4. Box plots showing significant differences in median fish densities among different reef morphologies found at Julians Ridge (LB=Low-relief bioeroded, MB=Moderate-relief bioeroded, HB=High-relief bioeroded). 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 morphologies.


Haemulon aurolineatum
(Tomtate)
Density (#/km^3)
3000
2500
2000
1500
1000
500
0
A
B
B
HB
LB
MB
Reef Morphology


Mycteroperca phenax
(Scamp)
Density (#/km^3)
20
15
10
5
0
A
AB
B
HB
LB
MB
Reef Morphology

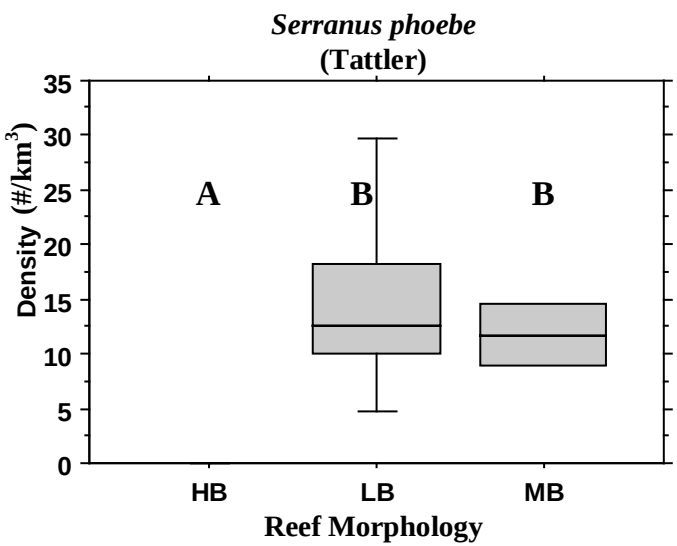

Serranus phoebe
(Tattler)
Density (#/km^3)
35
30
25
20
15
10
5
0
A
B
B
HB
LB
MB
Reef Morphology

Figure 5. Box plot showing significant differences in median densities of vermilion snapper (*Rhomboplites aurorubens*) between reef morpholiges found at Scamp Ridge (MB=Moderate-relief bioeroded, HB=High-relief bioeroded). 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 morphologies.

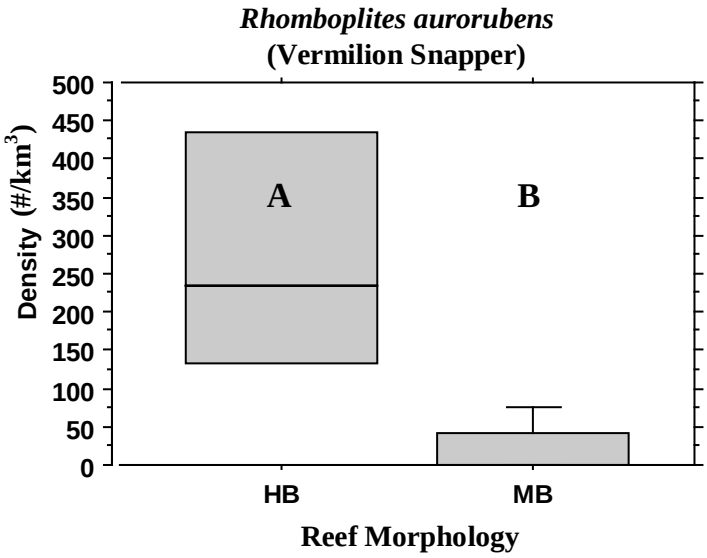

Rhomboplites aurorubens
(Vermilion Snapper)
Density (#/km^3)
500
450
400
350
300
250
200
150
100
50
0
A
B
HB
MB
Reef Morphology

Figure 6. Normal cluster analysis of species, by shelf-edge reef morphology. Dendrogram was constructed from a cluster analysis of Bray-Curtis similarity coefficients. SP=slab pavement, LB=Low-relief bioeroded, BB=blocked boulders, BBB=buried blocked boulders, MB=Moderate-relief bioeroded, HB=High-relief bioeroded.

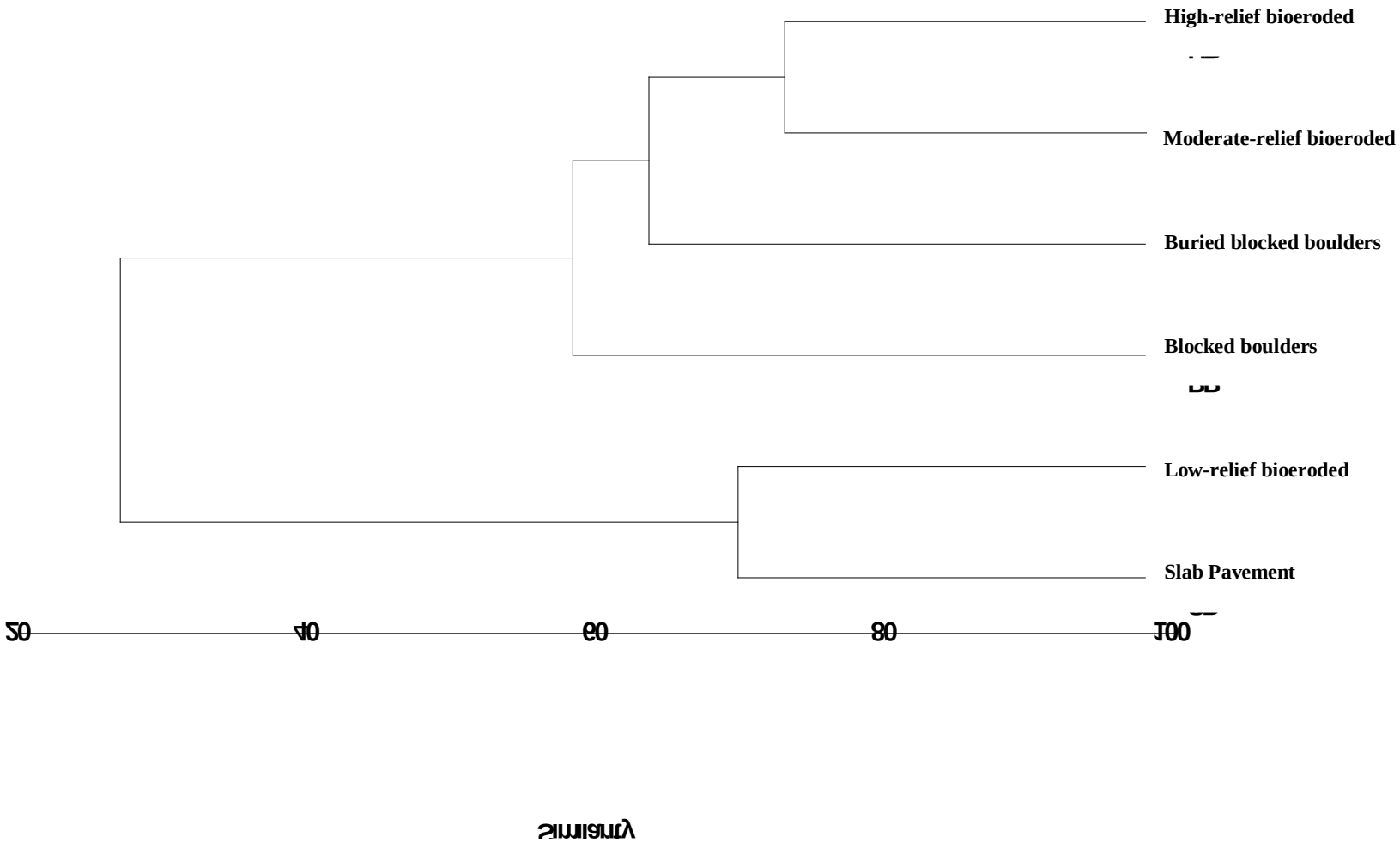
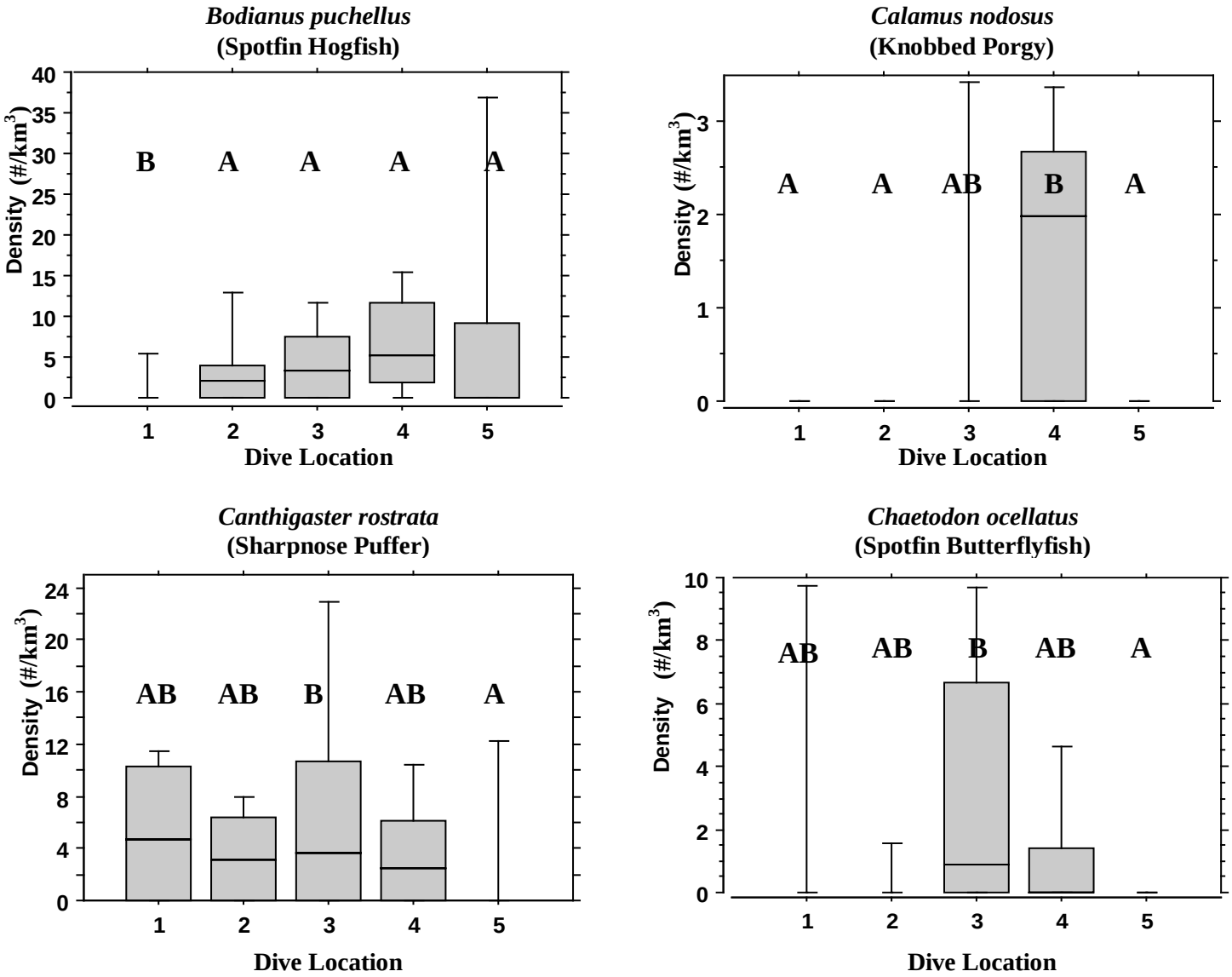
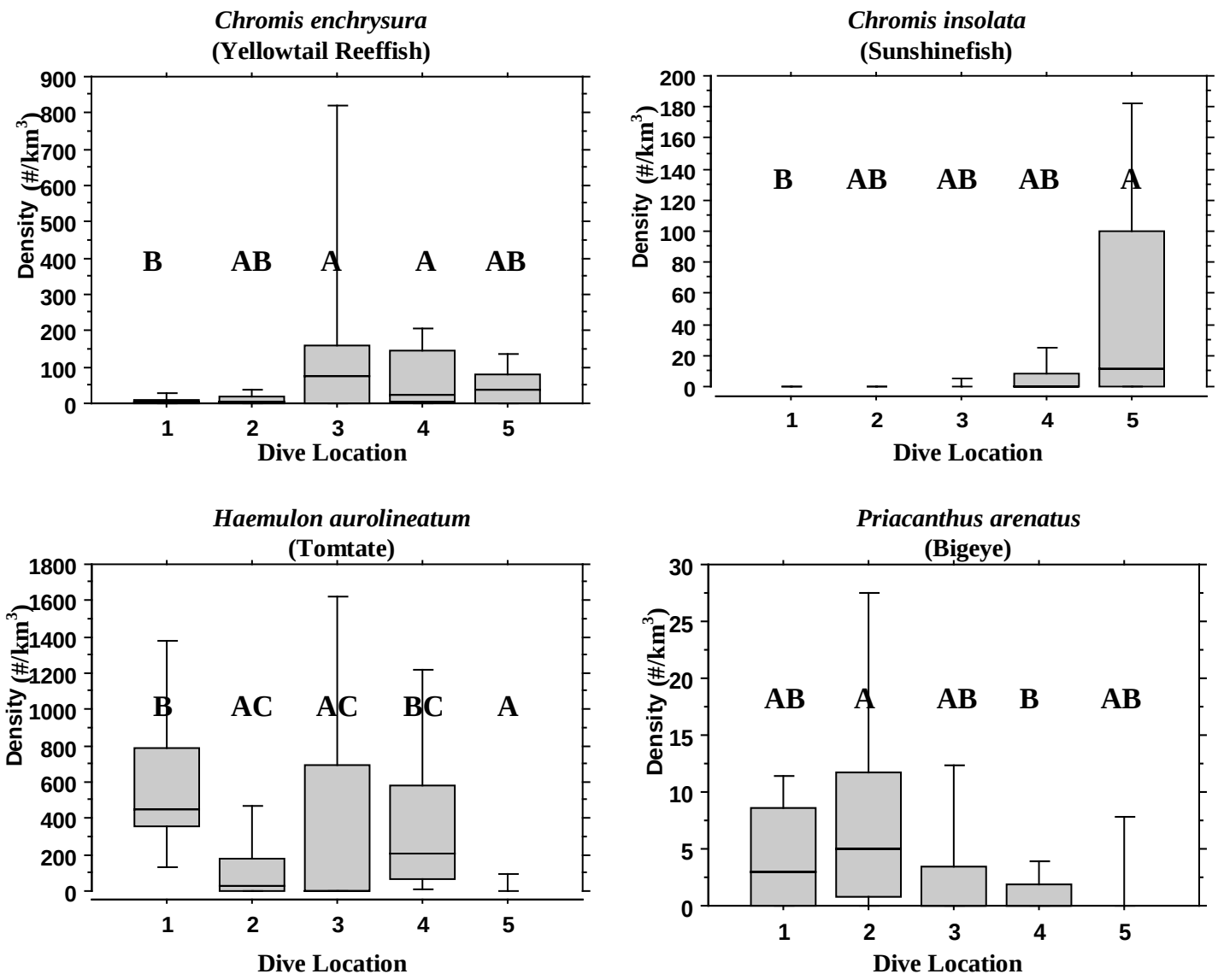
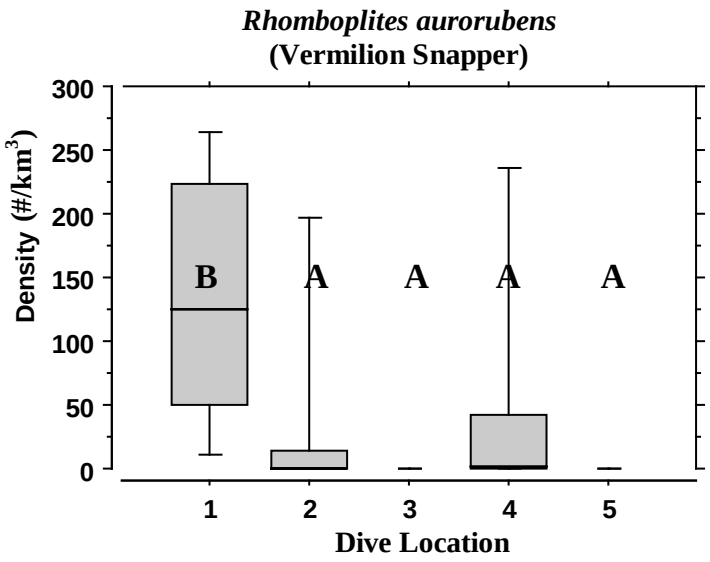

Similarity
100
80
60
40
20
Slab Pavement
Low-relief bioeroded
Blocked boulders
Buried blocked boulders
Moderate-relief bioeroded
High-relief bioeroded

Figure 7. Box plots showing significant differences in median densities among 2002 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.


Bodianus puchellus
(Spotfin Hogfish)
Density (#/km3)
B A A A A
Dive Location
Calamus nodosus
(Knobbed Porgy)
Density (#/km3)
A A AB B A
Dive Location
Canthigaster rostrata
(Sharpnose Puffer)
Density (#/km3)
AB AB B AB A
Dive Location
Chaetodon ocellatus
(Spotfin Butterflyfish)
Density (#/km3)
AB AB B AB A
Dive Location


Chromis enchrysura
(Yellowtail Reeffish)
Density (#/km3)
900
800
700
600
500
400
300
200
100
0
B
AB
A
A
AB
1
2
3
4
5
Dive Location
Chromis insolata
(Sunshinefish)
Density (#/km3)
200
180
160
140
120
100
80
60
40
20
0
B
AB
AB
AB
A
1
2
3
4
5
Dive Location
Haemulon aurolineatum
(Tomtate)
Density (#/km3)
1800
1600
1400
1200
1000
800
600
400
200
0
B
AC
AC
BC
A
1
2
3
4
5
Dive Location
Priacanthus arenatus
(Bigeye)
Density (#/km3)
30
25
20
15
10
5
0
AB
A
AB
B
AB
1
2
3
4
5
Dive Location


Rhomboplites aurorubens
(Vermilion Snapper)
Density (#/km^3)
300
250
200
150
100
50
0
B
A
A
A
A
1
2
3
4
5
Dive Location

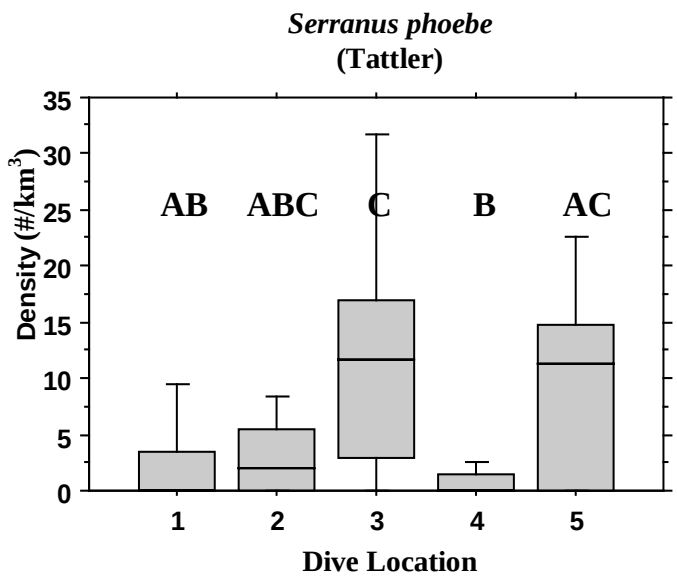

Serranus phoebe
(Tattler)
Density (#/km^3)
35
30
25
20
15
10
5
0
AB
ABC
C
B
AC
1
2
3
4
5
Dive Location

Figure 8. Normal cluster analysis of species, by shelf-edge dive location (2002). Dendrogram was constructed from a cluster analysis of Bray-Curtis similarity coefficients. S=Jacksonville Scarp, SR=Scamp Ridge, SAS=St. Augustine Scarp, GH=Georgetown Hole, JR=Julians Ridge.

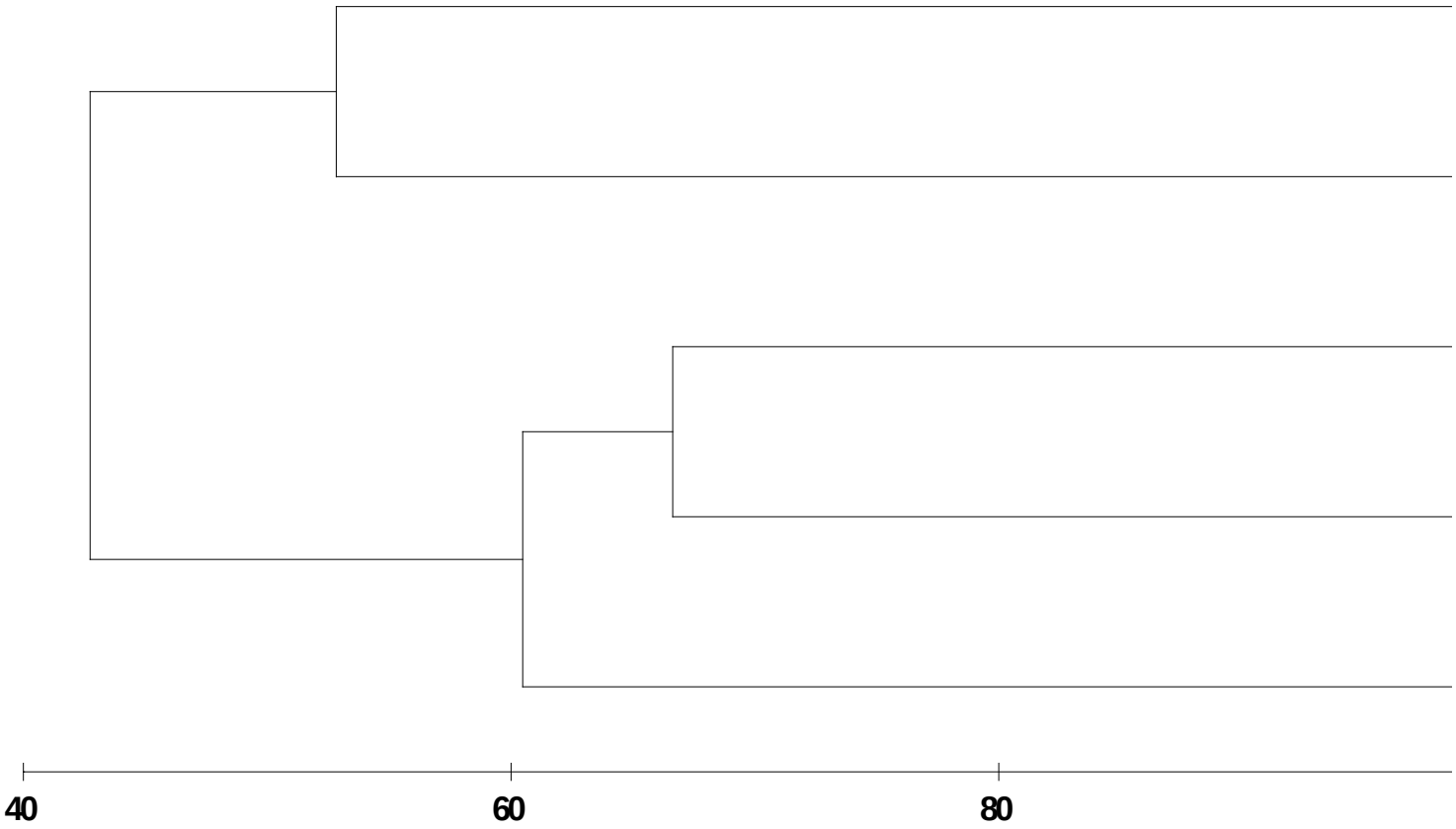
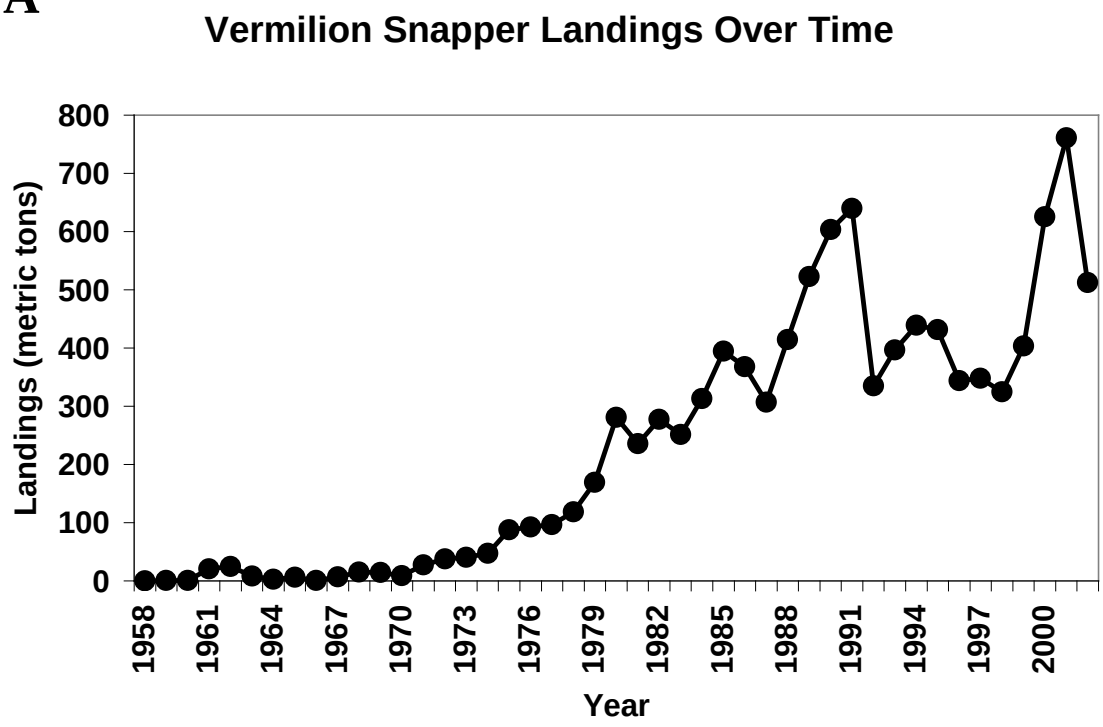

40
60
80

Figure 9. Catch data for vermilion snapper in the NMFS “south Atlantic” region (North Carolina to Key West). A=Commercial landings for vermilion snapper (1958-2002) taken from the NOAA NMFS database), B=Catch per unit effort (CPUE, catch per trap) for vermilion snapper (1988-2005) determined from a fishery-independent trapping survey (SCDNR, MARMAP).

A


Vermilion Snapper Landings Over Time
Landings (metric tons)
800
700
600
500
400
300
200
100
0
1958
1961
1964
1967
1970
1973
1976
1979
1982
1985
1988
1991
1994
1997
2000
Year

B

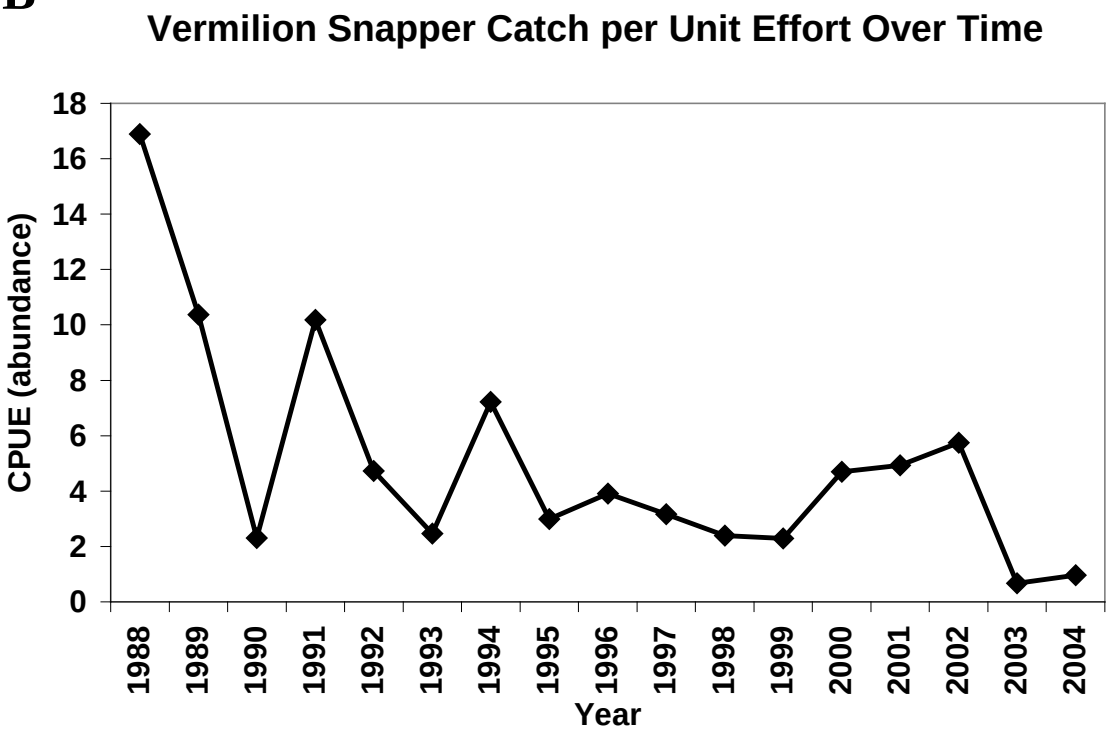
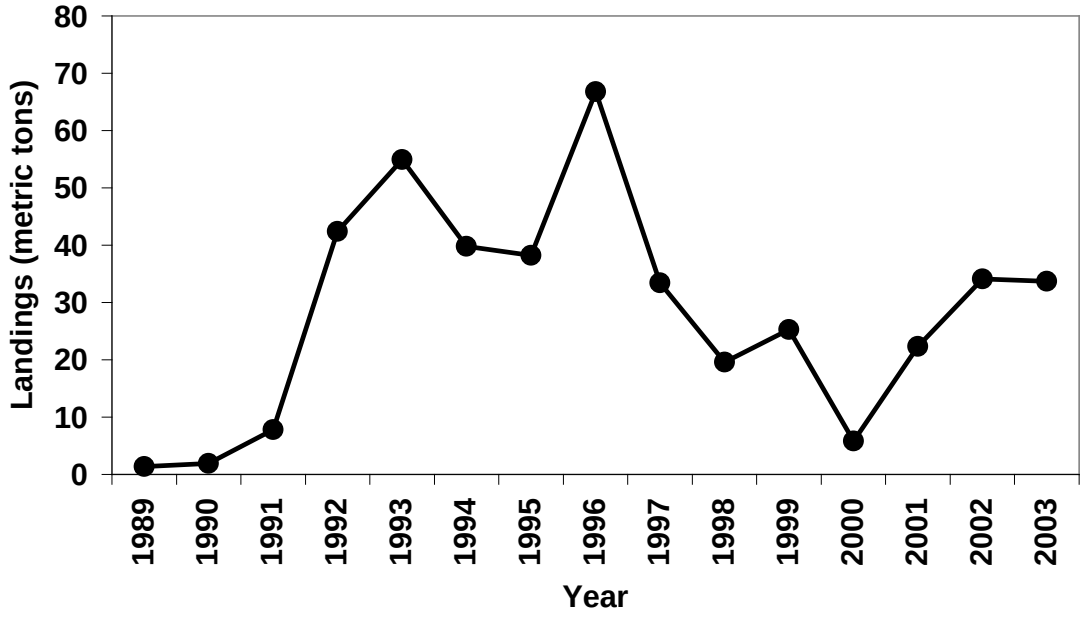

Vermilion Snapper Catch per Unit Effort Over Time
CPUE (abundance)
18
16
14
12
10
8
6
4
2
0
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
Year

Figure 10. Catch data for blackbelly rosefish in the NMFS “south Atlantic” region (North Carolina to Key West). A=Commercial landings for blackbelly rosefish (1989-2003) taken from the NOAA NMFS database, B=Catch per unit effort (CPUE,catch per 20 hooks) for blackbelly rosefish (1996-2003) determined from a fishery-independent vertical longline survey (SCDNR, MARMAP).

A


Blackbelly Rosefish Landings Over Time
Landings (metric tons)
80
70
60
50
40
30
20
10
0
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
Year

B

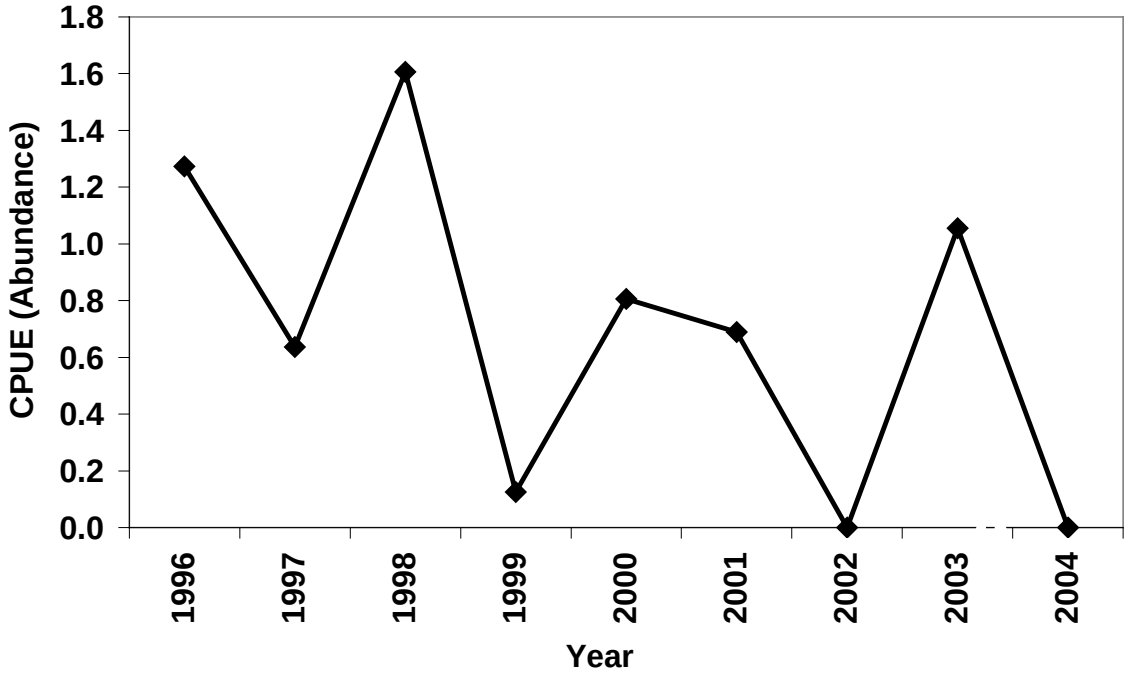
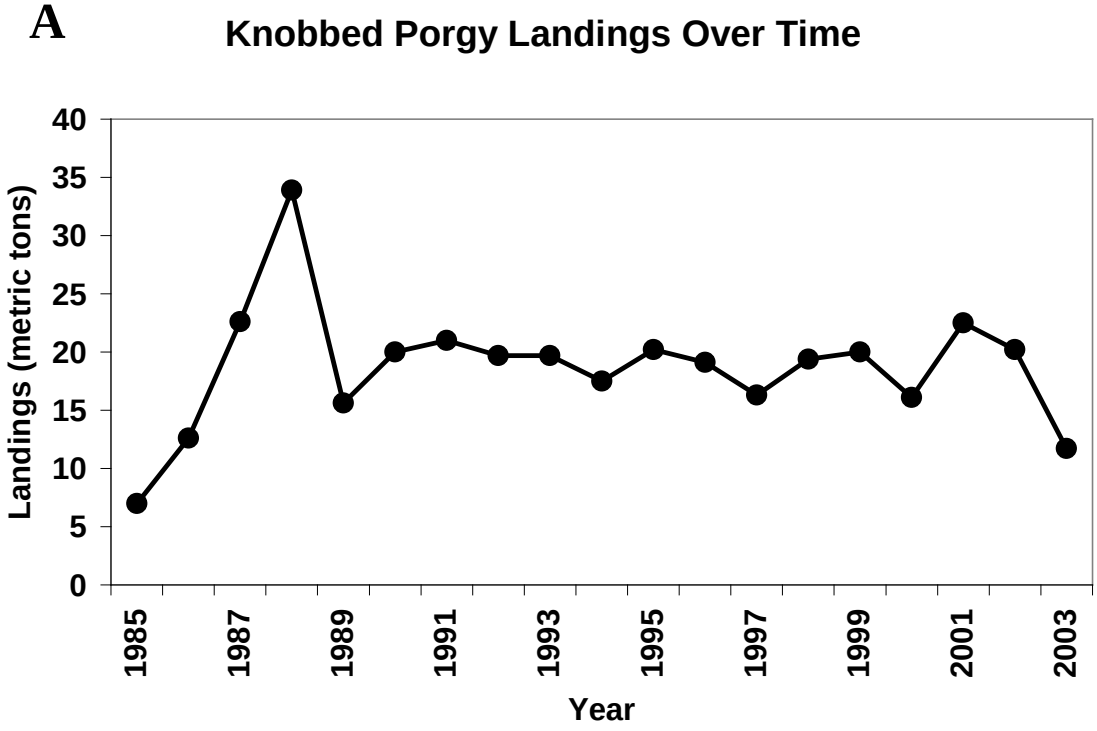

Blackbelly Rosefish Catch per Unit Effort Over Time
CPUE (Abundance)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1996
1997
1998
1999
2000
2001
2002
2003
2004
Year

Figure 11. Catch data for knobbed porgy in the NMFS "south Atlantic" region (North Carolina to Key West). A=Commercial landings for knobbed porgy (1985-2003) taken from the NOAA NMFS database, B=Catch per unit effort (CPUE, catch per trap) for knobbed porgy (1988-2004) determined from a fishery-independent trapping survey (SCDNR, MARMAP).

A


Knobbed Porgy Landings Over Time
Landings (metric tons)
40
35
30
25
20
15
10
5
0
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
Year

B

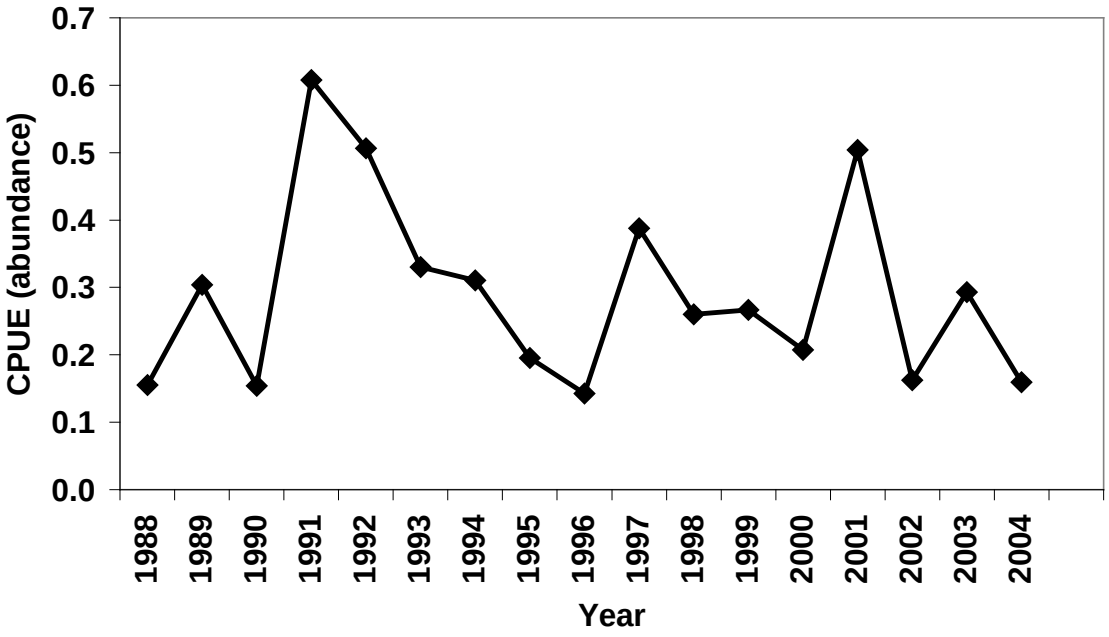
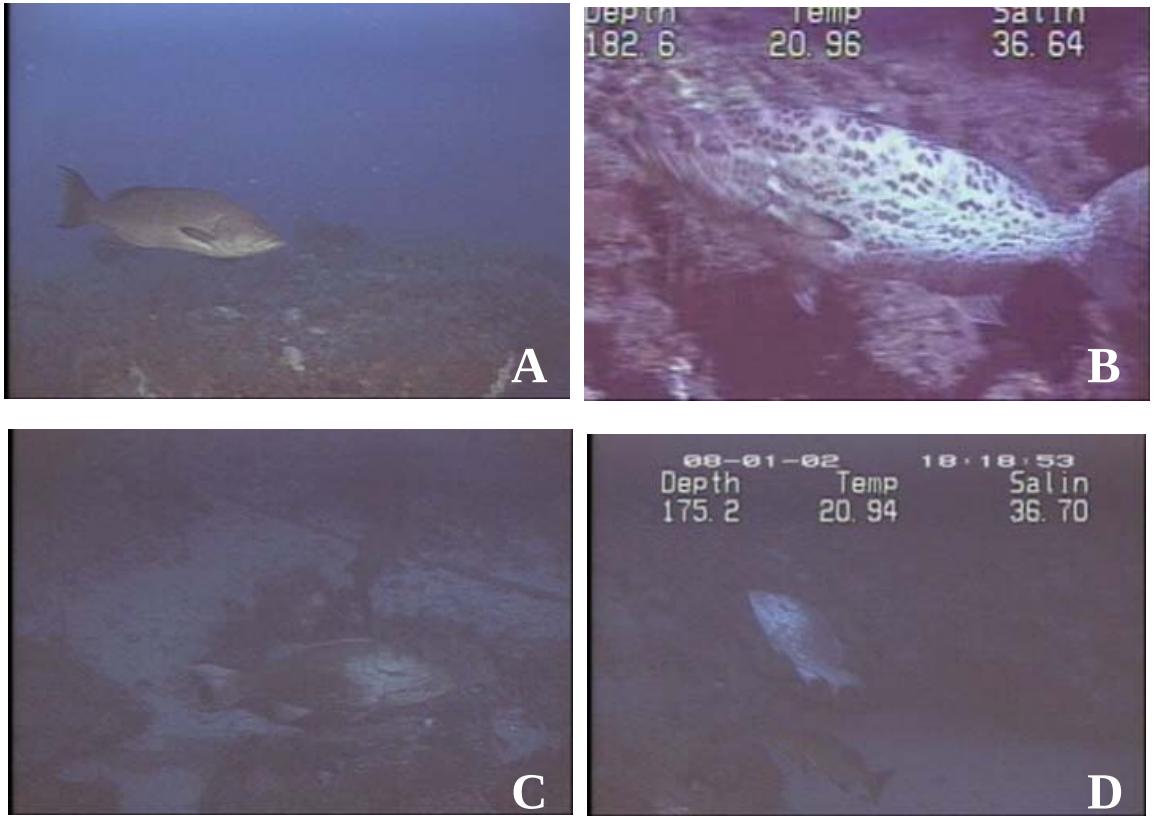

Knobbed Porgy Catch per Unit Effort Over Time
CPUE (abundance)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
Year

Figure 12. Reproductive behaviors seen during submersible dives. A=Scamp in brown phase, B=Scamp in cat paw phase, C=Scamp in gray-head phase, D=Scamp in gray-head phase courting brown female, E=Male hogfish, F=Female hogfish, G=Male hogfish splaying dorsal fin, H=Brightly colored male hogfish displaying to drab colored female hogfish, I=Red snapper school, J=Gravid speckled hind, K=Triggerfish guarding nest, L=Probable triggerfish nest.


A
Depth Temp Salin
182.6 20.96 36.64
B
C
08-01-02 18:18:53
Depth Temp Salin
175.2 20.94 36.70
D

E

F

G

07-30-02
18:52:58
Depth
Temp
Salin
171.61101218.60
36.46
H

08-02-02 19:29:53
Depth Temp Salin
172.4 20.88 36.54
I

J

08-04-02 16:47:30
Depth Temp Salin
164.1 20.58230105 36.49
K

L

Fig 13. Locations for reproductive behavior seen in five species within 2002 continental shelf-edge dive sites. Gray triangle=Gray triggerfish guarding nest, Black lightening bolt=Gravid speckled hind, Gray triangle=Red snapper school, Gray cross=Hogfish courting, White hexagon=Gray-head and cat paw scamp, White polygons=Proposed marine protected areas.

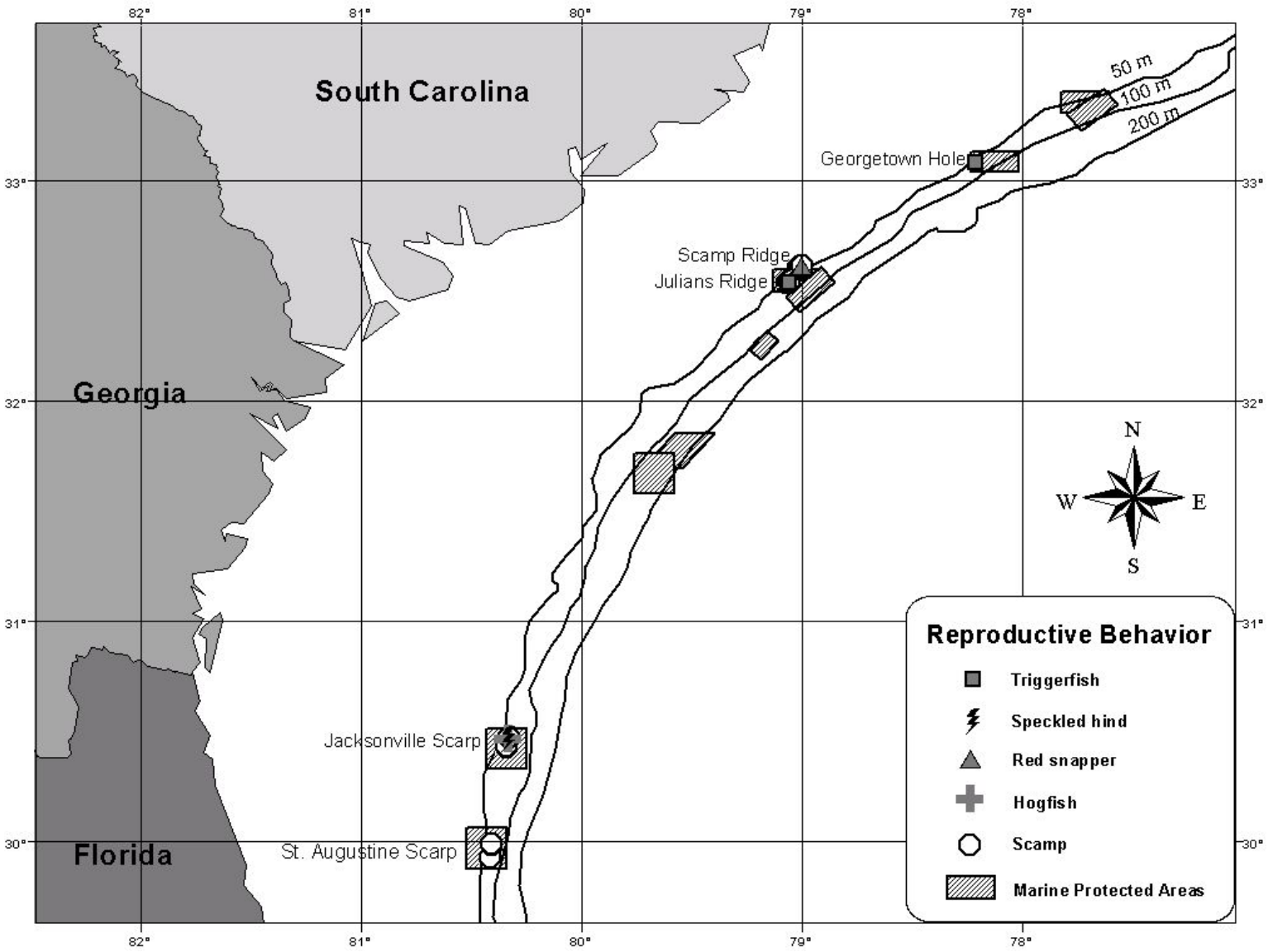
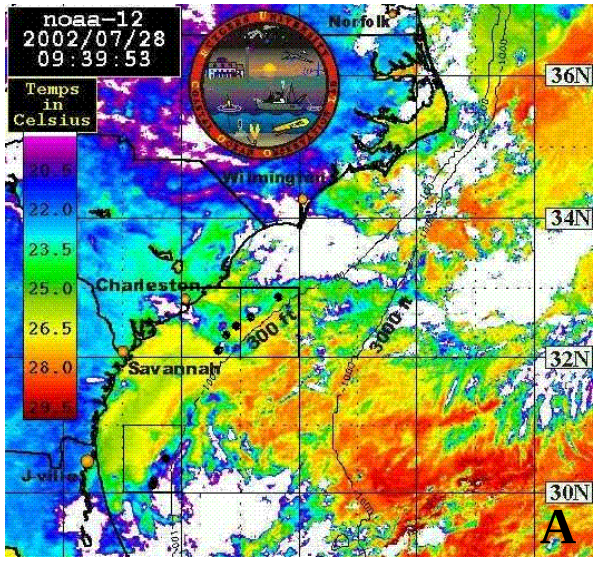
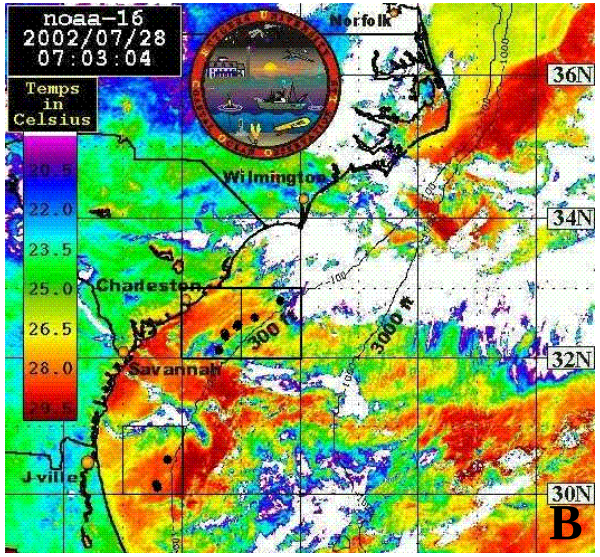

82°
81°
80°
79°
78°
33°
32°
31°
30°
South Carolina
Georgia
Florida
50 m
100 m
200 m
Georgetown Hole
Scamp Ridge
Julians Ridge
Jacksonville Scarp
St. Augustine Scarp
N
W
E
S
Reproductive Behavior
Triggerfish
Speckled hind
Red snapper
Hogfish
Scamp
Marine Protected Areas

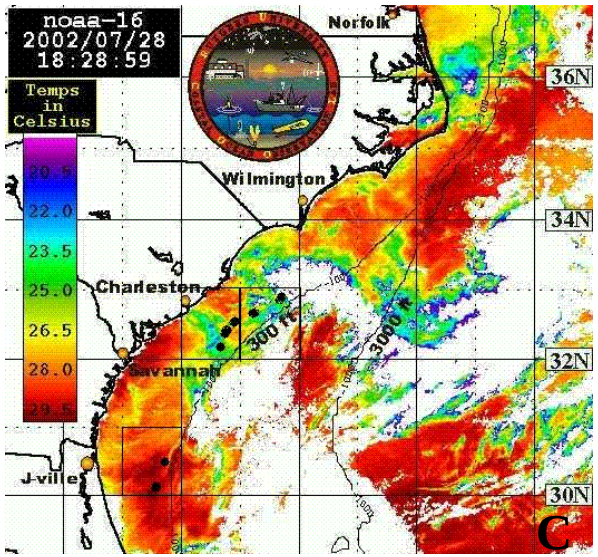
Figure 14. The red lionfish (*Pterois volitans*), an invasive species, was observed during submersible dives conducted in 2002.

21. 00
36. 68

Figure 15. Sea surface temperature imagery produced from NOAA's Geostationary Operational Environmental Satellites (noaa-12, noaa-16). Images were created using data collected by an AVHRR (advanced very high resolution radiometer) at Rutgers University. (Date, time, satellite): A=2002/07/28, 09:39:53, noaa-12; B=2002/07/28, 07:03:04, noaa-16; C=2002/07/28, 18:28:59, noaa-16; D=2002/07/30, 10:31:15. Black dots represent 2002 shelf-edge dive locations.


noaa-12
2002/07/28
09:39:53
Temps in Celsius
20.5
22.0
23.5
25.0
26.5
28.0
29.5
Norfolk
Wilmington
Charleston
Savannah
J-ville
300 ft
3000 ft
36N
34N
32N
30N
A


noaa-16
2002/07/28
07:03:04
Temps in Celsius
20.5
22.0
23.5
25.0
26.5
28.0
29.5
Norfolk
Wilmington
Charleston
Savannah
J-ville
300 ft
3000 ft
36N
34N
32N
30N
B


noaa-16
2002/07/28
18:28:59
Temps in Celsius
20.5
22.0
23.5
25.0
26.5
28.0
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Norfolk
Wilmington
Charleston
Savannah
J-ville
300 ft
3000 ft
36N
34N
32N
30N
C

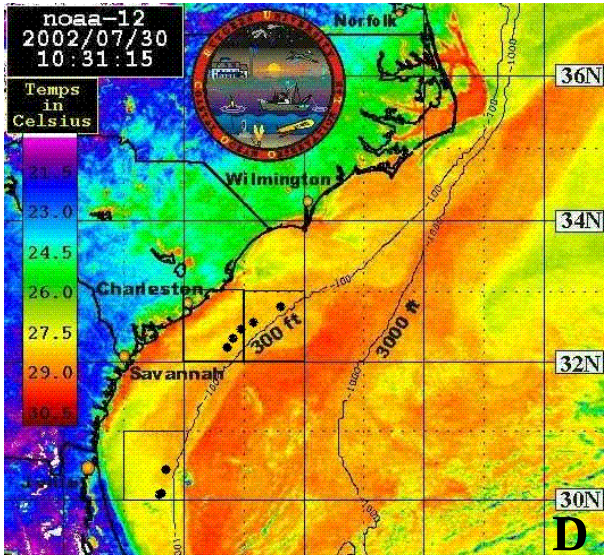
noaa-12
2002/07/30
10:31:15
Temps in Celsius
21.5
23.0
24.5
26.0
27.5
29.0
30.5
Norfolk
Wilmington
Charleston
Savannah
300 ft
3000 ft
36N
34N
32N
30N
D

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

Dive #	Location	Date mo-d-yr	Lat.	Long.	Hab.	D (m)	T (°C)	S (psu)	Total Tran. Area	Tran. #	Mean Tran. Area
1634	M3	07-14-1985	32.2701	-79.1617	SE	51	18.9	--	858	7	123 (+/- 40)
1635	M3	07-14-1985	32.2604	-79.1748	SE	52	19.1	--	1280	11	116 (+/- 49)
1636	M2	07-15-1985	32.4278	-78.9663	SE	54	19.5	--	2185	10	219 (+/- 81)
1637	M1	07-17-1985	32.4820	-78.8308	SE	51	19.9	--	1559	9	173 (+/- 77)
1638	D3	07-17-1985	32.5384	-78.4176	US	208	13.7	--	722	7	103 (+/- 26)
1639	D1	07-17-1985	32.7285	-78.1100	US	112	12.8	--	506	4	127 (+/- 46)
3289	St. Augustine Scarp	07-28-2002	29.9914	-80.2768	SE	55	20.0	36.5	1760	6	293 (+/- 72)
3290	St. Augustine Scarp	07-28-2002	29.9393	-80.2846	SE	55	20.0	36.5	3342	16	209 (+/- 78)
3291	Jacksonville Scarp	07-30-2002	30.4397	-80.2049	SE	54	18.6	36.4	2039	7	291 (+/- 102)
3292	Jacksonville Scarp	07-30-2002	30.4009	-80.2162	SE	51	19.0	36.5	2974	6	496 (+/- 279)
3293	Julian's Ridge	08-01-2002	32.3481	-79.0357	SE	50	--	--	4801	16	300 (+/- 143)
3294	Julian's Ridge	08-01-2002	32.3428	-79.0452	SE	55	21.0	36.6	4440	14	317 (+/- 119)
3295	Scamp Ridge	08-02-2002	32.4196	-78.9813	SE	47	22.1	36.6	6943	16	434 (+/- 134)
3296	Scamp Ridge	08-02-2002	32.4112	-78.9883	SE	48	21.1	36.6	5950	12	496 (+/- 113)
3297	Charleston Lumps S.	08-03-2002	32.6277	-78.3238	US	190	13.0	35.7	4784	13	368 (+/- 153)
3298	Charleston Lumps S.	08-03-2002	32.6193	-78.3186	US	192	13.2	35.7	5923	10	592 (+/- 248)
3299	Charleston Lumps N.	08-04-2002	32.7308	-78.1121	US	177	13.1	35.7	3447	12	287 (+/- 201)
3300	Georgetown Hole	08-04-2002	32.8505	-78.2551	SE	51	20.8	36.5	2319	15	155 (+/- 96)

Table 2. Six reef morphology categories are listed by 2002 shelf-edge dive sites. "X" denotes presence of reef morphology at dive site. 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**	

Table 3. Total transect volume (m^3) conducted entirely within each reef morphology category is listed by dive location. Number in parenthesis denotes the number of transects conducted within each category at that dive location.

Reef Morphology	**SAS**	**JS**	**JR**	**SR**	**GH**
Slab Pavement		1284 (3)			
Blocked Boulders	3988 (17)				
Buried Blocked Boulders		1900 (7)			
Low Relief Bioeroded Rock			3821 (12)		2319 (15)
Moderate Relief Bioeroded Rock			1895 (4)	4992 (11)	
High Relief Bioeroded Rock			1715 (7)	2068 (4)	

Table 4. Diversity parameters are listed for reef morphologies seen during 2002 shelf-edge dives. S= Median number of species, N=Total median density per km^3 of water, D=Margalef's index of species richness, J'=Pielou's evenness index, H'=Simpson index.

Reef Morphology	**S**	**N**	**D**	**J'**	**H' (log_e)**
Slab Pavement	5	22	1.29	0.83	1.33
Blocked Boulders	9	616	1.25	0.34	0.75
Buried Blocked Boulders	11	147	2.00	0.66	1.57
Low Relief Bioeroded Rock	3	85	0.45	0.71	0.78
Moderate Relief Bioeroded Rock	8	256	1.26	0.49	1.02
High Relief Bioeroded Rock	10	1,649	1.21	0.08	0.18

Table 5. Bray Curtis Similarity coefficients for 2002 shelf-edge reef morphologies. 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.

	SP	**BB**	**BBB**	**LB**	**MB**	**HB**
SP						
BB	15.94					
BBB	42.52	56.34				
LB	69.76	10.13	33.48			
MB	38.20	54.54	66.97	42.73		
HB	18.99	64.10	60.21	13.81	72.99	

Table 6. Diversity parameters are listed for 2002 shelf-edge dive locations. S= Median number of species, N=Total median density per km^3 of water, D=Margalef's index of species richness, J'=Pielou's evenness index, H'=Simpson index.

Dive Location	**S**	**N**	**D**	**J'**	**H' (log_e)**
Georgetown Hole	4	73	0.70	0.87	1.21
Scamp Ridge	10	264	1.61	0.38	0.87
Julian's Ridge	9	116	1.68	0.57	1.26
Jacksonville Scarp	9	66	1.91	0.76	1.68
St. Augustine Scarp	10	599	1.41	0.34	0.78

Table 7. Bray Curtis Similarity coefficients for 2002 shelf-edge dive locations.

	GH	**SR**	**JR**	**JS**	**SAS**
GH					
SR	40.54				
JR	52.84	56.22			
JS	38.37	63.31	59.13		
SAS	25.17	66.64	37.03	57.64	

Table 8. Mann-Whitney U test results for mean rank values for 1985 and 2002 fish densities. Bold p-values denote a significant difference between 1985 and 2002 densities ($p<0.05$).

Species	**1985 Mean Rank**	**2002 Mean Rank**	**p-value**
Bodianus pulchellus	51.5	45.8	0.3193
Calamus nodosus	59.1	40.9	**0.0007**
Canthigaster rostrata	35.8	55.8	**0.0006**
Centropristis ocyurus	76.7	29.7	**<0.0001**
Chaetodon ocellatus	57.0	42.3	**0.0114**
Chaetodon sedentarius	48.0	48.0	0.9970
Chromis enchrysura	51.5	45.8	0.3211
Haemulon aurolineatum	50.5	46.4	0.4826
Holacanthus ciliaris bermudensis	51.0	46.1	0.3948
Holocentrus adscensionis	32.3	58.0	**<0.0001**
Priacanthus arenatus	57.3	42.1	**0.0088**
Prognathodes aya	63.3	38.3	**<0.0001**
Rhomboplites aurorubens	58.7	41.2	**0.0026**
Serranus phoebe	48.2	47.9	0.9635
Anthias nicholsi	29.0	21.8	0.1192
Helicolenus dactylopterus	40.1	18.3	**<0.0001**
Laemonema barbatulum	41.0	18.00	**<0.0001**
Anthias nicholsi	29.0	21.8	0.1192

Table 9. Diversity parameters are listed for 1985 and 2002 shelf-edge and upper-slope habitats. S=Number of species, N=Total median density per km^3 of water, D=Margalef's index of species richness, J'=Pielou's evenness index, H'=Simpson index.

Year/Habitat	**S**	**N**	**D**	**J'**	**H' (log_e)**
1985 shelf-edge	12	358	1.87	0.64	1.60
2002 shelf-edge	9	142	1.61	0.64	1.40
1985 upper slope	3	132	0.41	0.92	1.01
2002 upper slope	2	38	0.27	0.70	0.48

Appendix 1. Species seen during submersible dives are listed with corresponding habitats, year, abundance, % total abundance, and density (per km^3). Species for each year are listed by decreasing abundance.

Habitat	Year	Species	Family	Abundance	% Total Abundance	Density (per km^3)
Shelf Edge	1985	*Rhomboplites aurorubens*	Lutjanidae	2,852	33.87	579.16
Shelf Edge	1985	*Haemulon aurolineatum*	Haemulidae	2,767	32.86	470.17
Shelf Edge	1985	*Chromis enchrysura*	Pomacentridae	1,153	13.69	311.77
Shelf Edge	1985	*Centropristis ocyurus*	Serranidae	274	3.25	73.13
Shelf Edge	1985	Pomacentridae	Pomacentridae	169	2.01	40.63
Shelf Edge	1985	*Equetus umbrosus*	Sciaenidae	126	1.50	28.07
Shelf Edge	1985	*Anthias nicholsi* (juveniles)	Serranidae	118	1.40	19.07
Shelf Edge	1985	*Chaetodon sedentarius*	Chaetodontidae	107	1.27	23.67
Shelf Edge	1985	Labridae	Labridae	101	1.20	33.90
Shelf Edge	1985	*Prognathodes aya*	Chaetodontidae	96	1.14	19.11
Shelf Edge	1985	*Bodianus pulchellus*	Labridae	90	1.07	16.37
Shelf Edge	1985	*Serranus phoebe*	Serranidae	87	1.03	26.31
Shelf Edge	1985	Unknown		84	1.00	16.72
Shelf Edge	1985	Carangidae	Carangidae	75	0.89	13.32
Shelf Edge	1985	*Chaetodon ocellatus*	Chaetodontidae	71	0.84	26.06
Shelf Edge	1985	*Holacanthus ciliaris bermudensis*	Pomacanthidae	64	0.76	14.66
Shelf Edge	1985	*Priacanthus arenatus*	Priacanthidae	53	0.63	17.85
Shelf Edge	1985	*Calamus nodosus*	Sparidae	50	0.59	10.09
Shelf Edge	1985	*Mycteroperca phenax*	Serranidae	16	0.19	2.58
Shelf Edge	1985	*Pagrus pagrus*	Sparidae	15	0.18	2.38
Shelf Edge	1985	*Balistes capriscus*	Balistidae	14	0.17	5.91
Shelf Edge	1985	*Canthigaster rostrata*	Tetraodontidae	9	0.11	2.08
Shelf Edge	1985	*Holocentrus adscensionis*	Holocentridae	8	0.10	1.98
Shelf Edge	1985	*Seriola dumerili*	Carangidae	6	0.07	0.84
Shelf Edge	1985	*Balistes vetula*	Balistidae	3	0.04	1.29
Shelf Edge	1985	*Epinephelus drummondhayi*	Serranidae	2	0.02	0.56
Shelf Edge	1985	Serranidae	Serranidae	2	0.02	0.36
Shelf Edge	1985	*Synodus* sp.	Synodontidae	2	0.02	0.58
Shelf Edge	1985	*Lachnolaimus maximus*	Labridae	1	0.01	0.40
Shelf Edge	1985	*Pseudupeneus maculatus*	Mullidae	1	0.01	0.00

Shelf Edge	1985	Rajiformes		1	0.01	0.18
Shelf Edge	1985	*Acanthostracion quadricornis*	Ostraciidae	1	0.01	0.00
Shelf Edge	1985	*Centropristis striata*	Serranidae	1	0.01	0.18
Shelf Edge	1985	*Epinephelus niveatus*	Serranidae	1	0.01	0.44
Shelf Edge	1985	*Liopropoma eukrines*	Serranidae	1	0.01	0.12
Total				**8,421**		**1,759.94**
Upper Slope	1985	*Anthias nicholsi*	Serranidae	286	73.15	240.99
Upper Slope	1985	*Helicolenus dactylopterus*	Sebastidae	62	15.86	54.87
Upper Slope	1985	*Laemonema barbatulum*	Moridae	37	9.46	33.69
Upper Slope	1985	Unknown		4	1.02	4.10
Upper Slope	1985	*Macroramphosus scolopax*	Centriscidae	2	0.51	1.05
Total				**391**		**334.70**
Shelf Edge	2002	*Haemulon aurolineatum*	Haemulidae	12,325	52.15	379.40
Shelf Edge	2002	Unknown juvenile swarm		3,155	13.35	111.55
Shelf Edge	2002	*Chromis enchrysura*	Pomacentridae	2,491	10.54	87.63
Shelf Edge	2002	*Rhomboplites aurorubens*	Lutjanidae	2,051	8.68	58.73
Shelf Edge	2002	Pomacentridae	Pomacentridae	595	2.52	17.67
Shelf Edge	2002	*Chaetodon sedentarius*	Chaetodontidae	337	1.43	11.25
Shelf Edge	2002	Labridae	Labridae	319	1.35	13.27
Shelf Edge	2002	*Equetus umbrosus*	Sciaenidae	235	0.99	6.97
Shelf Edge	2002	Serranidae	Serranidae	219	0.93	6.08
Shelf Edge	2002	*Chromis insolata*	Pomacentridae	210	0.89	13.15
Shelf Edge	2002	*Holocentrus adscensionis*	Holocentridae	187	0.79	7.01
Shelf Edge	2002	*Serranus phoebe*	Serranidae	159	0.67	5.88
Shelf Edge	2002	*Canthigaster rostrata*	Tetraodontidae	154	0.65	5.18
Shelf Edge	2002	*Bodianus pulchellus*	Labridae	154	0.65	5.42
Shelf Edge	2002	Unknown		135	0.57	4.49
Shelf Edge	2002	*Holacanthus ciliaris bermudensis*	Pomacanthidae	130	0.55	5.31
Shelf Edge	2002	*Mycteroperca phenax*	Serranidae	120	0.51	5.34
Shelf Edge	2002	*Prognathodes aya*	Chaetodontidae	119	0.50	4.19
Shelf Edge	2002	*Priacanthus arenatus*	Priacanthidae	95	0.40	3.49
Shelf Edge	2002	*Chaetodon ocellatus*	Chaetodontidae	56	0.24	1.74
Shelf Edge	2002	*Lutjanus buccanella*	Lutjanidae	40	0.17	1.42
Shelf Edge	2002	*Seriola dumerili*	Carangidae	36	0.15	1.78
Shelf Edge	2002	*Stegastes partitus*	Pomacentridae	31	0.13	0.68
Shelf Edge	2002	*Sargocentron bullisi*	Holocentridae	27	0.11	2.20
Shelf Edge	2002	*Calamus nodosus*	Sparidae	26	0.11	0.65

Shelf Edge	2002	*Pseudupeneus maculatus*	Mullidae	23	0.10	0.57
Shelf Edge	2002	*Ocyurus chrysurus*	Lutjanidae	22	0.09	0.76
Shelf Edge	2002	*Lutjanus campechanus*	Lutjanidae	17	0.07	0.70
Shelf Edge	2002	*Myripristis jacobus*	Holocentridae	16	0.07	0.33
Shelf Edge	2002	*Acanthostracion quadricornis*	Ostraciidae	13	0.06	0.51
Shelf Edge	2002	*Chromis scotti*	Pomacentridae	12	0.05	0.57
Shelf Edge	2002	*Centropristis ocyurus*	Serranidae	8	0.03	0.25
Shelf Edge	2002	*Liopropoma eukrines*	Serranidae	8	0.03	0.39
Shelf Edge	2002	*Chaetodipterus faber*	Ephippidae	8	0.03	0.24
Shelf Edge	2002	*Acanthurus* sp.	Acanthuridae	8	0.03	0.16
Shelf Edge	2002	*Holacanthus tricolor*	Pomacanthidae	7	0.03	0.35
Shelf Edge	2002	*Cephalopholis cruentata*	Serranidae	5	0.02	0.15
Shelf Edge	2002	*Mycteroperca microlepis*	Serranidae	5	0.02	0.15
Shelf Edge	2002	*Lachnolaimus maximus*	Labridae	5	0.02	0.17
Shelf Edge	2002	*Seriola rivoliana*	Carangidae	5	0.02	0.24
Shelf Edge	2002	*Synodus* sp.	Synodontidae	4	0.02	0.12
Shelf Edge	2002	*Pagrus pagrus*	Sparidae	4	0.02	0.17
Shelf Edge	2002	*Rypticus* sp.	Serranidae	4	0.02	0.23
Shelf Edge	2002	*Pterois volitans*	Scorpaenidae	4	0.02	0.09
Shelf Edge	2002	*Halichoeres bivittatus*	Labridae	4	0.02	0.04
Shelf Edge	2002	*Epinephelus drummondhayi*	Serranidae	3	0.01	0.19
Shelf Edge	2002	*Pomacanthus arcuatus*	Pomacanthidae	3	0.01	0.17
Shelf Edge	2002	Muraenidae	Muraenidae	3	0.01	0.20
Shelf Edge	2002	*Mulloidichthys martinicus*	Mullidae	3	0.01	0.06
Shelf Edge	2002	*Lutjanus griseus*	Lutjanidae	3	0.01	0.12
Shelf Edge	2002	Unknown Labridae 3	Labridae	3	0.01	0.18
Shelf Edge	2002	*Haemulon striatum*	Haemulidae	3	0.01	0.14
Shelf Edge	2002	*Balistes capriscus*	Balistidae	3	0.01	0.08
Shelf Edge	2002	*Balistes vetula*	Balistidae	3	0.01	0.07
Shelf Edge	2002	*Diplodus holbrookii*	Sparidae	2	0.01	0.06
Shelf Edge	2002	Scorpaenidae	Scorpaenidae	2	0.01	0.07
Shelf Edge	2002	*Centropyge argi*	Pomacanthidae	2	0.01	0.23
Shelf Edge	2002	*Prognathodes aculeatus*	Chaetodontidae	2	0.01	0.13
Shelf Edge	2002	*Sphyraena barracuda*	Sphyraenidae	1	0.00	0.03
Shelf Edge	2002	*Cephalopholis fulva*	Serranidae	1	0.00	0.04
Shelf Edge	2002	*Epinephelus morio*	Serranidae	1	0.00	0.04
Shelf Edge	2002	*Equetus* sp.	Sciaenidae	1	0.00	0.10

Moderate-relief bioeroded

Shelf Edge	2002	*Aluterus scriptus*	Monacanthidae	1	0.00	0.02
Shelf Edge	2002	*Stephanolepis hispidus*	Monacanthidae	1	0.00	0.02
Shelf Edge	2002	Unknown Labridae 1	Labridae	1	0.00	0.10
Shelf Edge	2002	Unknown Labridae 2	Labridae	1	0.00	0.10
Shelf Edge	2002	Holocentridae	Holocentridae	1	0.00	0.03
Shelf Edge	2002	*Fistularia* sp.	Fistulariidae	1	0.00	0.05
Shelf Edge	2002	*Dactylopterus volitans*	Dactylopteridae	1	0.00	0.03
Shelf Edge	2002	*Balistes* sp.	Balistidae	1	0.00	0.03
Shelf Edge	2002	*Aulostomus maculatus*	Aulostomidae	1	0.00	0.09
Total				**23,636**		**769.04**
Upper Slope	2002	*Anthias nicholsi*	Serranidae	520	73.65	44.78
Upper Slope	2002	*Helicolenus dactylopterus*	Sebastidae	92	13.03	8.82
Upper Slope	2002	Unknown		45	6.37	10.95
Upper Slope	2002	*Epinephelus niveatus*	Serranidae	16	2.27	2.50
Upper Slope	2002	*Gephyroberyx darwinii*	Trachichthyidae	14	1.98	1.85
Upper Slope	2002	*Caulolatilus microps*	Malacanthidae	6	0.85	0.34
Upper Slope	2002	*Laemonema barbatulum*	Moridae	4	0.57	0.16
Upper Slope	2002	Unknown A		4	0.57	0.28
Upper Slope	2002	*Scyliorhinus retifer*	Scyliorhinidae	2	0.28	0.13
Upper Slope	2002	Unknown B		2	0.28	0.16
Upper Slope	2002	*Synodus* sp.	Synodontidae	1	0.14	0.08
Total				**706**		**70.05**