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[Article]

Influence of Benthic Features and Fishing Pressure on Size and Distribution of Three Exploited Reef Fishes from the Southeastern United States

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Abstract.—Distribution, habitat preference, and size structure were examined for three commonly targeted bottom fishes (black sea bass *Centropristis striata*, gag *Mycteroperca microlepis*, and scamp *M. phenax*) in the southeastern United States. Fish communities and bottom characteristics of limestone ledges within Gray's Reef National Marine Sanctuary (located centrally along the southeastern continental shelf) were surveyed. Black sea bass occurred at 98% of the ledges and were evenly distributed throughout the sanctuary in much-higher numbers than either gags or scamps, which were concentrated at only 11% of the ledges. Gag or scamp presence was most strongly related to height of ledge undercut, whereas abundance of black sea bass was best explained by percent cover of sessile biota. In addition, lower abundance of black sea bass occurred in the presence of either gags or scamps, which are generally larger than black sea bass. In all three species, an abrupt decline in abundance was observed for size-classes above the size limit of the fishery. Also, modal size of gags or scamps was smaller and the percentage of fish exceeding the fishery size limit was lower in heavily fished areas than in less intensively fished areas.

Black sea bass *Centropristis striata*, gags *Mycteroperca microlepis*, and scamps *M. phenax* are among the most favored target species for bottom fishermen on the continental shelf of the southeastern United States from Florida to Virginia (Huntsman 1976; Matheson et al. 1986; Mercer 1989; McGovern et al. 2005). Most prior studies on the distribution of these protogynous species have been conducted at broad scales (tens to hundreds of kilometers) covering much of the southeastern shelf and have examined latitudinal, depth, or inshore–offshore differences in abundance or biomass among fish populations (Struhsaker 1969; Huntsman 1976; Miller and Richards 1980; Grimes et al. 1982; Wenner 1983; Barans and Henry 1984; Chester et al. 1984; Sedberry and Van Dolah 1984; Parker and Mays 1998; McGovern et al. 2005). These studies have identified distribution patterns at biogeographic scales; however, the variability in distribution of these fishes at finer, subregional scales (tens to thousands of meters) on the southeastern shelf has remained largely unknown. Reef and hard-bottom habitats have been estimated to cover about 23% of the southeastern shelf, and less than 2% of the shelf is classified as consisting of high-relief (>1-m) features (Parker et al. 1983). In many other regions, fish communities have been shown to differ significantly between adjacent reef patches in relation to local physiography, even when patches are separated by a short distance (e.g., Molles 1978; Chabanet et al. 1997; Chittaro 2004). The same is probably true for fish associated with adjacent hard-bottom patches of varying quality on the southeastern continental shelf, but this has not been quantified.

In addition, most prior studies on the habitat preferences of these three species have been limited to very general bottom classifications, such as live-bottom (Struhsaker 1969; Huntsman 1976; Miller and Richards 1980; Powles and Barans 1980; Grimes et al. 1982; Wenner 1983; Chester et al. 1984; Sedberry and Van Dolah 1984), sand bottom (Struhsaker 1969; Wenner et al. 1979), and shelf edge environments (Struhsaker 1969; Grimes et al. 1982; Barans and Henry 1984; Parker and Ross 1986; Gilmore and Jones 1992; Parker and Mays 1998; Quattrini and Ross 2006; Schobernd 2006). At best, ledge characteristics have only been coarsely categorized in height (e.g., small or large) and colonization density (e.g., sparse or dense sessile invertebrate coverage) and then related to fish assemblages (Parker et al. 1994; Riggs et al. 1996; Parker and Mays 1998; Quattrini and Ross 2006). Such studies have identified the general habitat type for the three species as hard bottom and ledges, but specific relationships between fish occurrence, abundance, or size and continuous-scale environmental data (e.g., degree of colonization by sessile invertebrates, vertical relief, ledge area, and overhang morphology) have not been quantified.

The influence of other forces that shape the

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distribution and abundance of the three species, such as recreational fishing, is in need of further study as well (SAFMC 1998). The effect of fisheries on populations of target species has been considered at broader scales by fishery managers in the southeastern United States, but less is known about impacts at subregional scales or at discrete localities. Recreational fishing effort has particularly increased in the region in recent decades (Ehler and Leeworthy 2002; NOAA 2007). Fishing with hook and line is the dominant approach, although some spearfishing also occurs. Fishermen in this area primarily target black sea bass, gags, and scamps. In many parts of the world, direct and indirect fish community effects from several forms of fishing (e.g., commercial, recreational, and artisanal) have been demonstrated (e.g., Russ and Alcala 1989; Grigg 1994; Jennings et al. 1995; Jennings and Polunin 1996; Chiappone et al. 2000; Westera et al. 2003; Dulvy et al. 2004). However, no comparable investigations of recreational fishing effects on these three species are available for areas within the southeastern United States (but see Sedberry et al. [1998] for a study of black sea bass).

The present study was conducted at Gray's Reef National Marine Sanctuary (GRNMS), a hard-bottom ecosystem located centrally along the continental shelf of the southeastern United States. In addition to having the range of bottom types, macroinfauna, and fish species representative of this shelf region (Powles and Barans 1980; Parker et al. 1983, 1994; Wenner 1983; Sedberry and Van Dolah 1984; Sedberry et al. 1998; Hyland et al. 2006), GRNMS has attributes useful for examining the effects of recreational fishing on local fish communities. Only hook-and-line fishing and spearfishing are allowed (NOAA 2006), nearly all effort is from the recreational sector (Ehler and Leeworthy 2002; NOAA 2006; G. Sedberry, GRNMS, personal communication), and the spatial distribution of fishing effort is not uniform throughout the sanctuary. Patterns of boat use and deposition of debris associated with fishing indicate that the north-central area of the sanctuary receives more fishing pressure than other areas (Kendall et al. 2007; Bauer et al., 2008). This results in the potential for differences to occur in the fish community between areas that are heavily used and those that are less used by fishermen.

Black sea bass, gags, and scamps are managed by the South Atlantic Fishery Management Council and are susceptible to overfishing. In fact, black sea bass and gags are presently overfished, and additional management measures are actively being sought and implemented (NOAA 2007; J. Kimmel, SAFMC, personal communication). More detailed knowledge of their habitat use and susceptibility to recreational fishing pressure is needed to inform management decisions (SAFMC 1998). The objectives of this study were to (1) map the spatial distribution of black sea bass, gags, and scamps at GRNMS, (2) quantify their habitat preferences, (3) describe their size structure, and (4) compare populations in heavily fished areas with those in less intensively fished areas.

Methods

Study area.—Gray's Reef National Marine Sanctuary is located on the continental shelf of the southeastern United States, 32.4 km offshore of Sapelo Island, Georgia (Figure 1). Average depth in the sanctuary is 18 m (range = 14–21 m). The ecological and socioeconomic importance of this area is due to the presence of a topographically complex system of limestone ledges that protrude above this otherwise flat region of the continental shelf. Commonly referred to as live-bottom areas, the rocky outcroppings within GRNMS support about 300 species of marine invertebrates (Gleason et al. 2007) and about 65 species of macroalgae (Searles 1988). These benthic communities provide habitat for over 180 fish species, including several that are of interest to the recreational and commercial bottom fishermen of the region (Sedberry and Van Dolah 1984; Gilligan 1989; Reef Environmental Education Foundation 2007).

Site selection.—Ledges were the focal bottom type of this study, because they constitute the primary habitat for the three species and are the areas most commonly used by the fishermen targeting these species. Ledge sites were selected randomly from recent benthic maps of GRNMS (Kendall et al. 2005). A new set of randomly selected sites was generated for each of three sampling periods: August 2004, May 2005, and August 2005. The total number of ledges visited was therefore maximized rather than conducting repeated measures at fewer sites. Only ledges that were at least 60 m long were surveyed; 60 m was the approximate minimum size (+10 m) needed to accommodate a 25-m-long transect sample unit, assuming that a transect was begun in the middle of the ledge and then conducted in a randomly chosen direction (i.e., left or right) along the ledge. If the random site selection process chose a ledge smaller than 60 m, the nearest ledge of suitable length was surveyed instead.

Survey methods.—Fish and benthic surveys were conducted in spring and summer months to coincide with the availability of a research vessel and diveable weather conditions. There were two components to the field survey: a fish count and benthic assessment; both occurred within a 25- × 4-m belt transect for a total area of 100 m^2 (Kendall et al. 2007). Transects were

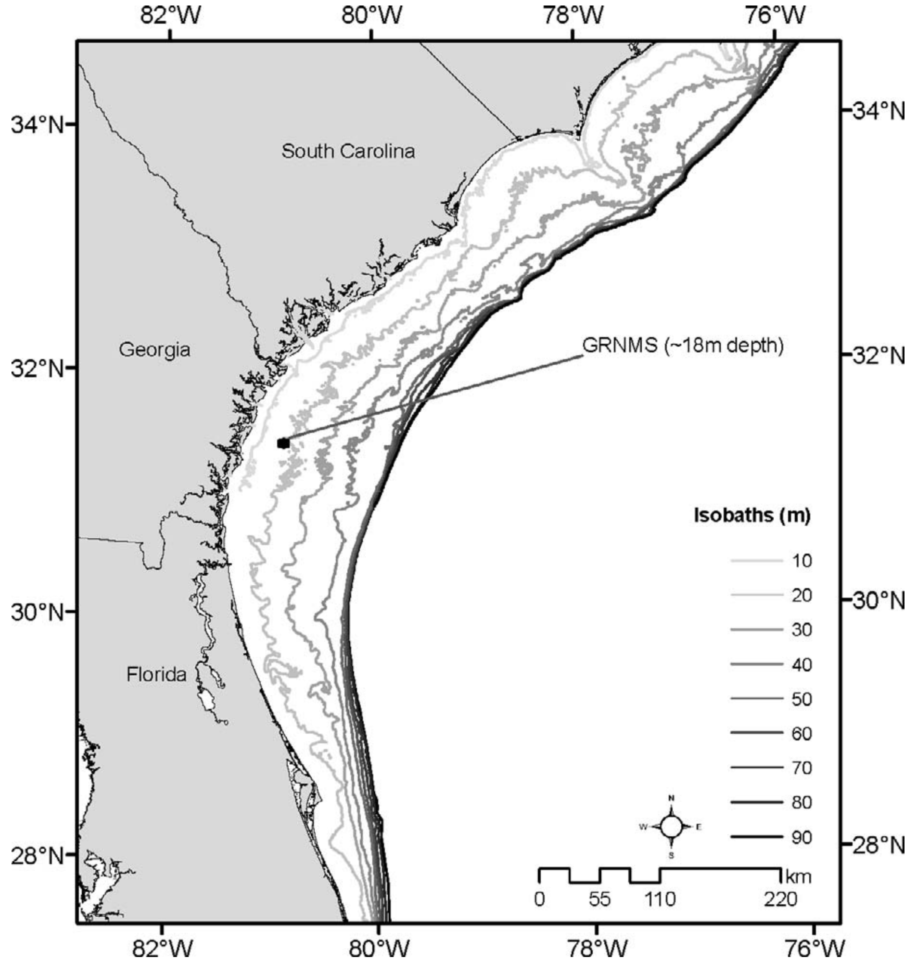


FIGURE 1.—Location of the Gray's Reef National Marine Sanctuary (GRNMS) along the southeastern U.S. continental shelf, where the distribution, habitat preferences, and size structure of black sea bass, gags, and scamps were studied.

conducted along the ledge face or lip (if undercut) and followed any turns or curves along it. Ledges in this area are usually not more than 2 m tall and may or may not have an overhang or undercut present. Conducting the transect along this axis ensured that it would (1) be entirely within the ledge bottom type and (2) survey fish on the underside, face, and top of the ledge. A fish surveyor faced toward the end of the transect and recorded all occurrences of black sea bass, gags, and scamps within the survey area while taking care not to double count these mobile fish. For each species, the number of individuals belonging to 10-cm size-classes (fork length) was tallied using visual estimation. The entire length of the transect was conducted at a constant speed and fixed time ($\sim$15 min) regardless of bottom complexity or number of fish present. A second diver followed behind the fish surveyor and recorded benthic variables at five random locations along the 25-m long transect. At each location, the second diver measured total ledge height, undercut height and width (if present), and percent cover of sessile invertebrates within a 1-m^2 quadrat.

Data analysis.—Since sampling periods were limited to the late spring and summer (May–August), seasonal differences in benthic communities were not explored and fish data were pooled for all analyses. Abundance and proportion of fish above or below the fishery size limit were plotted for each species by survey site and overlaid onto the benthic map of GRNMS to examine spatial distribution and fish size in heavily fished areas versus less intensively fished areas.

The study area was divided into regions of relatively high and relatively low fishing pressure based on the

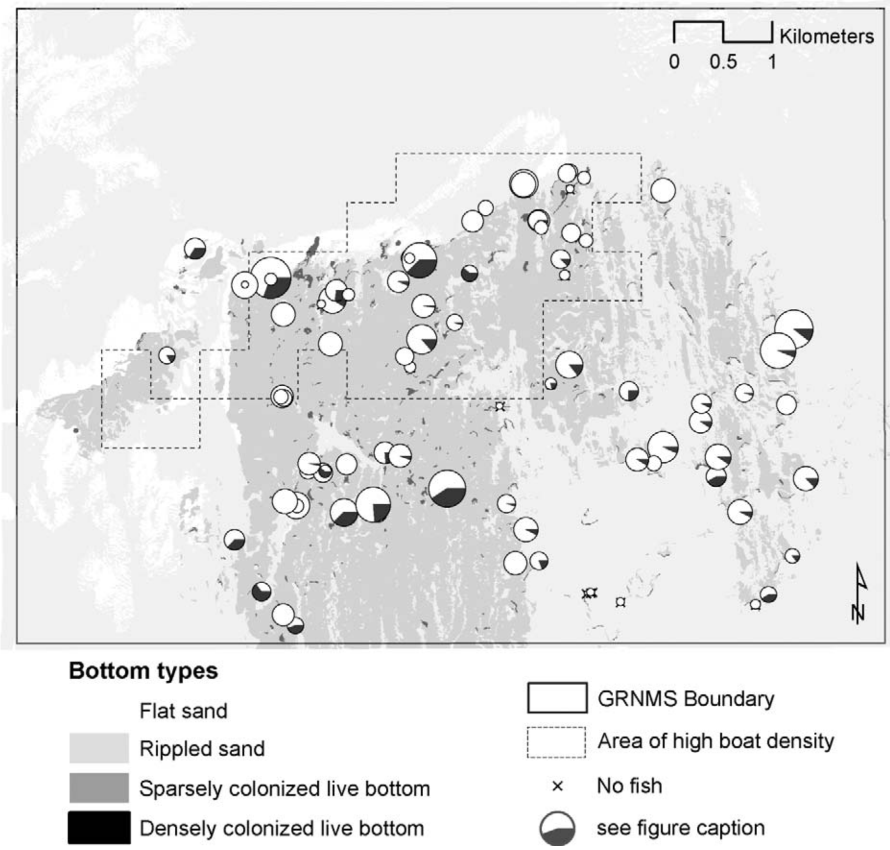


FIGURE 2.—Spatially explicit pie plot showing size and abundance of black sea bass observed at ledge sites within Gray's Reef National Marine Sanctuary (GRNMS) off the coast of Georgia. Shading in pies indicates the proportions of fish below (white) and above (shaded) the fishery size limit. Pie size is scaled to the total number of fish at each site; the largest pie represents 111 individuals.

observed spatial distribution of boats and fishing-related marine debris (Bauer et al., 2008). Opportunistic counts of fishing boats on 68 separate days during 1998–2004 indicated one intensively used region in the north-central portion of the study area (mean density ± SE = 1.13 ± 0.20 boats$\cdot$km$^{-2}\cdot$d^{-1}). This region harbors several well-known ledges and, perhaps more importantly, a National Oceanic and Atmospheric Administration (NOAA) data buoy (Station 41008; NOAA National Data Buoy Center) that provides a fixed reference point on the surface to visually orient fishermen to nearby ledges. Much-lower boat density was observed in the rest of the study area (0.05 ± 0.005 boats$\cdot$km$^{-2}\cdot$d^{-1}). During 57 surveys of marine debris in the area of higher boat density, 60 fishing-related items were found (1.053 items/survey). During 122 debris surveys in the area of low boat density, three fishing-related items were observed (0.025 items/survey). These boat and debris densities were used as surrogates to estimate the relative differences in fishing pressure between the two regions defined by Bauer et al. (2008).

Length frequency histograms were created for each species (sightings designated as occurring in the more intensively or less intensively fished areas). Mean (arithmetic) number and SE for fish in each size-class were calculated. The size-bin containing the size limit for the recreational fishery (SAFMC 2006) was noted on the plots, and the proportion of fish above or below that value was calculated for areas of high and low boat density. When the size limit fell within one of the 10-cm size-classes observed during fish surveys, the number of fish in that size-class was split proportionally above and below the limit. For example, the gag size limit is 61 cm (24 in total length), which was contained in the 60–70-cm size-class–. Therefore, 10% of the fish in that bin were assumed to be below the

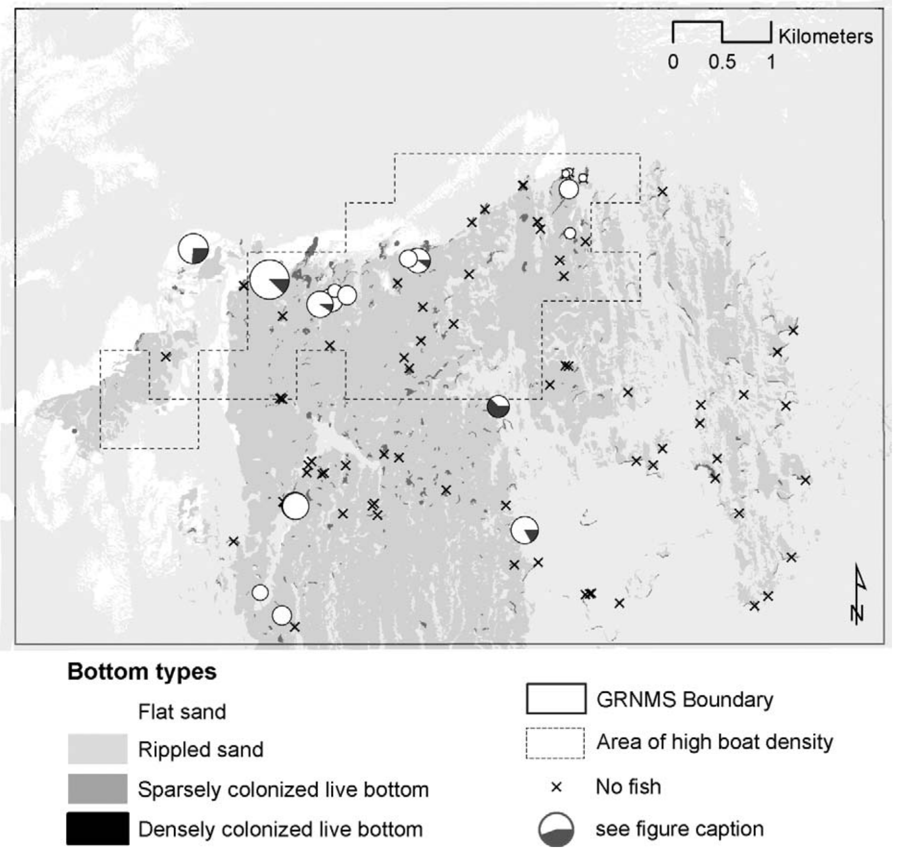


FIGURE 3.—Spatially explicit pie plot showing size and abundance of scamps observed at ledge sites within Gray's Reef National Marine Sanctuary (GRNMS) off the coast of Georgia. Shading in pies indicates the proportions of fish below (white) and above (shaded) the fishery size limit. Pie size is scaled to the total number of fish at each site; the largest pie represents 20 individuals.

size limit and 90% were assumed to be above the size limit.

Abundance, occurrence, and size of each fish species were also examined for relationships to specific ledge characteristics. The abundance and mean body length of black sea bass were examined for relations with explanatory variables by use of multiple regression. Explanatory variables were total percent cover of sessile biota, total ledge height, ledge area, and location (area of high or low boat density). Ledge area was used instead of ledge length to test for effects of the horizontal extent of ledges. Although ledges are narrow, linear features, many are variously curved, fork into multiple ledges, or form complex shapes that preclude straightforward measurement of length. All possible two-way interactions with location were examined. Undercut variables were not considered, since black sea bass were not observed to utilize ledge undercuts. Abundance was log transformed to meet statistical assumptions of regression.

Probability of gag or scamp occurrence was examined in relation to ledge variables by use of logistic regression. Abundances were too low to enable analysis beyond simple presence–absence. Diver observations of gags and scamps indicated that these species utilized the undercut of ledges. Therefore, relationships between gag or scamp presence–absence and undercut height, undercut width, ledge area, and location (area of high or low boat density) were considered, as were all possible two-way interactions with location. Mean gag or scamp size was also examined through multiple regression with the same explanatory variables.

The relationship between gag and scamp occurrence (presence–absence) and black sea bass abundance was also evaluated with multiple regression. Gags and scamps were combined for this analysis because they

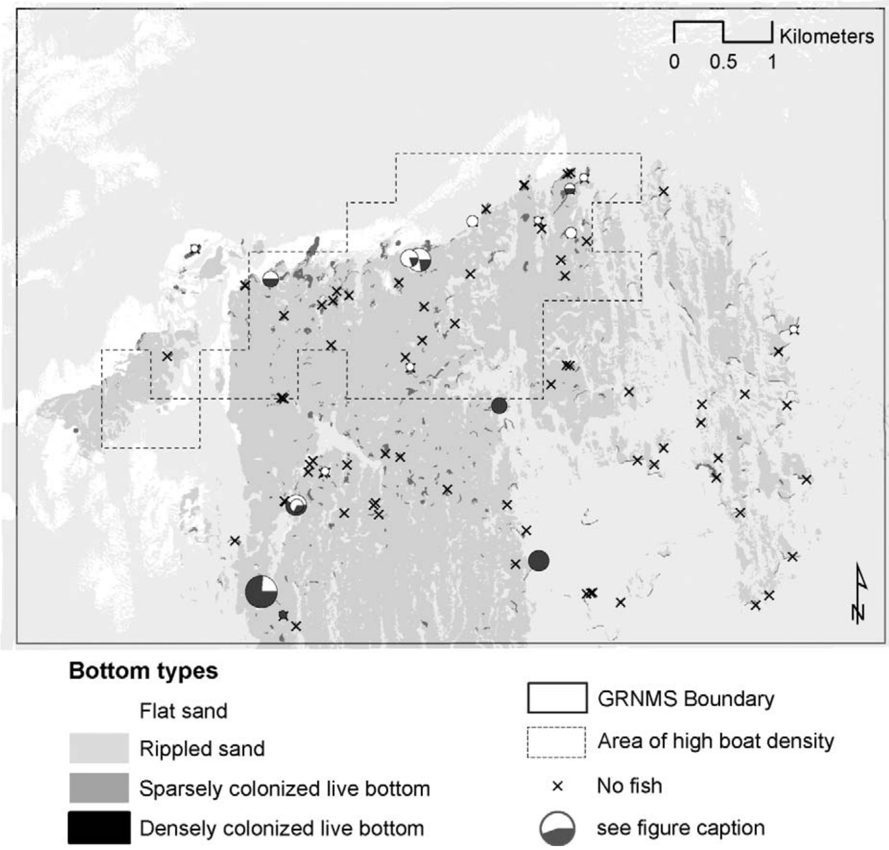


FIGURE 4.—Spatially explicit pie plot showing size and abundance of gags observed at ledge sites within Gray's Reef National Marine Sanctuary (GRNMS) off the coast of Georgia. Shading in pies indicates the proportions of fish below (white) and above (shaded) the fishery size limit. Pie size is scaled to total number of fish at each site; the largest pie represents 17 individuals.

often co-occur. The abundance of black sea bass was analyzed as the response variable; independent variables were gag and scamp presence–absence and any significant variables predicting black sea bass abundance and gag or scamp occurrence (i.e., ledge area, percent cover, or undercut height).

Results

Boat density was 22.6 times higher and incidence of fishing-related marine debris was 42.8 times higher in the north-central portion of the sanctuary than in the surrounding area. Ninety-two surveys were completed; 55 surveys were conducted in areas of low boat density, and 37 were conducted in areas of high boat density. A pie plot of black sea bass abundance for each ledge site indicated that this species did not exhibit a clumped distribution (Figure 2). In contrast, scamps and gags were seen at only a few sites that were clumped together (Figures 3, 4). Many were observed on the tall ledges in the north-central part of the sanctuary. Another concentration of fish was found on the tall ledges along or near the south-central boundary of the sanctuary. Black sea bass were much more abundant (mean ± SE = 28.0 ± 2.3 fish/100 m^2) than either gags (1.0 ± 0.2 fish/100 m^2) or scamps (2.0 ± 0.5 fish/100 m^2).

Size frequency histograms revealed that for all three species, fewer fish were observed in size-classes above the fishery size limit than in classes below the limit (Figure 5a–c). This pattern was common to areas of high and low boat density. Thirty percent of all black sea bass observed in the area of high boat density were above the fishery size limit. Similarly, 32% of all black sea bass in the area of low boat density were above the size limit. In contrast, the percentage of gags that exceeded the fishery size limit was only 13% in the area of high boat density versus 35% in the area of low boat density. A similar pattern was found for the percentage of scamps that were larger than the size limit (high boat density area: 24%; low boat density area: 44%). Modal fork length for black sea bass was about 20 cm in both areas. In contrast, gags had a modal size of about 40 cm in the area of high boat density and a much-higher modal size (~60–70 cm) in the area of low boat density. Similarly, scamps had a modal size of approximately 40 cm in the area of high boat density and a larger mode of about 50 cm in the area of low boat density; however, the scamp size distribution was much flatter and the sample size was much lower in the low boat density area relative to the high boat density area.

The abundance of black sea bass was significantly related to percent cover of sessile invertebrates and ledge area. Abundance was positively related to percent cover and negatively related to ledge area (Figure 6), although these two variables explained only 15% of the variability in the data. None of the variables tested was a significant predictor of mean black sea bass size.

Gag presence–absence was significantly related to the undercut height of ledges (Figure 7a). Scamp presence–absence was significantly related to undercut height of ledges and ledge area, although comparisons with a reduced model indicated that ledge area explained only 8% of the variability in the data (Figure 7b). No other variables or interactions, including location, were significantly related to presence–absence of either species. None of the variables tested was significantly related to mean size of gags or scamps.

The abundance of black sea bass was significantly related to gag and scamp presence–absence (Figure 8). When gags or scamps were present, the abundance of black sea bass was significantly lower, although only 17% of the variability in abundance was explained by the model.

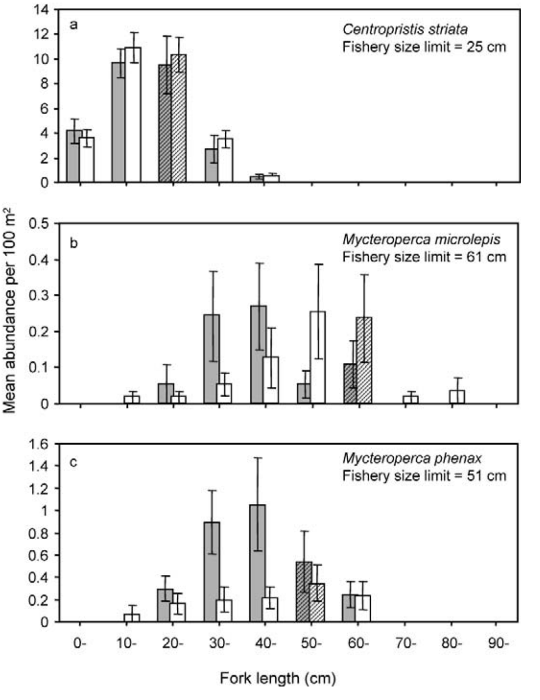
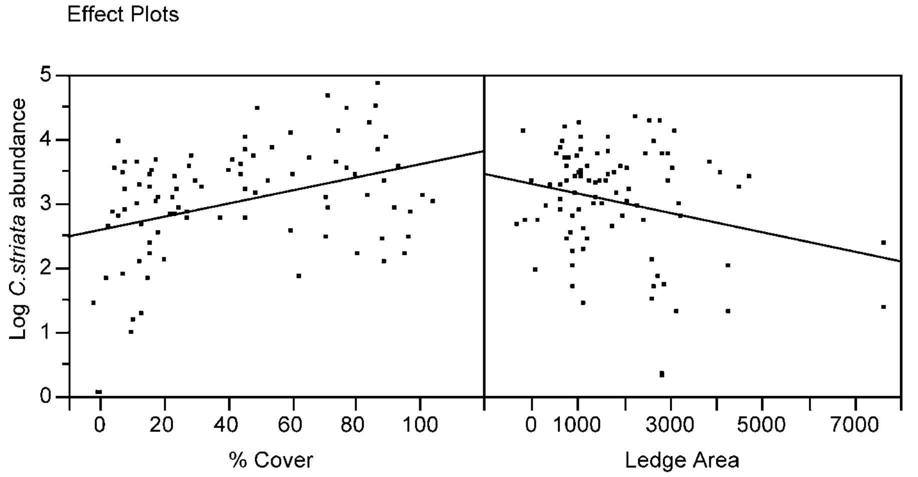


FIGURE 5.—Length frequency (±SE) histograms describing three bottom fishes targeted by the recreational fishery in areas of low boat density (white bars) and high boat density (gray bars) within Gray's Reef National Marine Sanctuary off the coast of Georgia: **(a)** black sea bass, **(b)** gags, and **(c)** scamps. The fishery size limit for each species is noted; hatched bars represent the size-class in which the size limit occurs. Abundance scale differs among panels.

Discussion

This study provides a spatial assessment of black sea bass, gags, and scamps in relation to fishing pressure and habitats at GRNMS. Gag and scamp spatial distributions were quite clumped on ledges in the north-central and south-central regions of the study area. Of the 92 ledges surveyed, only 20 had occurrences of these species; the majority of fish were observed in mixed-species groups on only 10 ledges. Extrapolation of this probability to the 447 ledge features present in the sanctuary (Kendall et al. 2005) suggests that less than 50 of the sanctuary's ledges would be expected to harbor a small group of gags or scamps. A very low level of focused bottom fishing or spearfishing on these few ledges could quickly reduce local abundance of these species within a short time. A recent study investigating the broad-scale movements of gags indicated that fish (at the latitude of the present study area) tended to stay around the same area but were the most prone to movement at a depth similar to our study depth (McGovern et al. 2005). In addition, gags and scamps spawn at shelf edge reefs (Sedberry et al. 2006), and mature adults probably undertake annual spawning migrations out of the sanctuary (Van Sant et al. 1994; McGovern et al. 2005; Sedberry et al. 2006). Further studies are required to determine (1) how quickly these species move across or along shelf habitats and (2) residence times at ledges in the study area; this information would allow estimation of the rate at which local populations may be replenished once overfished. In contrast, black sea bass occurred at 98% of the ledges surveyed and appeared evenly distributed throughout the sanctuary in much-higher numbers than either gags or scamps.

Mean fish density on ledges was 28 fish/100 m^2 for black sea bass, 1 fish/100 m^2 for gags, and 2 fish/100 m^2 for scamps. In a study conducted in 1985–1986, ledge densities of these species in the study area were twice as high (52, 4, and 2 fish/100 m^2, respectively; Parker et al. 1994). Differences in estimates between



ANOVA Whole Model

Source	DF	SS	MS	F Ratio	Prob>F
Model	2	10.8	5.4	7.5	0.001
Error	87	62.4	0.7		

Parameter Estimates

Term	Estimate	SE	t Ratio	Prob>|t|
Intercept	2.88	0.165	17.42	< 0.0001
Percent Cover	0.01	0.003	3.62	0.0005
Ledge Area	-0.0002	0.00006	-2.4	0.0184

$R^2 = 0.15$

Adj. $R^2 = 0.13$

FIGURE 6.—Regression of black sea bass abundance (fish/100 m^2) on percent cover or ledge area (m^2) at ledge sites within Gray's Reef National Marine Sanctuary off the coast of Georgia. Analysis of variance (ANOVA) results and parameter estimates are reported at bottom (DF = degrees of freedom; SS = sum of squares; MS = mean square; F and t = test statistics; Prob>F and Prob>t = P-values; adj. R^2 = adjusted coefficient of determination).

the two studies may be due to several factors, including (1) the respective biases of the video-based sampling method (Parker et al. 1994) and diver observation-based method (present study), (2) the inclusion of slightly broader seasonal sampling (May–November) by Parker et al. (1994), (3) the different base maps upon which sampling strategies were designed, and (4) some actual decline in fish density within the region over the last two decades.

Gag or scamp presence was most strongly related to undercut height of ledges, whereas abundance of black sea bass was best explained by percent cover of sessile biota. These findings represent the first quantitative assessment of habitat preferences for these species in relation to continuous environmental variables. This information is necessary to identify and prioritize among live-bottom and ledge areas in management of local populations. Qualitative diver observations agreed with these results and indicated that gags and scamps often retreated under ledges when approached, whereas black sea bass were never observed to use the undercut of a ledge. Interestingly, lower abundance of black sea bass occurred in the presence of either gags or scamps, which are generally much larger. Lower abundance of black sea bass at such sites could be due to predation (Matheson et al. 1986), competitive exclusion, or aggression by gags or scamps. We also showed that abundance of black sea bass was negatively influenced by ledge area, whereas presence of scamps was positively influenced. This suggests that

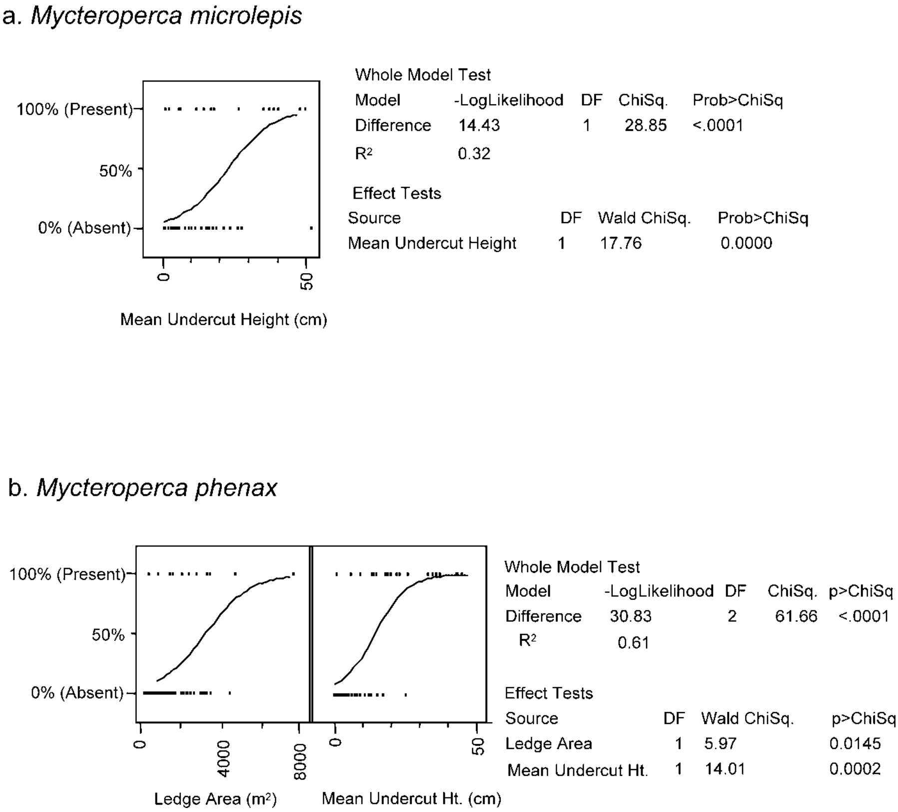
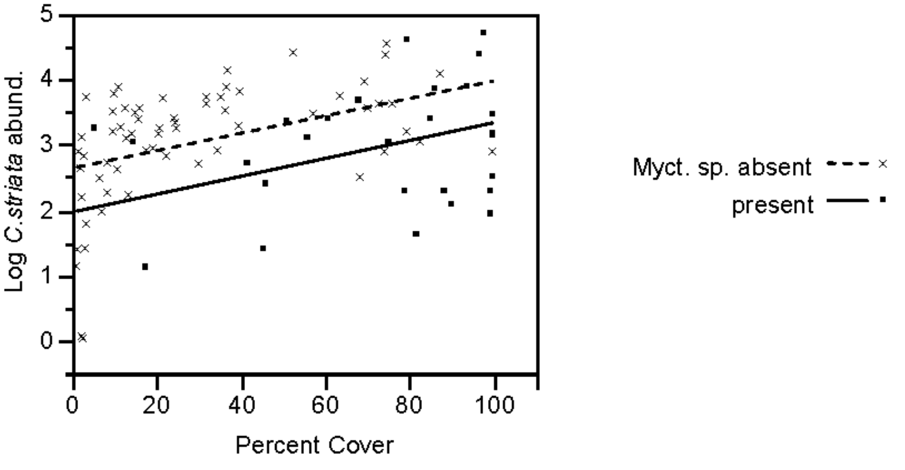


FIGURE 7.—Logistic regression models of fish presence–absence in relation to mean undercut height (cm) or ledge area (m^2) at ledge sites within Gray's Reef National Marine Sanctuary off the coast of Georgia: **(a)** gags and **(b)** scamps. Whole-model and effect test results are given to the right of each panel (DF = degrees of freedom; chisq = chi-square; Prob>chisq = P-value).

black sea bass avoid the ledges where the larger species are more likely to be present. Influences on distribution relative to the myriad of other local species, including prey, predators, and competitors, are possible but were not measured.

In areas of high and low boat density, fewer gags and scamps were observed in size-classes above the fishery size limit than in classes below the limit. This could be the result of selective removal of the largest fish by the fishery, as has been observed in other areas (Chiappone et al. 2000; Westera et al. 2003); it may also reflect ontogenetic emigration by large fish (McGovern et al. 2005). As with gags and scamps, fewer black sea bass were observed in size-classes above the fishery size limit than below the limit, which was also reported in a prior study (Sedberry et al. 1998). Emigration of larger fish is probably not a factor reducing the abundance of black sea bass, because they remain in the same specific area for their adult life in this part of their range (Mercer 1989; Parker 1990; Sedberry et al. 1998; Barkoukis 2006).

Relative fishing pressure was not a significant variable in determining mean fish size or presence–absence, but it did have an effect on gag and scamp size distributions. For example, modal size of gags was skewed toward smaller individuals by about 25 cm in the high boat density area relative to the low boat density area. Similarly, the modal size of scamps was about 15 cm smaller in the high boat density area than in the low boat density area, but the size distribution was flattened in the latter area. Our results and those of other studies (Watson and Ormond 1994; Wantiez et al. 1997) highlight the importance of using survey techniques that quantify the fish size distribution in addition to the mean and variance. The percentage of gags or scamps that were larger than the fishery size limit was higher in the low boat density area than in the high boat density area. Seasonal, ontogenetic, or depth-mediated migrations would not cause the observed differences in modal distribution between the heavily fished and less intensively fished areas of the sanctuary (e.g., McGovern et al. 2006). The sanctuary lies at a



ANOVA Whole Model

Source	DF	SS	MS	F Ratio	Prob > F
Model	2	12.2	6.1	8.71	0.0004
Error	87	60.9	0.7		
C. Total	89	73.2			

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	2.33	0.19	12.21	<.0001
p/a Myct.sp,	0.33	0.12	2.81	0.0061
Percent Cover	0.01	0.003	4.14	<.0001

Least Squares Means Table

Level	Least Sq Mean	Std Error	Mean
absent	3.23	0.113	3.06279
present	2.57	0.187	2.96506

Summary of Fit

R^2	0.17
Adj. R^2	0.15

FIGURE 8.—Regression model of black sea bass abundance (fish/100 m^2) in relation to percent cover and the presence or absence (p/a) of gags and scamps (*Mycteroperca* [Myct. sp.]) at ledge sites within Gray's Reef National Marine Sanctuary off the coast of Georgia. Analysis of variance (ANOVA) results, parameter estimates, and least-squares (least sq) means are reported at bottom (DF = degrees of freedom; SS = sum of squares; MS = mean square; std error = standard error; F and t = test statistics; Prob>F and Prob>t = P-values; adj. R^2 = adjusted coefficient of determination).

uniform depth. Ontogenetic migrations operate along an inshore–offshore axis at one to two orders of magnitude beyond the 3–5-km area where the different size patterns were seen. Size of fish undergoing seasonal spawning migrations would not differ between heavily fished and less intensively fished areas of the sanctuary. The difference in size distribution was apparent despite the presence of more preferred habitat within the fished area in the form of ledges with significantly higher undercut (Kendall et al. 2007). These considerations indicate that the most likely cause of the size distribution patterns is removal of large individuals by the fishery.

We demonstrated that the central area of GRNMS receives fishing effort that is 20–40 times higher than effort in the rest of the sanctuary. However, the exact level of effort and catch per unit effort (CPUE) are not quantifiable with present monitoring techniques. Similar shifts in size distribution of fished species in other regions have occurred (1) in response to fishing pressure reductions from implementation of marine protected areas (Watson and Ormond 1994; Wantiez et al. 1997; Westera et al. 2003; Ault et al. 2006), (2) along human population gradients (Dulvy et al. 2004), and (3) in relation to fishery characteristics (Chiappone et al. 2000). Such studies rarely quantify relative fishing effort as was done here (but see Dulvy et al. 2004), but all studies collectively demonstrate the need to understand the effects of various levels of fishing intensity. Additional activities should be initiated specifically to quantify fishing effort in different parts of the sanctuary and elsewhere along the southeastern United States and to determine the vulnerability of these species to recreational exploitation on a CPUE basis.

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References

Ault, J. S., S. G. Smith, J. A. Bohnsack, J. Luo, D. E. Harper, and D. B. McClellan. 2006. Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. Bulletin of Marine Science 78:633–654.

Barans, C. A., and V. J. Henry, Jr. 1984. A description of the shelf edge groundfish habitat along the southeastern United States. Northeast Gulf Science 7:77–96.

Barkoukis, A. M. 2006. A temporal and spatial analysis of fish trap catches at Gray's Reef National Marine Sanctuary, 1993–2005. Master's thesis. College of Charleston, Charleston, South Carolina.

Bauer, L., M. S. Kendall, and C. F. G. Jeffrey. 2008. Incidence of marine debris and its relationships with benthic features in Gray's Reef National Marine Sanctuary, Southeast USA. Marine Pollution Bulletin 56:402–413. DOI: 10.1016/j.marpolbul.2007.11.001.

Chabanet, P., H. Ralambondrainy, M. Amanieu, G. Faure, and R. Galzin. 1997. Relationships between coral reef substrata and fish. Coral Reefs 16:93–102.

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. Bulletin of Marine Science 34:267–279.

Chiappone, M., R. Sluka, and K. S. Sealey. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. Marine Ecology Progress Series 198:261–272.

Chittaro, P. M. 2004. Fish-habitat associations across multiple spatial scales. Coral Reefs 23:235–244.

Dulvy, N. K., N. V. C. Polunin, A. C. Mill, and N. A. J. Graham. 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Canadian Journal of Fisheries and Aquatic Sciences 61:466–475.

Ehler, R., and V. R. Leeworthy. 2002. A socioeconomic overview of Georgia's marine related industries and activities. National Oceanic and Atmospheric Administration, National Ocean Service, Silver Spring, Maryland.

Gilligan, M. R. 1989. An illustrated field guide to the fishes of Gray's Reef National Marine Sanctuary. NOAA Technical Memorandum NOS MEMD 25.

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). Bulletin of Marine Science 51:83–103.

Gleason, D. F., A. W. Harvey, and S. P. Vives. 2007. A guide to the benthic invertebrates and cryptic fishes of Gray's Reef. Georgia Southern University, Statesboro. Available: www.bio.georgiasouthern.edu/GR-inverts/. (June 2008).

Grigg, R. W. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. Marine Ecology Progress Series 103:25–34.

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. Bulletin of Marine Science 32:277–289.

Huntsman, G. R. 1976. Offshore headboat fishing in North Carolina and South Carolina. Marine Fisheries Review 38:13–23.

Hyland, J., C. M. Cooksey, W. L. Balthis, M. Fulton, D. Bearden, G. McFall, and M. Kendall. 2006. The soft-bottom macrobenthos of Gray's Reef National Marine Sanctuary and nearby shelf waters off the coast of

Georgia, USA. Journal of Experimental Marine Biology and Ecology 330:307–326.
Jennings, S., E. M. Grandcourt, and N. V. C. Polunin. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14:225–235.
Jennings, S., and N. V. C. Polunin. 1996. Effects of fishing effort and catch rates upon the structure and biomass of Fijian reef fish communities. Journal of Applied Ecology 33:400–412.
Kendall, M. S., L. J. Bauer, and C. F. G. Jeffrey. 2007. Characterization of the benthos, marine debris and bottom fish at Gray's Reef National Marine Sanctuary. NOAA Technical Memorandum NOS NCCOS 50.
Kendall, M. S., O. P. Jensen, C. Alexander, D. Field, G. McFall, R. Bohne, and M. E. Monaco. 2005. Benthic mapping using sonar, video transects, and an innovative approach to accuracy assessment: a characterization of bottom features in the Georgia Bight. Journal of Coastal Research 21:1154–1165.
Matheson, R. H., III, G. R. Huntsman, and C. S. Manooch. 1986. Age, growth, mortality, food, and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. Bulletin of Marine Science 38:300–312.
McGovern, J. C., G. R. Sedberry, H. S. Meister, T. M. Westendorff, D. M. Wyanski, and P. J. Harris. 2005. A tag and recapture study of gag, *Mycteroperca microlepis*, off the southeastern U.S. Bulletin of Marine Science 76:47–59.
Mercer, L. P. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)—black sea bass. U.S. Fish and Wildlife Service Biological Report 82.
Miller, G. C., and W. J. Richards. 1980. Reef fish habitat, faunal assemblages, and factors determining distributions in the South Atlantic Bight. Proceedings of the Gulf and Caribbean Fisheries Institute 32:114–130.
Molles, M. C. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. Ecological Monographs 48:289–305.
NOAA (National Oceanic and Atmospheric Administration). 2006. Gray's Reef National Marine Sanctuary final management plan/final environmental impact statement. NOAA, Savannah, Georgia.
NOAA (National Oceanic and Atmospheric Administration). 2007. Recreational fisheries statistics program. NOAA, Silver Spring, Maryland. Available: www.st.nmfs.gov/st1/index.html. (September 2007).
Parker, R. O., Jr. 1990. Tagging studies and diver observations of fish populations on live-bottom reefs of the U.S. southeastern coast. Bulletin of Marine Science 46:749–760.
Parker, R. O., Jr., A. J. Chester, and R. S. Nelson. 1994. A video transect method for estimating reef fish abundance, composition, and habitat utilization at Gray's Reef National Marine Sanctuary, Georgia. U.S. National Marine Fisheries Service Fisheries Bulletin 92:787–799.
Parker, R. O., Jr., D. R. Crosby, and T. D. Willis. 1983. Estimated amount of reef habitat on a portion of the U.S. South Atlantic and Gulf of Mexico continental shelf. Bulletin of Marine Science 33:935–940.
Parker, R. O., Jr., and R. W. Mays. 1998. Southeastern U.S. deepwater reef fish assemblages, habitat characteristics, catches, and life history. NOAA Technical Report NMFS 138.
Parker, R. O., Jr., and S. W. Ross. 1986. Observing reef fishes from submersibles off North Carolina. Northeast Gulf Science 8:31–49.
Powles, H., and C. A. Barans. 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Marine Fisheries Review 42:21–35.
Quattrini, A. M., and S. W. Ross. 2006. Fishes associated with North Carolina shelf-edge hardbottoms and initial assessment of a marine protected area. Bulletin of Marine Science 79:137–163.
Reef Environmental Education Foundation. 2007. REEF home page. Available: www.reef.org/. (September 2007).
Riggs, S. R., S. W. Snyder, A. C. Hine, and D. L. Mearns. 1996. Hardbottom morphology and relationship to the geologic framework: mid-Atlantic continental shelf. Journal of Sedimentary Research 66:830–846.
Russ, G. R., and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Marine Ecology Progress Series 56:13–27.
SAFMC (South Atlantic Fishery Management Council). 1998. Final habitat plan for the South Atlantic Region: essential fish habitat requirements for fishery management plans of the South Atlantic Fishery Management Council. Comprehensive amendment addressing essential fish habitat in fishery management plans of the South Atlantic Region. Amendment 10 to the Snapper Grouper Fishery Management Plan. SAFMC, Charleston, South Carolina.
SAFMC (South Atlantic Fishery Management Council). 2006. SAFMC home page. Available: www.safmc.net/. (September 2006).
Schobernd, C. M. 2006. Submersible observations of southeastern U.S. deep reef fish assemblages: habitat characteristics, spatial and temporal variation, and reproductive behavior. Master's thesis. College of Charleston, Charleston, South Carolina.
Searles, R. B. 1988. An illustrated field guide to the seaweeds of Gray's Reef National Marine Sanctuary. NOAA Technical Memorandum NOS MEMD 22.
Sedberry, G. R., and R. F. Van Dolah. 1984. Demersal fish associated with hard bottom habitat in the South Atlantic Bight of the USA. Environmental Biology of Fishes 11:241–258.
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. Proceedings of the Gulf and Caribbean Fisheries Institute 50:452–481.
Sedberry, G. R., O. Pashuk, D. M. Wyanski, J. A. Stephen, and P. Weinbach. 2006. Spawning locations of Atlantic reef fishes off the southeastern U.S. Proceedings of the Gulf and Caribbean Fisheries Institute 57:463–514.
Struhsaker, P. 1969. Demersal fish resources: composition, distribution, and commercial potential of the continental shelf stocks off southeastern United States. Fishery Industrial Research 4:261–300.
Van Sant, S. B., M. R. Collins, and G. R. Sedberry. 1994. Preliminary evidence from a tagging study for a gag

(*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. Proceedings of the Gulf and Caribbean Fisheries Institute 43:417–428.

Wantiez, L., P. Thollot, and M. Kulbicki. 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. Coral Reefs 16:215–224.

Watson, M., and R. F. G. Ormond. 1994. Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. Marine Ecology Progress Series 109:115–129.

Wenner, C. A. 1983. Species associations and day–night variability of trawl-caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. U.S. National Marine Fisheries Service Fisheries Bulletin 81:537–552.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight II. Spring 1974. South Carolina Marine Resources Center Technical Report 40.

Westera, M., P. Lavery, and G. Hyndes. 2003. Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park. Journal of Experimental Marine Biology and Ecology 294:145–168.