

INFLUENCE OF HARD BOTTOM MORPHOLOGY ON FISH ASSEMBLAGES OF THE CONTINENTAL SHELF OFF GEORGIA, SOUTHEASTERN USA

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ABSTRACT

Various reef types worldwide have inconsistent relationships among fish assemblage parameters and benthic characteristics, thus there is a need to identify factors driving assemblage structure specific to each reef type and locale. Limestone ledges are known to be key habitats for bottom fish on the continental shelf of the southeastern USA, however, the specific factors that link them to fish assemblages have not been quantified. Bottom fishes and habitat characteristics on ledges were surveyed at a study site located centrally in the southeastern USA continental shelf. Species richness, diversity, abundance, and biomass of fish were higher at ledges than on flat bottom. Species richness, abundance, and biomass of fish were well explained by ledge variables including percent cover of sessile invertebrates, total height, and height of undercut recesses. Multivariate analyses based on biomass of individual species at ledges revealed two fish assemblages associated with four ledge types. One assemblage was associated with ledges that were tall, heavily colonized with sessile invertebrates, large in area, and did or did not have undercuts. The other assemblage was associated with ledges that were short, not undercut, smaller in area, and were or were not heavily colonized by invertebrates. Seafloor classification schemes presently used in the region do not adequately capture hard bottom diversity to identify the location and extent of essential fish habitats for ecological and fisheries purposes. Given that ledges cover only ~1% to 5% of the southeastern USA continental shelf, they merit the highest levels of consideration in regional research, conservation, and management plans.

The coast off the southeastern United States (Cape Canaveral, Florida to Cape Hatteras, North Carolina) is characterized by a gradually sloping continental shelf comprised of three general bottom types: open sand (~70% of the shelf), flat hard-bottom often with little to no vertical relief that is sparsely colonized by sessile invertebrates (~25% of the shelf), and ledges or rocky outcrops with vertical relief up to several meters tall (~0.1 to 10 m) typically with dense colonization of sessile invertebrates (< ~5% of the shelf) (Struhsaker, 1969; Miller and Richards, 1980; Powles and Barans, 1980; Parker et al., 1983; Riggs et al., 1996; Bauer et al., 2008). The flat hard-bottom and ledge ecosystems of this region, both of which are locally termed “live bottom,” are characterized by a mixture of tropical and temperate reef fish species that are the focus of recreational and commercial fisheries (Struhsaker, 1969; Huntsman, 1976; Chester et al., 1984; SEAMAP-SA, 2001; Quattrini and Ross, 2006; Kendall et al., 2008).

Many studies have been conducted off the southeastern USA on fish communities over live bottom on the continental shelf (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., 1979a,b; Quattrini and Ross, 2006), 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 and Sedberry, 2009). Most of these studies were conducted at broad scales covering much of the region and examined differences in assemblage structure between inshore and offshore shelf communities or latitudinal changes in biogeography. The distribution of bottom types throughout the region have been summarized at coarse spatial (1×1 degree of latitude and longitude cells) and categorical resolution (hard bottom, possible hard bottom, or no hard bottom) (SEAMAP-SA, 2001).

Despite the abundance of research in this shelf region, very little quantitative analysis has been done to identify the specific habitat associations of fish communities (but see Parker et al., 1994; Quattrini and Ross, 2006; Kendall et al., 2008). Flat hard-bottom and limestone ledges are known to be key habitats for bottom fish in the region; however, the factors that make these features attractive to various components of the fish community have not been quantified. Even studies that have focused on individual species of bottom fish often have not quantified their fine-scale habitat preferences (Matheson et al., 1986; Mercer, 1989; Gilmore and Jones, 1992; Harris et al., 2002; McGovern et al., 2005). At best, gross ledge height has been categorized as small, medium, and large, or sparsely, moderately, or densely colonized by sessile invertebrates and then related to fish assemblages (Parker et al., 1994; Riggs et al., 1996; Quattrini and Ross, 2006). Although all of these studies have provided a wealth of biogeographic information on the region and an understanding of the general habitat associations of bottom fish, the more detailed structural attributes of benthic habitat that influence the composition of the fish assemblage have remained unknown.

In contrast to the lack of detailed studies on shelf habitats of the southeastern USA, much prior research has been focused on defining fine-scale habitat associations of fishes in coral reef environments although often with conflicting results (Risk, 1972; Luckhurst and Luckhurst, 1978; Molles, 1978; Roberts and Ormond, 1987; Chabanet et al., 1997; Friedlander and Parrish, 1998; Öhman and Rajasuriya, 1998; Gratwicke and Speight, 2005). In these studies, the total abundance, species richness, diversity, and assemblage structure of reef fish have variously been correlated with benthic characteristics such as rugosity, vertical relief, coral cover, and other environmental variables. These benthic characteristics typically influence fish assemblages differently among reef types and localities thus it is necessary to identify the factors that influence community structure of fishes that are specific to reef types and localities.

An important next step in understanding fish distributions on the continental shelf of the southeastern USA is analysis of how fish community structure varies with habitat features measured on continuous rather than categorical scales because many habitat characteristics vary continuously rather than discretely. For example, how ledge height, area, and percent cover of sessile biota relate to resident fish assemblages has not been quantified. The combined knowledge of fine-scale habitat requirements for fish assemblages and the growing capabilities of sonar and other seafloor mapping systems to map those habitats at commensurate resolution provide a powerful combination of tools to enable spatially explicit, ecosystem based management of the region.

The objective of this study was to quantify the habitat associations of bottom fish communities at a site centrally located on the inner continental shelf of the southeastern USA. In particular, we evaluated the differences in fish assemblages between flat live bottom and ledge habitats and quantified the physical attributes of ledges that are correlated with fish assemblages.

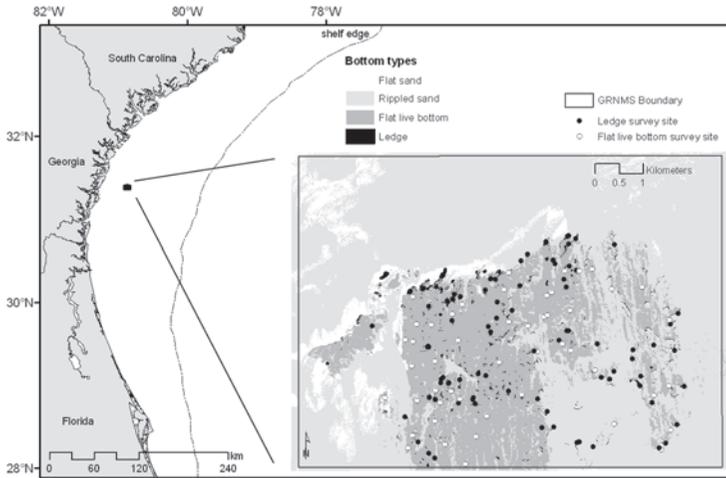


Figure 1. Gray's Reef National Marine Sanctuary study area off Georgia, southeastern USA, with inset showing bottom features and sampling sites.

METHODS

The study was conducted at Gray's Reef National Marine Sanctuary (GRNMS) which is located centrally on the inner/mid continental shelf of the southeastern USA. The study area lies at the center of the Carolinian biogeographic province, 32 km offshore of Sapelo Island, Georgia (Fig. 1). GRNMS possesses all of the bottom types representative of this region of the continental shelf including sand plains, flat live bottom, and limestone ledges with a range of vertical relief. Live bottom within GRNMS has been shown to support ~300 species of marine invertebrates (www.bio.georgiasouthern.edu/GR-inverts/) and ~65 species of macroalgae (<http://graysreef.noaa.gov/seaweed.html>). In turn, these benthic substrates and communities provide habitat for as many as 181 fish species (Sedberry and Van Dolah, 1984; Gilligan, 1989; Parker et al., 1994; Sedberry et al., 1998; Kendall et al., 2007).

SITE SELECTION.—Flat live bottom and ledge survey sites were randomly chosen using benthic maps digitized from bathymetry and side-scan sonar data (Fig. 1) (Kendall et al., 2005). Twice as many sampling surveys were devoted to the ledge bottom type given the higher abundance and diversity of bottom fish expected there based on prior studies (Gilligan, 1989; Parker et al., 1994).

There were two components to the field survey: fish community assessment and benthic assessment. Both survey components occurred within a 25×4 m belt transect. For sites on flat live bottom, surveys were conducted in a randomly selected compass heading. A 25 m buffer was used during placement of sites on flat live bottom to ensure that surveys did not cross bottom type boundaries. For ledge sites, surveys were conducted along the ledge and followed any curves rather than along a constant random compass heading. Consequently, only ledges a minimum of 60 m long were allowed during site selection. A ledge 60 m long was the minimum size (+10 m) to accommodate a 25-m long transect that began in the middle of the ledge and then was conducted in a randomly chosen direction (i.e., left or right) along the ledge.

FIELD METHODS.—Field surveys were conducted in August 2004, May 2005, and August 2005 to coincide with the availability of research vessels and diveable weather conditions. Two divers surveyed the 25×4 m belt transect at each site for a total surveyed area of 100 m^2 . One diver was responsible for visual identification, counts, and size estimation of fish species. The second diver characterized benthic features based on percent cover of sessile benthic organisms and ledge dimensions. Once at a site, the fish surveyor attached a tape measure to the substrate and began the survey. As the tape rolled out, the diver looked forward toward

the end of the transect and recorded all fish species to the lowest taxonomic level possible within the survey area. The entire length of the transect survey was conducted at a constant speed and for a fixed time period of 15 min regardless of bottom complexity or number of fish present. This speed allowed a thorough assessment of the fish community regardless of substrate complexity. The number of individuals of each species was tallied in 10 cm size class increments. Several similar looking pairs of fish species that were observed often moved too quickly, kept a distance from divers, or remained far under recesses of ledges to allow consistent identification to the species level and were therefore identified only to the genus level. Those species were *Seriola dumerili* (Risso, 1810) and *Seriola rivoliana* (Valenciennes in Cuvier and Valenciennes, 1833), *Pareques umbrosus* (Jordan and Eigenmann, 1889) and *Pareques acuminatus* (Bloch and Schneider, 1801), and *Decapterus macarellus* (Cuvier, 1833) and *Decapterus punctatus* (Cuvier, 1829).

Ledge surveys were conducted along the ledge face or lip if undercut. This allowed fish on the underside (if undercut), face, and top of the ledge to be surveyed. Preliminary observation of fish communities and ledge features indicated that the 4 m wide transect captured fish associated with the ledge rather than adjacent habitats. Beyond the scarp and first 1–2 m of the top of the ledge, the substrate rapidly transitions into flat live bottom. Transects at ledge sites were conducted solely along this edge and not on top of it.

Data on the percent cover of sessile biota at both flat live bottom and ledge sites were recorded within five 1 m² quadrats that were randomly placed along the transect. The quadrat was divided into 100 smaller 10 × 10 cm squares with string (1 small square = 1% cover) to enable estimation of percent cover of sessile biota (Kendall et al., 2007; Bauer et al., 2008). Additionally at ledge sites, several ledge dimensions were measured at each quadrat position. Total height was measured from the base of the ledge to the top of the substrate behind it but excluded the height of sessile organisms that were attached to the substrate. Undercut width was measured from the leading face of the ledge to the farthest recess underneath. Undercut height, the height under the ledge, was estimated visually using the quadrat as a reference. Values recorded at each quadrat were averaged for a given ledge and the averages were used in subsequent analyses.

DATA ANALYSIS.—Since survey periods were separated by only four months, seasonal differences were not explored and data were pooled across all time periods for analyses. Our scope of inference is limited to the summer time period given that seasonal changes are known to occur in the fish assemblage of this area (Sedberry and Van Dolah, 1984; Parker et al., 1994).

The probability of encounter, mean abundance (\pm SE), and biomass (\pm SE) within a 100 m² transect are provided for each species by bottom type. Probability of encounter was defined as the proportion of surveys in a given bottom type on which a species was observed. No standard error is given when a species was observed during fewer than three surveys although mean abundance and biomass were calculated. Mean values were rounded to the nearest whole number and SE was rounded to tenths. Biomass was calculated using the length-weight relationship $W = aL^b$, where L is length in centimeters and weight is in grams. The mid-point of each size class was used as the value of L . For example, if a fish were in the 10–20 cm size class its length (L) for biomass estimation was assumed to be 15 cm. Values of the terms (a) and (b) for each species were obtained from the FishBase database (Froese and Pauly, 2005). For species with more than one length-weight relationship defined, values for the most recent study nearest GRNMS were used. For species with no length-weight relationship published, terms for a morphologically similar species were used. It should be noted that length-weight parameters can change over time in response to such factors as fishing pressure, or they can be erroneously uploaded into FishBase and must therefore be interpreted cautiously as the database is periodically updated.

Species richness, the Shannon index of diversity (H'), abundance, and biomass of all fish observed at each survey were calculated. Distributions could not be transformed to meet the assumptions of parametric statistics. Therefore, differences between ledge surveys vs those

on flat live bottom for these variables were tested using non-parametric Wilcoxon tests based on ranked data.

Preliminary analysis corroborated the findings of prior studies and indicated that ledges harbored a significantly higher abundance (20 times higher), biomass (7 times higher), and species richness (2 times higher) and also possessed a different assemblage of fish than flat live bottom (Parker et al., 1994; Kendall et al., 2007). Therefore, the 92 ledge sites were investigated in greater detail through multiple regression and non-metric multidimensional scaling (MDS) to determine which physical attributes of the ledges were associated with the fish assemblage.

Response variables representing the fish community in multiple regression analyses were species richness, diversity, abundance, and biomass of fish. Predictor variables included percent cover of sessile invertebrates, total ledge height, undercut height, undercut width, and total area of ledges. Ledge area was calculated from benthic maps (Kendall et al., 2005) in a Geographic Information System. Linear correlations among predictor variable pairs ranged from 0.28 to 0.83. All predictor variables were included in initial models. Backwards selection in regression models was used to retain only significant variables. Fish abundance and biomass were log transformed to meet statistical assumptions.

Biomass of the individual fish species at ledge sites was used as the basis for MDS ordinations. Biomass was chosen for analysis over simple fish abundance because much of the prior literature in this region has been on fisheries productivity for which biomass is the better indicator. Preliminary analyses indicated that results were similar for either metric. Data were analyzed using the software Primer v6 (Clarke and Warwick, 2001). Only species occurring at a minimum of 5% of ledge sites were included to prevent those species lacking sufficient records from obscuring regular assemblage patterns. Two sites were eliminated from analysis due to highly unusual fish communities that were consistently isolated in preliminary ordinations. One had an extremely low species richness and the other had immense schools of three pelagic species: *Caranx crysos*, *Chloroscombrus chrysurus*, and *Scomberomorus regalis* (Bloch, 1793). Data from the remaining 90 sites were square root transformed to reduce the disparity between rare and common species and then used to construct a Bray-Curtis similarity matrix. Ordination plots were then constructed from the similarity matrix and cross checked based on hierarchical cluster analysis using the group average mode. Similarity percentages were then used to determine which species were most responsible for separation of the fish assemblages identified in the MDS and cluster analysis and also for determining which species typified each group.

To determine which ledge variables were most influential in explaining the pattern in the fish assemblage observed at each site, we used the BIOENV procedure within Primer v6. Spearman rank correlation was calculated between the fish assemblages and all possible combinations of ledge variables to determine which ledge variables best explained the similarities among sites.

RESULTS

In total, 143 sites were surveyed including 92 ledge and 51 flat live bottom locations (Fig. 1). The number of ledges surveyed represented 21% of all ledges within GRNMS (Kendall et al., 2005). Site depths ranged from 16 to 20 m.

Visual census recorded 75 fish species (or species groups) (Table 1). Thirty-four of the 75 species observed in the study were found on flat live bottom habitat. Two species, *Centropristis striata* (seen on 98% of flat live bottom surveys) and *Stenotomus* spp. (seen on 90%) were encountered most frequently. These two species were also the most numerically abundant and had the highest biomass (Table 1).

Seventy-two of the 75 species observed in the study were found on ledge habitat. Four species were encountered most frequently: *C. striata* (seen on 98% of ledge

Table 1. Fish species observed on flat live bottom and the two types of ledges identified in the MDS and cluster analyses. Within each of the two ledge types based on cluster analysis, the percent of surveys on which the species was encountered and the average abundance and biomass (and standard error) are provided. For species which had zero values for probability of encounter, abundance and biomass are left blank. No standard error is given when a species was observed on fewer than three surveys although mean abundance and biomass are provided. Also note that mean values are rounded to the ones digit and SE is rounded to tenths which results in some low values appearing as zeros.

Genus species Authority	Variable	Flat live bottom		Ledge	
		Value	SE	Value	SE
<i>Abudefduf saxatilis</i> (Linnaeus, 1758)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	
<i>Acanthostracion quadricornis</i> (Linnaeus, 1758)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			3	
Antennariidae	percent of surveys	0		2	
	mean abundance			0	
	mean biomass (g)			0	
<i>Apogon pseudomaculatus</i> Longley, 1932	percent of surveys	0		49	
	mean abundance			3	0.5
	mean biomass (g)			6	1.1
<i>Archosargus probatocephalus</i> (Walbaum, 1792)	percent of surveys	0		33	
	mean abundance			2	0.7
	mean biomass (g)			3,041	839.7
<i>Archosargus rhomboidalis</i> (Linnaeus, 1758)	percent of surveys	25		20	
	mean abundance	2	0.5	1	0.3
	mean biomass (g)	139	47.8	652	507.7
<i>Balistes capriscus</i> Gmelin, 1789	percent of surveys	0		26	
	mean abundance			1	0.3
	mean biomass (g)			846	290.6
<i>Calamus bajonado</i> (Bloch and Schneider, 1801)	percent of surveys	0		3	
	mean abundance			0	0.0
	mean biomass (g)			176	120.5
<i>Calamus calamus</i> (Valenciennes, 1830)	percent of surveys	0		10	
	mean abundance			0	0.1
	mean biomass (g)			229	98.5
<i>Calamus penna</i> (Valenciennes, 1830)	percent of surveys	0		5	
	mean abundance			0	0.1
	mean biomass (g)			49	33.0
<i>Caranx bartholomaei</i> (Cuvier, 1833)	percent of surveys	8		3	
	mean abundance	0	0.1	0	0.0
	mean biomass (g)	13	6.9	15	13.2
<i>Caranx crysos</i> (Mitchill, 1815)	percent of surveys	22		24	
	mean abundance	5	2.4	21	13.4
	mean biomass (g)	3,026	1,560.2	14,278	9,082.1
<i>Caranx ruber</i> (Bloch, 1793)	percent of surveys	0		7	
	mean abundance			1	0.6
	mean biomass (g)			290	200.5

Table 1. Continued.

Genus species Authority	Variable	Flat live bottom		Ledge	
		Value	SE	Value	SE
<i>Centropristis ocyurus</i> (Jordan and Evermann, 1887)	percent of surveys	33		41	
	mean abundance	1	0.5	1	0.3
	mean biomass (g)	65	34.4	106	29.5
<i>Centropristis striata</i> (Linnaeus, 1758)	percent of surveys	98		98	
	mean abundance	13	1.5	28	2.3
	mean biomass (g)	1,327	193.3	4,111	524.0
<i>Chaetodipterus faber</i> (Broussonet, 1782)	percent of surveys	2		12	
	mean abundance	1		7	3.4
	mean biomass (g)	182		3,070	1,572.9
<i>Chaetodon ocellatus</i> (Bloch, 1787)	percent of surveys	0		2	
	mean abundance			0	
	mean biomass (g)			0	
<i>Chilomycterus schoepfi</i> (Walbaum, 1792)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			1	
<i>Chloroscombrus chrysurus</i> (Linnaeus, 1766)	percent of surveys	12		12	
	mean abundance	8	4.5	24	12.4
	mean biomass (g)	578	289.2	5,176	3,023.0
Congridae	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			3	
<i>Coryphopterus glaucofraenum</i> Gill, 1863	percent of surveys	0		5	
	mean abundance			0	0.0
	mean biomass (g)			0	0.1
<i>Decapterus</i> spp.	percent of surveys	6		10	
	mean abundance	1	0.5	195	118.7
	mean biomass (g)	240	205.4	908	540.5
<i>Diodon hystrix</i> Linnaeus, 1758	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			19	
<i>Diplectrum formosum</i> (Linnaeus, 1766)	percent of surveys	43		33	
	mean abundance	4	0.9	1	0.4
	mean biomass (g)	71	21.4	57	22.3
<i>Diplodus holbrookii</i> (Bean, 1878)	percent of surveys	6.00		34	
	mean abundance	0	0.4	4	1.0
	mean biomass (g)	30	26.7	483	112.4
<i>Echeneis naucrates</i> Linnaeus, 1758	percent of surveys	2		0	
	mean abundance	0			
	mean biomass (g)	23			
<i>Epinephelus morio</i> (Valenciennes, 1828)	percent of surveys	0		7	
	mean abundance			0	0.0
	mean biomass (g)			102	43.7
<i>Equetus lanceolatus</i> Linnaeus, 1758	percent of surveys	6		16	
	mean abundance	0	0.1	0	0.1
	mean biomass (g)	22	15.3	26	10.9

Table 1. Continued.

Genus species Authority	Variable	Flat live bottom		Ledge	
		Value	SE	Value	SE
<i>Ginglymostoma cirratum</i> (Bonnaterre, 1788)	percent of surveys	0		3	
	mean abundance			0	0.0
	mean biomass (g)			1,006	776.9
<i>Gymnothorax saxicola</i> Jordan and Davis, 1891	percent of surveys	8		1	
	mean abundance	0	0.0	0	
	mean biomass (g)	25	14.6	0	
<i>Haemulon aurolineatum</i> Cuvier, 1830	percent of surveys	4		48	
	mean abundance	0		931	494.5
	mean biomass (g)	4		1,897	644.2
<i>Haemulon plumierii</i> (Lacépède, 1801)	percent of surveys	0		11	
	mean abundance			0	0.2
	mean biomass (g)			240	153.8
<i>Haemulon</i> spp.	percent of surveys	2		1	
	mean abundance	0		0	
	mean biomass (g)	0		0	
<i>Halichoeres bivittatus</i> (Bloch, 1791)	percent of surveys	61		89	
	mean abundance	6	1.1	15	1.6
	mean biomass (g)	194	48.0	290	37.0
<i>Halichoeres caudalis</i> (Poey, 1860)	percent of surveys	51		45	
	mean abundance	3	0.8	1	0.2
	mean biomass (g)	115	30.8	57	12.6
<i>Holacanthus bermudensis</i> Goode, 1876	percent of surveys	0		20	
	mean abundance			1	0.2
	mean biomass (g)			603	180.5
<i>Hypleurochilus geminatus</i> (Wood, 1825)	percent of surveys	0		17	
	mean abundance			0	0.1
	mean biomass (g)			0	0.1
<i>Lutjanus analissacom</i> (Cuvier, 1828)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			12	
<i>Lutjanus campechanus</i> (Poey, 1860)	percent of surveys	2		9	
	mean abundance	0		0	0.1
	mean biomass (g)	29		473	256.9
<i>Microgobius carri</i> Fowler, 1945	percent of surveys	12		12	
	mean abundance	0	0.1	0	0.1
	mean biomass (g)	0	0.1	1	0.6
<i>Micropogonias undulatus</i> (Linnaeus, 1766)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			2	
<i>Muraena retifera</i> Goode and Bean, 1882	percent of surveys	0		11	
	mean abundance			0	0.0
	mean biomass (g)			43	15.9
<i>Mycteroperca microlepis</i> (Goode and Bean, 1879)	percent of surveys	0		20	
	mean abundance			1	0.2
	mean biomass (g)			2,586	1,073.1

Table 1. Continued.

Genus species Authority	Variable	Flat live bottom		Ledge	
		Value	SE	Value	SE
<i>Mycteroperca phenax</i> Jordan and Swain, 1884	percent of surveys	0		24	
	mean abundance			2	0.5
	mean biomass (g)			3,035	883.7
<i>Nicholsina usta</i> (Valenciennes, 1840)	percent of surveys	8		0	
	mean abundance	0	0.1		
	mean biomass (g)	2	1.5		
<i>Ogcocephalus nasutus</i> (Cuvier, 1829)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			1	
<i>Ogcocephalus radiatus</i> (Mitchill, 1818)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			3	
<i>Opsanus tau</i> (Linnaeus, 1766)	percent of surveys	25		61	
	mean abundance	0	0.1	1	0.1
	mean biomass (g)	56	17.7	188	27.1
<i>Pagrus pagrus</i> (Linnaeus, 1758)	percent of surveys	0		2	
	mean abundance			0	
	mean biomass (g)			45	
<i>Parablennius marmoreus</i> (Poey, 1876)	percent of surveys	0		28	
	mean abundance			1	0.2
	mean biomass (g)			1	0.3
<i>Paralichthys albigutta</i> Jordan and Gilbert, 1882	percent of surveys	8		16	
	mean abundance	0	0.0	0	0.2
	mean biomass (g)	31	21.0	309	150.3
<i>Pareques</i> spp.	percent of surveys	2		55	
	mean abundance	0		55	22.8
	mean biomass (g)	0		6,013	3,411.1
<i>Pomacanthus paru</i> (Bloch, 1787)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	
Pomacanthidae	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	
<i>Prionotus ophryas</i> Jordan and Swain, 1885	percent of surveys	2		0	
	mean abundance	0			
	mean biomass (g)	4			
<i>Prionotus scitulus</i> Jordan and Gilbert, 1882	percent of surveys	0		4	
	mean abundance			0	0.0
	mean biomass (g)			6	3.0
Triglidae	percent of surveys	12		11	
	mean abundance	0	0.0	0	0.0
	mean biomass (g)	22	10.8	8	3.3
<i>Ptereleotris calliurus</i> (Jordan and Gilbert, 1882)	percent of surveys	10		5	
	mean abundance	0	0.1	0	0.1
	mean biomass (g)	1	1.0	0	0.3
<i>Ptereleotris helenae</i> (Randall, 1968)	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	

Table 1. Continued.

Genus species Authority	Variable	Flat live bottom		Ledge	
		Value	SE	Value	SE
<i>Raja eglantheria</i> Bosc, 1800	percent of surveys	2		0	
	mean abundance	0			
	mean biomass (g)	48			
<i>Rhinobatos lentiginosus</i> Garman, 1880	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			11	
<i>Rypticus maculatus</i> Holbrook, 1855	percent of surveys	2		39	
	mean abundance	0		1	0.4
	mean biomass (g)	1		167	71.8
<i>Scomberomorus maculatus</i> (Mitchill, 1815)	percent of surveys	4		7	
	mean abundance	2		3	1.7
	mean biomass (g)	537		970	599.0
Scorpaenidae	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			1	
<i>Seriola</i> spp.	percent of surveys	4		9	
	mean abundance	0		0	0.2
	mean biomass (g)	149		276	198.7
<i>Serraniculus pumilio</i> Ginsburg, 1952	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	
<i>Serranus subligarius</i> (Cope, 1870)	percent of surveys	47		88	
	mean abundance	2	0.6	13	1.4
	mean biomass (g)	6	3.4	25	2.8
<i>Sphyraena barracuda</i> (Edwards, 1771)	percent of surveys	0		7	
	mean abundance			0	0.1
	mean biomass (g)			162	81.5
Sphyraenidae	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	
<i>Stegastes variabilis</i> (Castelnau, 1855)	percent of surveys	0		10	
	mean abundance			0	0.2
	mean biomass (g)			1	0.6
<i>Stenotomus</i> spp.	percent of surveys	90		80	
	mean abundance	20	4.1	24	2.8
	mean biomass (g)	1,677	313.0	3,007	430.0
<i>Stephanolepis hispidus</i> (Linnaeus, 1766)	percent of surveys	0		8	
	mean abundance			0	0.0
	mean biomass (g)			14	5.5
Syngnathidae	percent of surveys	0		1	
	mean abundance			0	
	mean biomass (g)			0	
Synodontidae	percent of surveys	12		2	
	mean abundance	0	0.1	0	
	mean biomass (g)	71	54.4	9	
<i>Urophycis earlli</i> (Bean, 1880)	percent of surveys	4		26	
	mean abundance	0		1	0.4
	mean biomass (g)	2		283	79.4
<i>Xyrichtys novacula</i> (Linnaeus, 1758)	percent of surveys	2		1	
	mean abundance	0		0	
	mean biomass (g)	1		0	

surveys), *Halichoeres bivittatus* (89%), *Serranus subligarius* (88%), and *Stenotomus* spp. (80%) were (Table 1). The most numerically abundant species on ledges were schooling juvenile fish such as *Haemulon aurolineatum* and *Decapterus* spp. that were particularly abundant during August surveys. Also quite abundant at all times were *Pareques* spp., *C. striata*, and *Stenotomus* spp. (Table 1). Pelagic schooling fish such as *C. crysos* had by far the highest biomass (mean biomass of $14,278 \pm 9082$ g 100 m⁻²). Bottom associated fish with high biomass were *Pareques* sp. (6013 ± 3411 g 100 m⁻²), *C. striata* (4111 ± 524 g 100 m⁻²), *Archosargus probatocephalus* (3041 ± 840 g 100 m⁻²), *Mycteroperca phenax* (3035 ± 884 g 100 m⁻²), and *Mycteroperca microlepis* (2586 ± 1073 g 100 m⁻²).

Species richness, diversity, abundance, and biomass of fish at ledge sites were all significantly higher than on flat live bottom sites (Fig. 2A–D). The regression of ledge variables on fish community metrics indicated that only a few ledge characteristics influenced the overall fish assemblage. Species richness and abundance of fish had significant positive relationships with both mean percent cover of sessile invertebrates and total ledge height (Figs. 3A,B, Table 2A,B). These two-variable models for fish richness and abundance explained 66% and 70% of the variability in the data respectively. Fish diversity (H') had a significant positive relationship with ledge area and a significant negative relationship with mean undercut height (Fig. 3C, Table 2C), however, these variables explained only 12% of the variability in the data. Fish biomass was significantly related to total height and undercut height of ledges, which

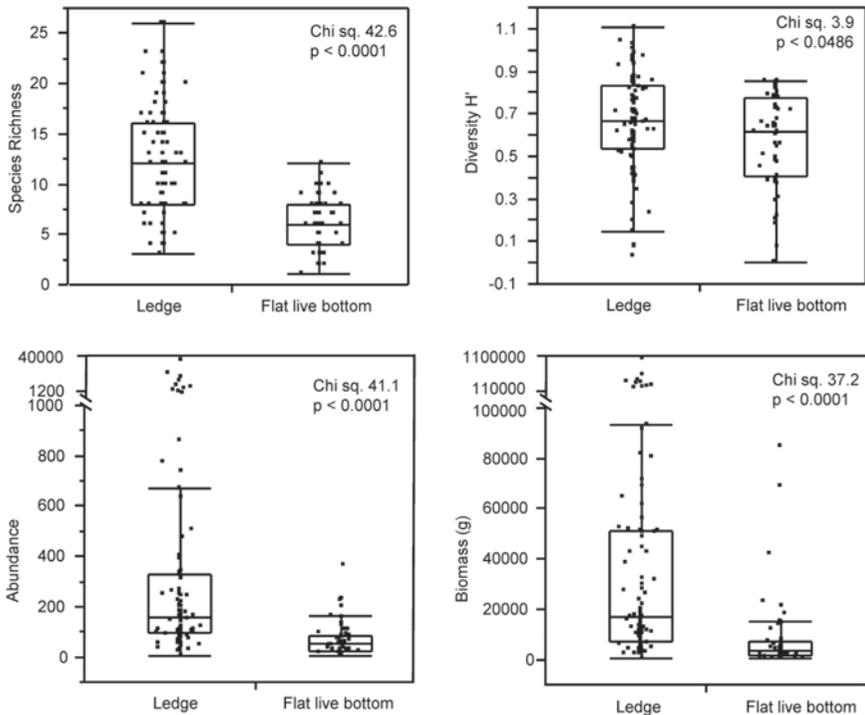


Figure 2A–D. Species richness, Shannon Diversity (H'), abundance, and biomass of fish on 100 m² surveys within each bottom type. Results from Wilcoxon tests are provided below each comparison. Box plots denote median and interquartile range. Extreme values of biomass and abundance are not shown. Points are scattered within each class for visibility.

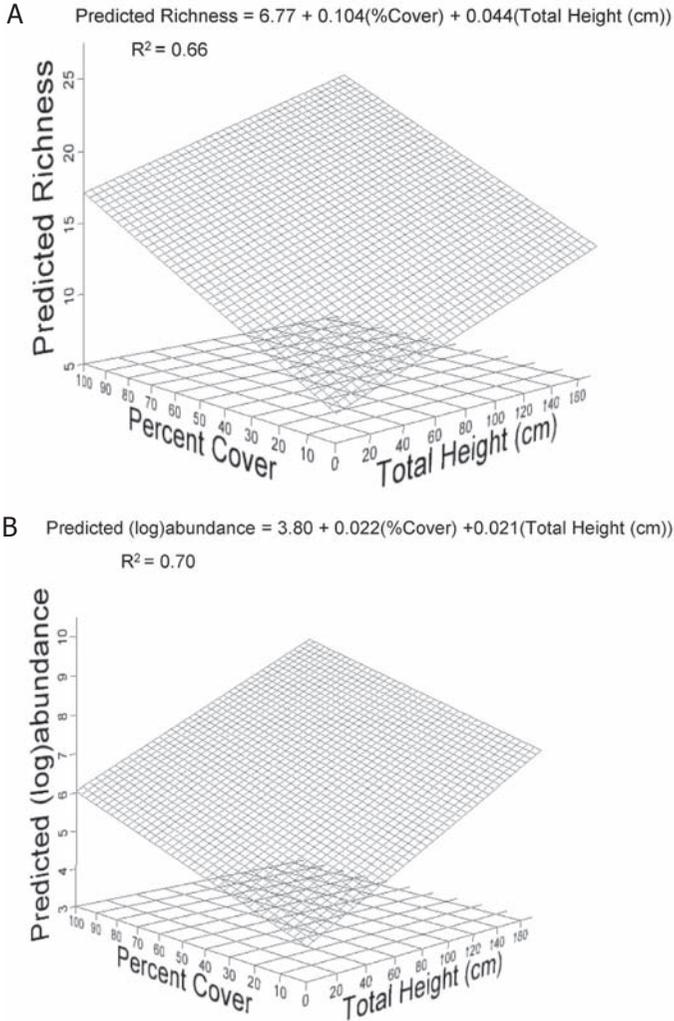
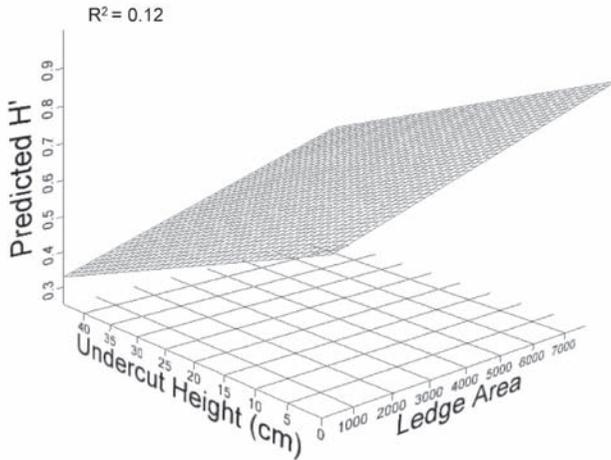


Figure 3. Multiple regression model of (A) species richness of fish at ledge sites, (B) (log) abundance of fish at ledge sites, (*opposite page*) (C) diversity of fish at ledge sites, and (D) (log) biomass of fish at ledge sites.

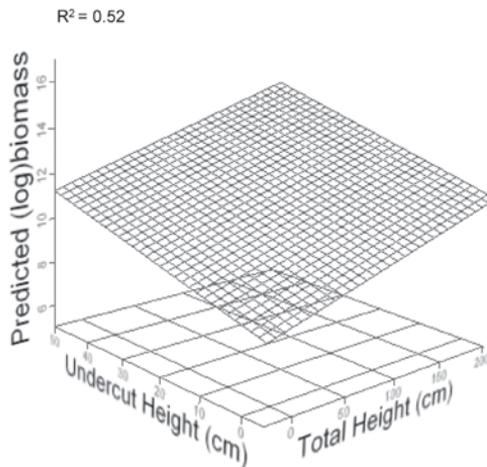
together explained 52% of the variability in the data (Fig. 3D, Table 2D). Undercut width was not a significant variable in predicting values for any fish community metric.

The MDS ordination based on biomass of individual species at each ledge site indicated that fish communities on ledges could be separated into two groups (A and B in Fig. 4). The moderate two-dimensional stress (0.17) indicated that the detail of the plot must be cautiously interpreted but that the overall ordination was correct. Cluster analysis confirmed that the fish assemblage consisted of two distinct groups. Bubble plots of the ledge characteristics associated with these two groups indicated that each occurred with specific ledge types (Fig. 4). Group A consisted of fish associated with ledges that were tall (mean: 55 ± 6.7 cm SEM), heavily colonized with

C Predicted H' = 0.64 + -0.007 (Undercut Height (cm)) + 0.000(Ledge Area)



D Predicted (log)biomass = 9 + 0.015 (Total Height (cm)) + 0.052 (Undercut Height (cm))



sessile invertebrates (72% covered \pm 4.7), and larger in area (2800 \pm 320 m²). Within this group, ledges may or may not have been undercut. Group B consisted of fish associated with ledges that were short (14 \pm 1.4 cm), not undercut, and smaller in area (1280 \pm 130 m²). Within this group, ledges may or may not have been heavily colonized by sessile invertebrates. The split between groups A and B occurred at a ledge height of 0.25 m.

The average of the Bray-Curtis dissimilarities between pairs of sites in groups A and B was 79.5%. The fish species most responsible for this were *Pareques* spp. (8.1%), *A. probatocephalus* (7.4%), *M. phenax* (6.8%), and *Stenotomus* spp. (5.0%). All but *Stenotomus* spp. were typical of group A. Within group A, the average Bray-Curtis similarity between all pairs of sites was 37.6%. Group B was typified by *Stenotomus* spp. and had average Bray-Curtis similarity of 45.6%. Rarely if ever seen in group B,

Table 2. Multiple regression model of:

(A) Species richness of fish at ledge sites.

ANOVA					
Source	DF	SS	MS	F Ratio	
model	2	1,836	918	85.9	
error	89	951	11	Prob > F	
c. total	91	2,787		< 0.0001	
Parameter Estimates					
Term		Estimate	Std Error	t ratio	Prob > t
intercept		6.77	0.55	12.29	< 0.0001
mean percent cover		0.1	0.01	7.88	< 0.0001
mean total height		0.04	0.01	3.07	0.0028

(B) (log)abundance of fish at ledge sites.

ANOVA					
Source	DF	SS	MS	F Ratio	
model	2	149	74.6	105.2	
error	89	63	0.7	Prob > F	
c. total	91	212		< 0.0001	
Parameter Estimates					
Term		Estimate	Std Error	t ratio	Prob > t
intercept		3.8	0.14	26.8	< 0.0001
mean percent cover		0.02	0	6.6	< 0.0001
mean total height		0.02	0	5.8	< 0.0001

(C) Diversity of fish at ledge sites.

ANOVA					
Source	DF	SS	MS	F Ratio	
model	2	0.57	0.28	6.09	
error	89	4.14	0.05	Prob > F	
c. total	91	4.71		0.0033	
Parameter Estimates					
Term		Estimate	Std Error	t ratio	Prob > t
intercept		0.64	0.04	17.8	< 0.0001
mean undercut height		-0.01	0	-3.3	0.0013
area		0	0	2.3	0.0261

(D) Biomass of fish at ledge sites.

ANOVA					
Source	DF	SS	MS	F Ratio	
model	2	92	46.02	48.2	
error	89	84.9	0.95	Prob > F	
c. total	91	177		< 0.0001	
Parameter Estimates					
Term		Estimate	Std Error	t ratio	Prob > t
intercept		9	0.14	65.1	< 0.0001
mean undercut height		0.02	0.01	2.62	0.0103
area		0.05	0.02	3.19	0.002

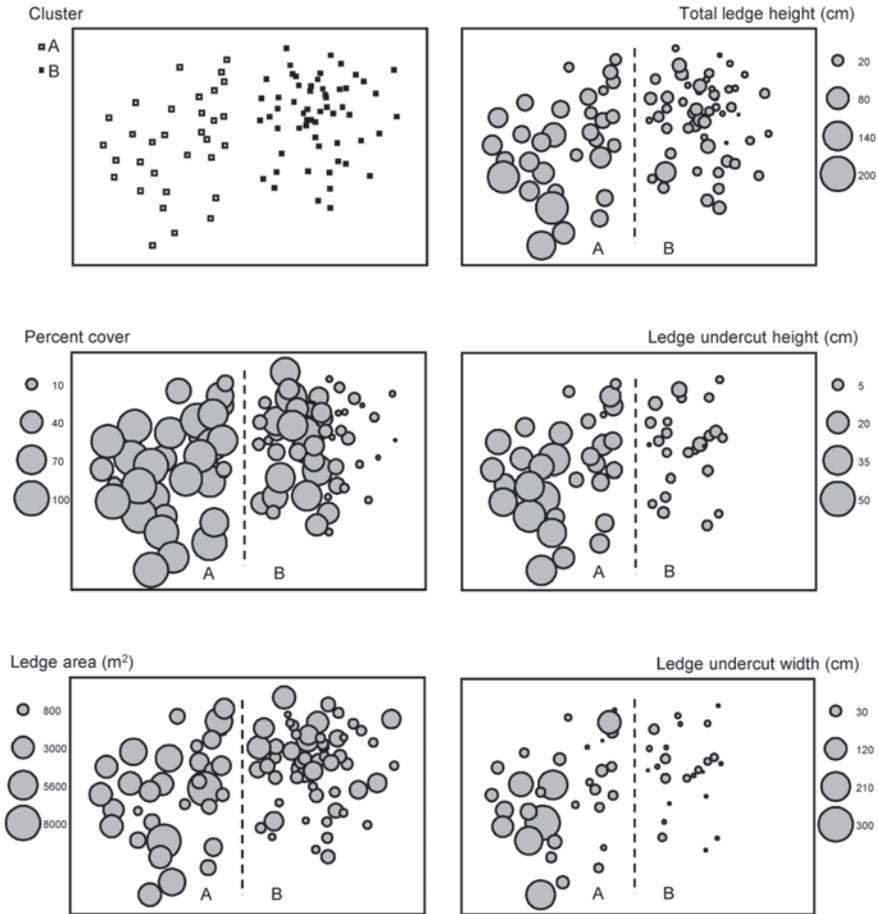


Figure 4. MDS of fish communities based on biomass at ledge sites ($n = 90$). Two dimensional stress of the ordination plot was 0.17. The dotted line separates the fish assemblage into two groups labeled A and B based on the ordination and confirmed by cluster analysis. Bubble plots denote the individual characteristics of each ledge site.

but often seen in group A were *M. phenax*, *Holacanthus bermudensis*, *Decapterus* spp., *Lutjanus campechanus*, *Calamus calamus*, and *Haemulon plumieri*.

The BIOENV procedure indicated that all ledge variables were at least partially influential in determining the similarity in fish assemblages among sites. The full model included percent cover, total height, undercut height, undercut width, and area of ledges and yielded a correlation of $\rho = 0.622$ ($P < 0.01$). The best models with fewer variables resulted in gradually reduced correlation and did not allow a clear choice for a more parsimonious number of explanatory variables or display a large drop in correlation (Table 3).

Table 3. Variables and correlations for the ten best models resulting from the BIOENV procedure.

	Correlation (ρ)	Percent cover	Ledge height	Undercut height	Undercut width	Ledge area
1	0.622	X	X	X	X	X
2	0.612	X	X	X	X	
3	0.606	X	X	X		X
4	0.600	X	X		X	X
5	0.598	X	X		X	
6	0.597	X	X	X		
7	0.588	X		X	X	X
8	0.586		X	X	X	X
9	0.585	X		X	X	
10	0.597		X	X	X	

DISCUSSION

Fish assemblages of the southeastern USA shelf differ over soft bottom and hard bottom habitats (e.g., Struhsaker, 1969; Parker et al., 1994). Our results demonstrate that major differences are also present among various types of hard bottom habitat. Species richness, diversity, abundance, and biomass of fish were all significantly higher at ledge sites than on flat live bottom sites. Two times higher species richness and 2–10 times higher fish density on high relief (ledge) live bottom relative to flat live bottom appear to be typical results in the region (Grimes et al., 1982; Barans and Henry, 1984; Parker et al., 1994; Quattrini and Ross, 2006; this study). This indicates that the bulk of fish diversity and biomass is concentrated not merely over all live bottom, but much more specifically over ledges. Given that ledges cover < 1% of the seafloor in the study site (Kendall et al., 2005) and are thought to cover only slightly greater proportions of the wider continental shelf (Miller and Richards, 1980; Parker et al., 1983; Barans and Henry, 1984), they merit the highest levels of attention in regional research and management plans (Quattrini and Ross, 2006).

Our results indicate that abundance, species richness, biomass, and assemblage composition of bottom fish on ledges can be predicted from just a few easily quantifiable environmental variables: ledge height, undercut height, percent cover of sessile invertebrates, and ledge area. Ledge height and area can be readily measured over large shelf areas and at sufficiently fine scales through remote sensing techniques such as multibeam sonar (e.g., Kendall et al., 2005). Quantifying cover of sessile invertebrates through sonar backscatter is an area of advancing research (Kendall et al., 2005; Brown and Collier, 2008). Quantifying the undercut characteristics of ledges via remote sensing is a challenging area of research, but can easily be done *in situ*.

Many studies outside the southeastern USA shelf have examined the relationship between structure of fish communities and benthic variables although with inconsistent results. The relationships between fish abundance, species richness, diversity, biomass, and benthic characteristics appear to be somewhat localized phenomena. Different reef types and regions have unique correlations between fish community parameters and benthic characteristics with few rules common to all systems (Roberts and Ormond, 1987; Chabanet et al., 1997; Öhman and Rajasuriya, 1998). Species richness of bottom fish in our study was positively correlated with ledge height. This highlights the importance of vertical relief in adding niche space to the benthos off the southeastern USA. Working in a variety of reef types and regions worldwide,

many studies have found species richness of bottom fish to be positively correlated with rugosity or vertical relief of the substrate [fringing reefs in the Netherlands Antilles (Luckhurst and Luckhurst, 1978); rock reefs in Gulf of California (Molles, 1978); coral reefs in Hawaii (Friedlander and Parrish, 1998); coral vs sandstone reefs in Sri Lanka (Öhman and Rajasuriya, 1998); artificial reefs in the British Virgin Islands (Gratwicke and Speight, 2005)] although this relationship was not ubiquitous [fringing reef in the Red Sea (Roberts and Ormond, 1987; Öhman and Rajasuriya, 1998)]. At our study site, species richness was also positively correlated with percent cover of sessile biota. The three dimensional planar plot of this relationship indicates that either high percent cover or total height (or both) of ledges can be related to high richness values. Similarly, species richness of fish has been correlated with diversity of benthic cover [Roberts and Ormond, 1987; reefs on Reunion Island, Indian Ocean (Chabanet et al., 1997; Gratwicke and Speight, 2005)] or cover of particular bottom types such as hard bottom and live coral in other systems [(limestone reefs at GRNMS (Parker et al., 1994; Öhman and Rajasuriya, 1998; Gratwicke and Speight, 2005)] although, again results have been inconsistent among regions (Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987).

Fish abundance in the present study was also significantly correlated with percent cover of sessile biota and ledge height, which together explained 70% of the variability in the data. Links between fish abundance and benthic characteristics have been more difficult to identify in other regions with only weak or no correlation found with rugosity [patch reef in the US Virgin Islands (Risk, 1972; Luckhurst and Luckhurst, 1978; Öhman and Rajasuriya, 1998; Gratwicke and Speight, 2005)], cover of particular bottom types (Roberts and Ormond, 1987; Öhman and Rajasuriya, 1998), or other benthic variables (Risk, 1972; Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987).

Diversity (H') of fish has also been elusive to link with benthic characteristics. Fish diversity has been positively correlated with benthic variables such as rugosity or reef height (Risk, 1972; Molles, 1978; Öhman and Rajasuriya, 1998) and live coral cover (Öhman and Rajasuriya, 1998) but not with substrate diversity (Risk, 1972) and not in all studies or reef types investigated (Luckhurst and Luckhurst, 1978; Öhman and Rajasuriya, 1998). Unlike fish abundance and species richness, fish diversity at our study site was not significantly related to ledge height and percent cover. Instead, fish diversity was positively related to ledge area and counter to expectations, negatively related to undercut height. A large undercut would presumably allow a greater niche space, a larger number of species, equitable distribution of community membership, and therefore higher diversity, but this was not the case. In fact, larger undercuts were marked by the presence of large schools of a few species such as *Haemulon* sp. and *Pareques* sp., the latter of which were regularly observed utilizing the undercut of ledges. Such large monotypic schools lowered the overall values of fish diversity at undercut ledges even in the presence of a larger number of species.

Comparisons with previous studies on the inner shelf region off the southeastern USA revealed some striking differences in fish community structure. Parker et al. (1994) conducted video surveys of fish also within GRNMS. Their sampling design was similar to the present study in that survey sites were randomly placed and stratified by bottom type including ledge and live bottom. Surveys were conducted in August 1985, November 1985, May 1986, and August 1986. Apart from the November

survey, this allowed excellent comparison to the present study given that the same months were sampled.

Overall fish density on ledges observed by Parker et al. (1994) was 9–20 fish m^{-2} based on video surveys in August. The same month in the present study fell at the high end of this range with an average of 21 fish m^{-2} on ledges. In addition, Parker et al. (1994) identified 55 fish to the species level on ledges, comparable to the 54 we identified in the present study. Sampling effort was too low on ledges in May 1986 ($n = 3$) by Parker et al. (1994) to justify similar comparisons for that month alone. Despite a similar density and overall number of species on ledges recorded by the two studies, the particular species that comprised each list were quite different. Over one third of the species identified in each study were not recorded by the other (comparison generously assumed probable matches for fish identified to species level in one study but only genus or family in the other). Specifically, 22 of the species seen in the present study were not encountered by Parker et al. (1994), and conversely, Parker et al. (1994) included 18 species not encountered in the present study. These discrepancies include not only rarely observed species but also quite common ones. For example, two species in the family Acanthuridae were routinely recorded by Parker et al. (1994) but were never observed on our visual transects. Similarly, on our visual surveys, two very different species, the bottom dwelling *Urophycis earlii* and the pelagic *C. crysos*, were among the most common and abundant species encountered, respectively, but were absent in the video surveys of Parker et al. (1994). The respective biases of video vs visual survey techniques alone cannot account for these differences. The additional survey in November by Parker et al. (1994) may account for some of the 18 species observed in that study that were not encountered in the August and May visual surveys of the present assessment, however, this does not explain the 22 species observed with visual assessment but not video. It is also probable that the older, more general maps (Hunt, 1974) used to guide initial site selection by Parker et al. (1994) led to the sampling of somewhat different habitats than the much more detailed maps used to guide survey design in the present study (Kendall et al., 2005). Despite these influences, the differences in species composition between these studies are striking and suggest that some considerable change in community structure between the two studies occurred. Unlike a trend toward more tropical species found on deeper live bottom off North Carolina (Parker and Dixon, 1998), neither study had differing proportions of tropical versus temperate species nor pelagic vs benthic species; The assemblages were simply different. This could be due to random variation in recruitment prior to the two studies, which may have resulted in stochastically changed community composition at this shelf location on the scale of decades. Without quantitative observations during the 20 yr interval between these studies and additional regular monitoring in the future, the variability and stability of fish community patterns at shelf sites such as GRNMS cannot be determined (Quattrini and Ross, 2006).

Other studies conducted in this region of the continental shelf were based on bottom trawls (Sedberry and Van Dolah, 1984) and fish traps (Sedberry et al., 1998), both over hard bottom. Trawls caught 48 species (summer, Sedberry and Van Dolah, 1984) whereas traps collected only 15 species (Sedberry et al., 1998). Trawl sampling revealed much lower fish density of 0.1 m^{-2} than either the present study or that of Parker et al. (1994). Due to different biases in trawl, trap, video, and visual assessment

techniques and the specific habitats that were sampled, more detailed comparisons among these studies are problematic.

Basic ledge dimensions allowed good prediction of not only species richness and abundance of fish, but also which species assemblage was likely to occur. For example, the large fish associated with fisheries (e.g., *M. phenax*, *L. campechanus*) occurred primarily in association with ledges > only 0.25 m. This breakpoint in ledge height was defined by fish assemblage composition and is a much lower threshold than previously used to quantify significantly different ledge communities. For example, two distinct fish communities were also observed on the shelf edge off North Carolina based on ledge height. Communities differed for ledges with large (> 2 m) vs small (< 0.5 m) vertical profiles (Quattrini and Ross, 2006) as defined using a geologically based classification scheme (i.e., Riggs et al., 1996) instead of a biologically derived breakpoint. In addition to ledge height, however, our results demonstrate the importance of other ledge variables including percent cover, undercut height, undercut width, and ledge area in predicting fish assemblages.

The best available summary of seafloor characterization data for the southeastern USA was recently produced by the Southeast Area Monitoring and Assessment Program- South Atlantic (SEAMAP-SA) in an effort to identify the location and extent of hard bottom habitats on the continental shelf and locate essential fish habitats (SEAMAP-SA, 2001). In this program, diverse data sources were queried and used to attribute large grid cells (1 minute latitude by 1 minute longitude) with one of three classifications: hard bottom present somewhere within the cell, possible hard bottom present, or no hard bottom. The database does not distinguish between flat live bottom and ledges, degree of colonization by sessile invertebrates, or other more detailed attributes among hard bottom types. Our findings and those of other recent studies (Parker et al., 1994; Quattrini and Ross, 2006; Kendall et al., 2008) indicate that the coarse spatial scale and classification scheme should be refined where datasets allow to reflect the significant differences in fish communities among hard bottom types. Fish assemblages at our study site were divided into two distinct groups, each of which included two ledge types. Very basic seafloor classification schemes (e.g., SEAMAP-SA, 2001) and those based on geology (e.g., Riggs et al., 1996), while useful for their specific purposes and the technology available at the time, do not adequately capture the needed aspects of hard bottom diversity and its associated fish assemblage structure. Defining ledge types based on their fish assemblages provides a more meaningful classification of habitats for ecological and fisheries purposes.

While the findings here represent an important advancement in understanding the linkages between southeastern USA fish communities and their associated habitats, two lines of additional research are needed for our results to have maximum benefit for continental shelf science and management. First, high resolution benthic maps of the continental shelf must be produced to determine the spatial extent, height, cover, and undercut characteristics of ledges. All of these variables except for ledge undercut can be characterized with present multibeam sonar and backscatter technology. The present classification schemes and suite of mapping products for shelf ecosystems by SEAMAP-SA would be excellent for prioritizing areas in need of more detailed mapping. Second, similar studies must be undertaken to determine if the same suite of ledge characteristics governing species distribution at our study area on the inner continental shelf operate on the different fish communities found in the deeper water of the outer continental shelf (Quattrini and Ross, 2006).

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