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Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A.

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Synopsis

Demersal fish communities associated with hard bottom habitats in the South Atlantic Bight were investigated in three depth zones (inner, middle and outer shelf) between 30° and 33°N latitudes. Fishes were sampled with trawls and baited fishing gear, and were observed by remotely operated underwater television. Most demersal hard bottom fishes demonstrated seasonal differences in abundance in each depth zone, especially at the inner and outer shelf stations. Diversity values from trawl catches were higher in winter than summer at inner and outer shelf stations, but lower in winter at middle shelf stations. Species richness was higher in summer than in winter at most stations, but H' diversity patterns were more influenced by community evenness. Diversity values were higher than those reported for similar depths in the Middle Atlantic Bight. Mean biomass of demersal teleosts for all stations combined was slightly greater in winter than in summer. There was no significant difference in biomass between stations in summer, however, middle shelf stations had significantly greater biomass than inner or outer shelf stations in winter. Biomass estimates from the hard bottom areas studied were considerably higher than those reported in the literature for sand bottom areas in the South Atlantic Bight, but less than those reported for tropical reefs. Cluster analysis revealed differences in community composition between day and night trawl tows at all stations, and greater seasonal differences in species composition at inner and outer shelf stations than at middle shelf depths. Underwater television provided useful complementary data to trawl catches, documented the presence of large fishes which avoided the trawl, and provided information on the community composition at high relief stations which could not be trawled.

Introduction

The continental shelf in the South Atlantic Bight is characterized by smooth sandy bottom with occasional rock outcrops forming hard bottom areas, often covered with a thin sand layer (Fig. 1). These hard bottom areas support large numbers of sponges, corals, ascidians and other sessile invertebrates as well as many species of tropical and subtropical fishes (Struhsaker 1969, Miller & Richards 1980). There is little quantitative data on distribution and abundance of demersal fishes associated with hard bottom in the South Atlantic Bight because of the difficulties in sampling rocky, high relief bottom. Most published studies of shelf fishes in this area have concentrated on assemblages found over sand bottom with only limited reference to hard bottom areas (Struhsaker 1969, George & Staiger 1978, Wenner et al. 1980). Miller & Richards (1980) examined trawl logs from several exploratory fishing vessels and categorized hard bottom habitats based on depth, thermal stability, and indicator reef species; however, they provided little quantitative data on abundance of these and other hard bottom species. Powles & Barans (1980) gave biomass estimates for some hard bottom fishes, but their study was primarily directed at testing the effectiveness of trawls, traps, diver observations and underwater television as sampling methods for these fishes. Grimes et al. (1982) reported the cross-shelf distribution of 113 species of hard bottom fishes, based mainly on hook- and-line collections, and Wenner (1983) compared trawl collections over hard bottom with

Fig. 1. Underwater photographs of a hard bottom station (IS03) with low relief rock outcrops (A) and hard bottom covered with sand (B). Black sea bass, *Centropristis striata,* are associated with the rock outcrops in photograph A. A school of tomtate, *Haemulon aurolineatum,* a solitary sheepshead, *Archosargus probatocephalus,* and two red porgy, *Pagrus pagrus,* are visible in photograph B.

Table 1. Physical characteristics of each station. Latitude and longitude are the approximate center of each station.

Station	Depth extremes (m)	Bottom temperature(°C)		Rock relief (m)	Latitude (N)	Longitude (W)
		Winter	Summer			
IS01	16–18	14.6	25.6	0–0.5	32°29.7′	79°42.5′
IS02	16–22	12.3	28.4	0–2	31°23.6′	80°53.1′
IS03	20–22	14.5	23.3	0–2	30°37.1′	80°10.6′
MS01	25–35	14.9	24.9	0–1	31°44.2′	80°13.4′
MS02	23–29	16.1	23.5	0–0.5	31°20.9′	80°20.9′
MS03	34–38	15.6	21.4	0–2	30°54.0′	80°36.3′
OS01	58–67	16.1	16.9	0–0.5	31°32.0′	79°44.3′
OS02	47–58	18.9	24.0	0–2	31°08.1′	79°55.0′
OS03	54–63	18.9	15.2	0–2	30°25.7′	80°12.4′

tows made over sand bottom and noted higher diversity and biomass and a different species composition of catches in hard bottom areas.

Because of the importance of hard bottom habitat to fisheries in the South Atlantic Bight (Grimes et al. 1982), there has recently been increased study of the life history, population dynamics, behavior and fishery of species associated with this habitat (Huntsman 1976, Miller & Richards 1980, Grimes et al. 1982, Manooch & Barans 1982, Waltz et al. 1982, Wenner 1983). The present study was initiated to provide additional quantitative data on the distribution, abundance, biomass and community structure of demersal fishes from several hard bottom areas in this region. This report summarizes the results of that study and examines seasonal, latitudinal and depth-related patterns in these parameters.

Methods

Study area

Nine hard bottom stations were chosen for study between 30° and 33° N latitude. Three stations were located within each of three bathymetric zones, representing inner shelf (IS), middle shelf (MS) and outer shelf (OS) depths (Fig. 2). Rock relief ranged in height from no relief to greater than 2 m and ranged in extent from areas of hard pan with

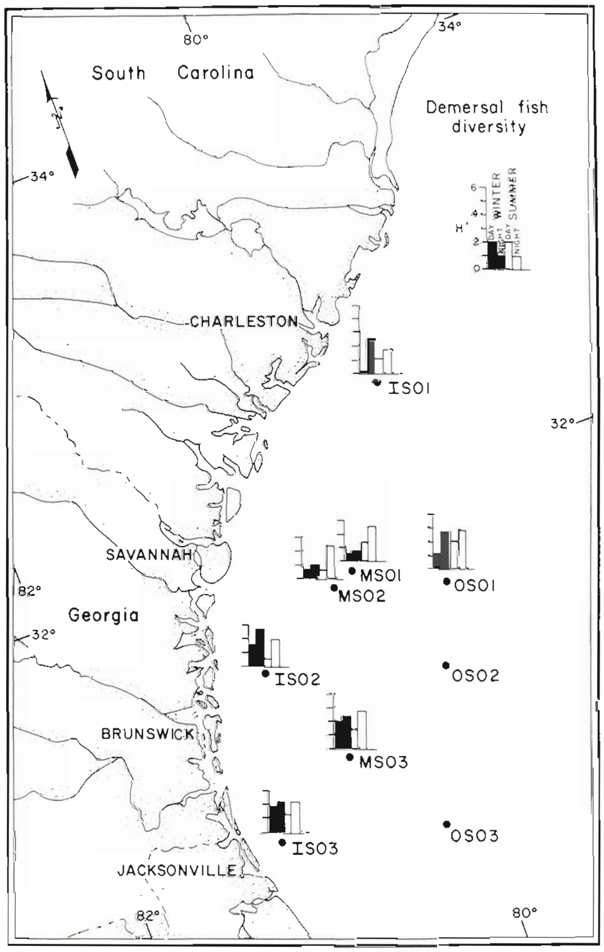

Fig. 2. Station locations and Shannon diversity (H′) for pooled replicate samples of demersal fishes at each station, by light phase and season.

few rock outcroppings to areas with a heavy incidence of outcroppings. Sites selected were generally greater than 1 km^2. Physical characteristics of each station are presented in Table 1.

Sampling

Sampling was conducted in winter (15 January to 26 March) and again in summer (4 August to 18 September) 1980. Prior to removal sampling, each station was surveyed using underwater television and fathometer, and bottom temperature was measured with a reversing thermometer. The television surveys were designed to provide information on the physical characteristics as well as on the occurrence of fishes at each station. Bottom type (sand versus hard bottom), occurrence of large attached invertebrates (sponges, corals) and occurrence of fishes were continuously observed on the television monitor and recorded on videotape; observations and Loran C coordinates were logged at two minute intervals. All subsequent sampling was attempted within the boundaries of known hard bottom as defined by television reconnaissance.

Trawl sampling for fishes consisted of standard tows with a 40/54 high rise trawl (Hillier 1974). This net is very effective in sampling fishes on rough bottom (Smith 1977). The trawl had a 12.2 m headrope and a 16.5 m footrope. The net was equipped with steel doors and rubber rollers, and had stretch-mesh dimensions of 20.3 cm in the wings, 10.2 cm in the body, and 0.6 cm in the codend. Six replicate tows, three day and three night, were attempted at all low to moderate relief sites. Only five successful tows (two night) were completed at IS02 in summer. Trawl samples were standardized by towing the net at 100 RPM (about 6.5 km h^{-1}) for a distance of five Loran C microsecond units. This resulted in an average trawl distance of about one kilometer.

At high relief outer shelf stations which could not be trawled (OS02 and OS03), television transects and catches made with baited fishing gear were used to characterize the fish fauna. Removal gears were fished simultaneously in two sets at each station, one set at dawn and one at dusk. Each set consisted of two baited Antillean S-traps (122 cm × 122 cm × 61 cm) and four vertical longlines (10 hooks each) fished for about one hour, and three snapper reels fished while the vessel drifted over the area during a set. Because baited fishing gears are very selective, the results of this effort were used only to supplement the television observations at high relief stations. Television transects at the inner and middle shelf sites were analyzed primarily for comparison of this assessment technique across the shelf.

Fishes collected in the trawl and on baited gears were sorted to species, counted, and weighed. Large catches of abundant species were subsampled by weight for abundance estimates.

Data analysis

Biomass of demersal teleost fishes was calculated as mean catch per tow for the replicate trawls done on each station. Because previous investigations (Taylor 1953, Struhsaker 1969) have shown that trawl catches are usually distributed as a negative binomial, a $\log_e (x + 1)$ transformation was made on the data (Elliot 1977). Retransformed mean biomass estimates per tow were calculated for each station from transformed values following the methodology of Bliss (1967). Biomass was also calculated as kilograms of fish per hectare of area swept by the trawl. Area swept by the trawl (a) was determined for each collection by the following equation modified from Klima (1976):

$$a = \frac{D\,(0.6\,H)}{10\,000\,m^2\ ha^{-1}} ,$$

where D = bottom distance in meters covered by the trawl, as calculated from start and end Loran C coordinates, and H is the trawl headrope length in meters. The average area swept by our trawl for all stations was estimated to be 4.3 ha per station. Occasional large elasmobranchs (such as *Dasyatis centroura* and *Ginglymostoma cirratum*) were not included in biomass estimates because even a single occurrence of these species would significantly alter the estimates.

Numerical classification techniques (cluster analysis) were used to compare the similarity be-

Table 2. A listing of the most abundant demersal fishes collected by trawl during winter (w) and summer (s) 1980, by station. This list includes all species ranked in the ten most abundant species at any one station in either season. n = number of fish collected for each species; N = total number of all fishes collected at a station for each season.

Species	Station IS01		IS02		IS03		MS01		MS02		MS03		OS01	
	w	s	w	s	w	s	w	s	w	s	w	s	w	s
	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)	n (%N)
Synodus foetens	6 (0.8)	9 (0.2)	6 (1.6)	12 (0.2)	35 (1.0)	5 (0.2)	15 (0.7)	4 (0.1)	11 (0.1)	8 (0.1)	15 (0.3)	1 (0.1)	3 (1.5)	8 (1.5)
Synodus poeyi							1 (0.1)	5 (0.2)	3 (<0.1)	3 (<0.1)		6 (0.4)	38 (18.6)	13 (2.5)
Porichthys plectrodon		60 (1.4)		33 (0.6)	5 (0.1)	20 (0.7)		1 (<0.1)		2 (<0.1)		16 (1.0)		
Urophycis regia	319 (40.1)		17 (4.5)		16 (0.4)						4 (0.1)		18 (8.8)	
Urophycis spp.	13 (1.6)		11 (2.9)											
Ophidion holbrooki	4 (0.5)	22 (0.5)	3 (0.8)	19 (0.4)	22 (0.6)	8 (0.3)		48 (1.6)	15 (0.1)	14 (0.1)	18 (0.3)	13 (0.8)		7 (1.3)
Centropristis ocyurus	10 (1.3)	30 (0.7)		20 (0.4)	1 (<0.1)	13 (0.4)	1 (0.1)	48 (1.6)	2 (<0.1)	5 (0.1)	27 (0.5)	16 (1.0)	5 (2.4)	22 (4.2)
Centropristis striata	22 (2.8)	194 (4.7)	22 (5.8)	161 (3.2)	29 (0.8)	60 (2.0)	2 (0.1)	6 (0.2)	38 (0.4)	33 (0.3)	7 (0.1)	8 (0.5)		
Diplectrum formosum	2 (0.2)	51 (1.2)		40 (0.8)	17 (0.5)	2 (0.1)	12 (0.6)	26 (0.8)	32 (0.3)	8 (0.1)	70 (1.2)			
Serranus phoebe								1 (<0.1)					2 (1.0)	52 (9.9)
Priacanthus arenatus		1 (<0.1)		1 (<0.1)	1 (<0.1)	8 (0.3)	5 (0.2)	4 (0.1)	11 (0.1)	10 (0.1)	2 (<0.1)	1 (0.1)	1 (0.5)	
Apogon pseudomaculatus		25 (0.6)		59 (1.2)				163 (5.3)		18 (0.2)		38 (2.3)		9 (1.7)
Lutjanus campechanus						2 (0.1)	8 (0.4)	2 (0.1)	9 (0.1)		7 (0.1)	4 (0.2)		1 (0.2)
Rhomboplites aurorubens		1 (<0.1)			934 (26.4)	15 (0.5)	6 (0.3)	399 (13.0)	138 (1.3)	460 (4.7)	2449 (42.2)	192 (11.8)	13 (6.4)	141 (26.9)
Haemulon aurolineatum		435 (10.5)		1587 (31.2)	1530 (43.2)	921 (31.0)	859 (39.4)	799 (26.0)		479 (4.9)	2127 (36.6)	179 (11.0)		
Orthopristis chrysoptera		1 (<0.1)	3 (0.8)	8 (0.2)	30 (0.8)	14 (0.5)								
Calamus leucosteus		38 (0.9)	17 (4.5)	1 (<0.1)	24 (0.7)	33 (1.1)	56 (2.6)	31 (1.0)	89 (0.8)	52 (0.5)	53 (0.9)	2 (0.1)	26 (12.8)	53 (10.1)
Lagodon rhomboides		1 (<0.1)	78 (20.5)	15 (0.3)	168 (4.8)	20 (0.7)			1 (<0.1)		28 (0.5)			
Pagrus pagrus							6 (0.3)	10 (0.3)	18 (0.2)	4 (<0.1)	7 (0.1)		63 (30.9)	14 (2.7)
Stenotomus aculeatus	177 (22.3)	2942 (71.2)	174 (45.8)	2721 (53.4)	472 (13.2)	1730 (58.2)	1163 (53.3)	1443 (46.9)	9559 (89.4)	8580 (88.1)	735 (12.6)	1015 (62.2)	1 (0.5)	2 (0.4)
Equetus lanceolatus		1 (<0.1)		1 (<0.1)	2 (0.1)	1 (<0.1)		3 (0.1)	621 (5.8)	2 (<0.1)	115 (2.0)	15 (0.9)		
Equetus sp. nov.													3 (1.5)	17 (3.2)
Equetus umbrosus		8 (0.2)	20 (5.3)	16 (0.3)	175 (5.0)	30 (1.0)	8 (0.4)	10 (0.3)	14 (0.1)	1 (<0.1)	5 (0.1)	26 (1.6)		145 (27.6)
Mullus auratus						1 (<0.1)		1 (<0.1)			21 (0.4)			
Scorpaena brasiliensis	2 (0.2)	8 (0.2)	3 (0.8)	26 (0.5)	3 (0.1)	8 (0.3)	3 (0.1)	2 (0.1)		1 (<0.1)	7 (0.1)	11 (0.7)		2 0.4)
Scorpaena calcarata	2 (0.2)	8 (0.2)		2 (<0.1)		1 (<0.1)	2 (0.1)			2 (0.1)	3 (0.1)	6 (0.4)		10 (1.9)
Prionotus carolinus	164 (20.6)	120 (2.9)		187 (3.7)	1 (<0.1)			1 (<0.1)	1 (<0.1)	10 (0.1)				
Prionotus spp.	23 (2.9)			1 (<0.1)	6 (0.2)									
Syacium papillosum	19 (2.4)	11 (0.3)	8 (2.1)	57 (1.1)	6 (0.2)	6 (0.2)	8 (0.4)	4 (0.1)	1 (<0.1)		10 (0.2)	6 (0.4)	22 (10.8)	2 (0.4)
Aluterus schoepfi		1 (<0.1)		3 (0.1)			8 (0.4)	11 (0.4)	31 (0.3)	6 (0.1)	16 (0.3)	24 (1.5)		
Monacanthus hispidus	3 (0.4)	141 (3.4)	1 (0.3)	40 (0.8)	5 (0.1)	32 (1.1)	4 (0.2)	19 (0.6)	33 (0.3)	18 (0.2)	28 (0.5)	11 (0.7)		
Lactophrys quadricornis	2 (0.2)	4 (0.1)	1 (0.3)	16 (0.3)	7 (0.2)	5 (0.2)	5 (0.2)	3 (0.1)	24 (0.2)	2 (<0.1)	16 (0.3)	1 (0.1)		
Total n	768	3812	364	5026	3489	2935	2172	3044	10652	9718	5770	1591	175	498
Total N	795	4132	380	5093	3538	2972	2183	3078	10689	9743	5809	1631	204	525
Total %N	96.6	92.3	95.8	98.7	98.6	98.8	99.5	98.9	99.6	99.7	99.3	97.5	85.8	94.9

tween trawl collections (normal analysis) and to elucidate species assemblages (inverse analysis). To reduce the effects of the contagion generally present in trawl collections (Taylor 1953), the data were transformed [$\log_{10}$ (x + 1)] before analysis. Additionally, only species that occured in at least three trawl collections were included in this analysis because the chance occurrence of rare species provides little information on the basic patterns of community structure. Similarity was measured by the Bray-Curtis index (Bray & Curtis 1957) and similarity matrices were expressed in the form of dendrograms generated using a flexible sorting strategy (Lance & Williams 1967, Clifford & Stephenson 1975), with $\beta = -0.25$.

Subsequent to cluster analysis, species groups were chosen from the inverse classification by utilizing a variable stopping rule (Boesch 1977). Nodal analysis was then used to determine the constancy and fidelity of each species group to the seven trawlable stations. Constancy (values range from 0 to 1) is a measure of the frequency of occurrence of a species group among all samples at a station, and fidelity (values range from −1 to +1) is an expression of the constancy of a species group to collections at one station over all collections at all stations (Boesch 1977). Because normal cluster analysis resulted in grouping of collections from different stations, and because of the interest in describing faunal affinities of species groups with regard to our selected study areas, site groups as defined by normal analysis were not used in normal-inverse comparisons by nodal analysis. Instead, fidelity and constancy of species groups as defined by inverse analysis were compared to each station.

Another measure of community structure, species diversity, was calculated for pooled replicate tows at each site by H′ and its components, evenness and species richness (Margalef 1958, Pielou 1975).

Television analysis

Six 20-minute videotape transects were analyzed at each station: three recorded during the day and three at night. Lengths of transects (m) were measured between start and end Loran C coordinates. During review of each videotape transect, two independent observers viewed the tapes and counted fish seen on the monitor screen for every ten-second interval of tape. An average of the two counts was used for time intervals in which the two observers could not agree on the number of fish seen. For large schools of fish, which were impossibe to count, abundance was estimated (e.g. 50, 75 or 100 fish) for the ten second interval in which they occurred. The tape was viewed a third time by both observers to identify fishes which had been counted but not identified during earlier viewings. Fish counts were summarized as numbers per 100 m of transect. Fish density (number of individuals per hectare) was calculated by estimating the area viewed by the camera and multiplying the transect length by the estimated horizontal field of view (3.4 m) based on measurements made in a swimming pool.

Results

Quantitative assessment of fish captured by trawl

A total of 62,840 fishes representing 54 families, 98 genera and 128 species were taken in 83 trawl collections during both seasons. Of these, 50,771 individuals and 122 species belonged to the demersal fish community and the remaining pelagic fishes were mainly carangids and clupeids. A complete listing of species collected at each station is available from the senior author.

Dominant and economically important species

Ten species made up 94.2% of the total number of demersal fishes collected by trawl during both seasons, and the two most abundant species, *Stenotomus aculeatus* and *Haemulon aurolineatum* made up 78.1% of the total. Other abundant species were *Rhomboplites aurorubens, Equetus lanceolatus, Centropristis striata, Prionotus carolinus, Calamus leucosteus, Equetus umbrosus, Urophycis regia* and *Monacanthus hispidus*. Ranking of these and other dominant species changed seasonally and by station within a season (Table 2).

The southern porgy (*Stenotomus aculeatus*) and tomtate (*Haemulon aurolineatum*) were more numerous in summer than in winter. Generally, *S. aculeatus* was the most abundant species and *H. aurolineatum* was the second most abundant species at all stations, except OS01, in summer. In winter, *S. aculeatus* was one of the three most abundant species at all stations except OS01. Southern porgy were most numerous at MS02 and most individuals were captured during the day at all stations in both winter (70.6%) and summer (63.1%). *Haemulon aurolineatum* were taken only at IS03, MS01 and MS03 in winter with maximum numbers taken at MS03. In summer, this species was abundant at all stations except OS01. In contrast to *S. aculeatus,* most tomtate were captured at night in both winter (54.2%) and summer (83.4%).

Vermilion snapper (*Rhomboplites aurorubens*) were most abundant at middle shelf stations with no apparent seasonal pattern. They were generally not abundant at inner shelf stations, except at IS03, where they were the second ranking species in winter. *R. aurorubens* was the most numerous species at MS03 in winter and was the second most abundant species collected at that site in summer. This species was common at OS01, especially in summer. During winter, vermilion snapper occurred in approximately equal numbers in day (52.2%) and night (47.8%) trawls, but they were most abundant in day trawls (72.6%) during summer.

Other dominant species also demonstrated seasonal differences in abundance. *Equetus lanceolatus, Urophycis regia* and, to a lesser extent, *Calamus leucosteus* were more abundant in winter. Jackknife fish (*E. lanceolatus*) occurred in maximum numbers at middle shelf stations and were never taken at OS01. In winter, most jackknife fish (98.0%) were captured during the day; however, the few specimens taken during the summer were all caught at night. Spotted hake (*U. regia*) were collected only in winter, and mainly at inner shelf stations. All but one specimen were taken at night. Whitebone porgy (*C. leucosteus*) were collected during both seasons at all stations except IS01, where none were caught in winter. Abundance was highest at middle shelf stations. Whitebone porgy were more abundant in day trawls in winter (81.1%) and summer (70.6%).

Centropristis striata, Prionotus carolinus, Monacanthus hispidus and *Equetus umbrosus* were more abundant during the summer. Black sea bass (*C. striata*) were caught in the trawl at all stations, except OS01, during both seasons. Although seasonal differences in abundance were minor at middle shelf stations, all inner shelf stations had significantly larger catches in summer than in winter. Most black sea bass were caught at night in winter (86.7%) and summer (97.0%). Northern searobin (*P. carolinus*) were abundant only at inner shelf stations. They occurred in approximately equal numbers during both seasons at IS01, but were only found at IS02 in summer. This species was rare at

Table 3. Abundance and biomass estimate for trawl-caught demersal teleosts during winter and summer, 1980.

Station	Estimated (retransformed) mean catch per tow		Number of individuals ha^{-1} of swept area		Estimated (retransformed) mean catch (kg) per tow		Biomass (kg ha^{-1} of swept area)	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
IS01	673.1	913.4	174.8	1000.7	2.782	48.653	3.288	54.497
IS02	79.6	1872.5	81.3	1132.2	7.390	45.754	8.929	38.667
IS03	1252.5	675.3	858.2	926.9	69.085	40.994	65.283	49.049
MS01	1105.1	1069.8	472.4	657.3	65.489	50.754	33.949	41.129
MS02	1775.0	1946.1	2031.1	2358.2	149.693	53.437	168.000	69.456
MS03	1559.6	332.9	1253.4	435.0	9.044	23.925	90.926	35.100
OS01	45.2	108.7	48.6	141.6	14.232	18.738	15.831	24.397

Table 4. Community structure values (number of individuals, number of species, Shannon diversity (H′), evenness (J′) and species richness (SR) for pooled replicate samples.

Station	Season	Number of individuals	Number of species	H′	J′	SR
IS01	winter	795	30	2.58	0.53	4.34
	summer	4132	35	1.75	0.34	4.08
IS02	winter	380	22	2.73	0.61	3.54
	summer	5093	48	2.01	0.36	5.51
IS03	winter	3538	40	2.42	0.45	4.77
	summer	2972	39	1.77	0.33	4.75
MS01	winter	2183	29	1.56	0.32	3.64
	summer	3078	45	2.30	0.41	5.48
MS02	winter	10689	38	0.77	0.15	3.99
	summer	9743	42	0.80	0.15	4.46
MS03	winter	5809	43	2.08	0.38	4.85
	summer	1630	39	2.20	0.41	5.14
OS01	winter	204	20	3.04	0.70	3.57
	summer	525	32	3.21	0.64	4.95

other stations and all but one specimen were caught at night. Planehead filefish (*M. hispidus*) were collected at all inner and middle shelf stations with catches higher in summer than in winter at inner shelf stations and at MS01. Most specimens of *M. hispidus* were taken at night in winter (77.0%) and summer (94.3%). Cubbyu (*E. umbrosus*) were slightly more abundant in summer, and demonstrated pronounced seasonal differences in abundance at OS01. Although not captured during winter at the outer shelf stations, this was the most abundant species at those sites in summer. All cubbyu were captured at night.

Other less abundant species demonstrated seasonal or diel abundance patterns. *Apogon pseudomaculatus* were captured only during the summer and only at night. All *Ophidion* spp. (*O. beani, O. holbrooki, O. selenops*) were captured at night. Most *Centropristis ocyurus* (96.6%), *Syacium papillosum* (96.6%) and *Scorpaena* spp. (98.2%) were captured at night, whereas most *Holacanthus bermudensis* (74.2%) and *Mullus auratus* (95.7%), were trawled during the day. Most *Lagodon rhomboides* (88.4%) were captured during winter, and 85.5% of these occurred in night trawls.

Several other species, including some economically valuable species, were not dominant in the overall catches but were common at some stations. Red porgy (*Pagrus pagrus*), were common at middle and outer shelf stations. In winter, *P. pagrus* was the most abundant species at OS01 and was a dominant species at MS02. In summer, red porgy were dominant only at OS01. None were caught at inner shelf stations, and most red porgy were caught during the day. Red snapper (*Lutjanus campechanus*) and gag (*Mycteroperca microlepis*) were taken primarily at middle shelf stations. These species were infrequently caught by the trawl and sample sizes were too small to determine seasonal or geographical patterns of abundance.

Abundance, biomass and community structure

At inner shelf stations, overall fish abundance was highest in summer when inshore waters warmed up (>22° C). Increased abundance in summer was particularly pronounced at IS01 and IS02 (Table 3). Station IS03 had a smaller seasonal difference in fish abundance, and difference in temperature was not as great (Table 1). Little seasonal difference in abundance was evident for demersal teleosts at MS01 and MS02, but at MS03 differences were similar in magnitude to the two northermost inner shelf stations, with abundance higher in winter. In general, the inner and middle shelf hard bottom fish communities were characterized by a few

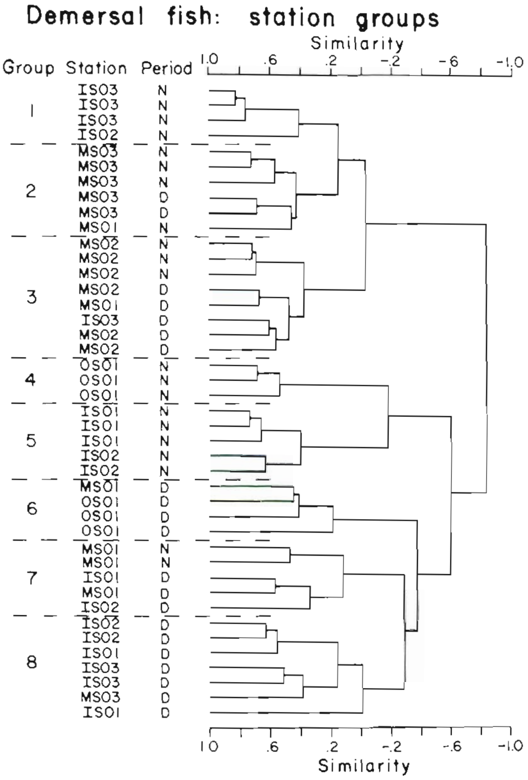

Fig. 3. Normal cluster dendrogram of winter trawl collections of demersal fishes. D = day trawls and N = night trawls.

abundant species, several species of intermediate abundance and a large number of rare species, many of which were represented by a single specimen. During both seasons, fish abundance was lowest at OS01.

Mean biomass per tow of demersal teleosts at all stations was 44.052 kg in winter and 30.974 kg in summer. Mean catch per tow values were significantly different between stations for winter catches ($F_{6,35} = 3.57$, $p<0.01$, ANOVA) when catches at MS02 and MS03 were significantly greater than other stations (Duncan Multiple Range Test, a = 0.05). No significant difference was observed between stations for summer catches ($F_{6,34} = 0.98$, $p>0.50$, ANOVA). When catches from both seasons were combined, biomass (kg ha^{-1}) was highest at middle shelf depths and lowest at the outer shelf station (Table 3).

Diversity of trawl catches varied with light phase, depth and season (Table 4, Fig. 2). The effect of light phase on diversity was the most consistent, with night trawls having higher H′ diversity values than day trawls at every station (Fig. 2). Between seasons, diversity was highest at inner shelf stations during winter (Table 4). Since species richness varied little seasonally at IS01 and IS03, increased diversity at these stations in winter is due to increased evenness. Species richness at IS02 was actually much greater in summer, but the strong dominance of the community by *S. aculeatus* and *H. aurolineatum* (Table 2) resulted in a lower evenness value and a resultant lower H′ diversity. Diversity of middle shelf stations was equal to or lower than inner shelf stations, especially at MS02 where large numbers of *S. aculeatus* dominated during both winter and summer (Table 2). Unlike inner shelf sites, diversity at middle shelf sites was higher during summer when the two most abundant species were not as dominant, and species

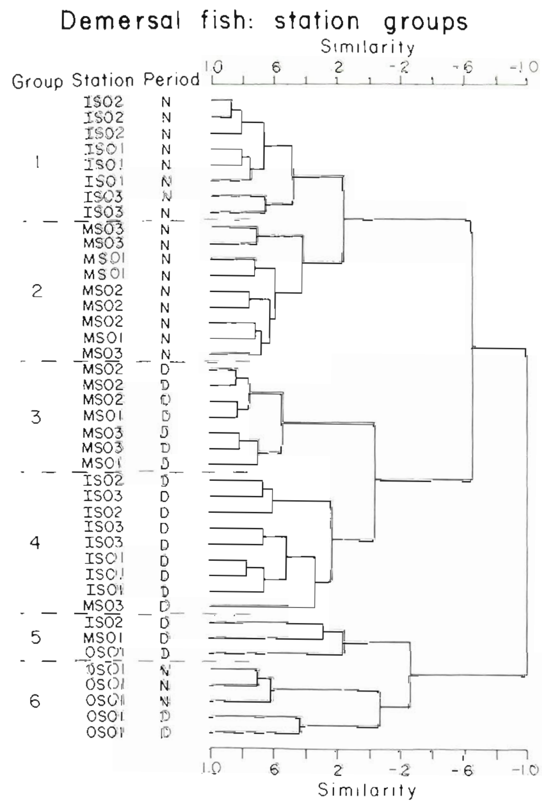

Fig. 4. Normal cluster dendrogram of summer trawl collections of demersal fishes. D = day trawls and N = night trawls.

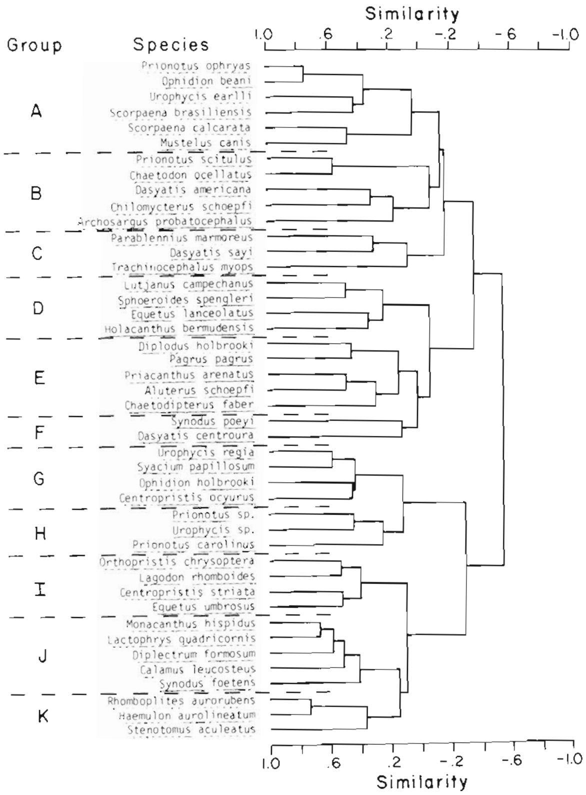

Fig. 5. Inverse cluster dendrogram of winter trawl collections of demersal fishes.

richness increased. Diversity (H′) was highest at station OS01 during both seasons. Although species richness was comparable to other stations with low H′ diversity (e.g. MS02), no species were very abundant or strongly dominant at OS01.

Normal cluster analysis also demonstrated the importance of light phase in influencing the community composition of trawl collections (Figs. 3, 4), since most collections within a season grouped together based on sampling period. Differences in faunal composition by depth were also apparent within each light phase, particularly during the summer. However, no distinct latitudinal patterns were detected in the normal cluster analysis.

Winter inverse and nodal analyses indicated that several species frequently co-occurred within a particular depth zone. Species groups B, H and I (Fig. 5) were more faithful to inner shelf stations (Fig. 6) and included hard bottom species (*C. ocellatus, A. probatocephalus, C. striata, E. umbrosus*) as well as coastal or open shelf species (*Prionotus* spp., *Urophycis* sp., *O. chrysoptera*) which frequently occur inshore (Struhsaker 1969). Species groups C–E demonstrated moderate to high constancy and fidelity to middle shelf stations in winter. These groups comprised common to abundant hard bottom species (*E. lanceolatus, H. aurolineatum, S. aculeatus*), including species of commercial importance (*L. campechanus, P. pagrus, R. aurorubens*). Other species which were ubiquitous across the shelf (Groups G and J) were more frequent (higher in constancy) at middle shelf stations. Only species Group F, which was composed of deep-living sand bottom species, demonstrated faithfulness to OS01 in winter.

In summer, some species groups (Groups A–C) had high constancy at inner shelf stations, while several other groups (Groups G–J) rarely occurred at those depths (Figs. 7, 8). Three groups (Groups E–G) were generally faithful to inner shelf stations and, as in winter, consisted of inshore hard bottom and open shelf species. Two species groups were faithful to middle shelf depths (Groups H and J) in summer. These included two economically valuable species, red snapper (*L. campechanus*) and gag (*M. microlepis*). As in winter, several species (Group C), including the vermilion snapper (*R. aurorubens*), that were ubiquitous across the shelf were more frequent at middle shelf depths. Species Group D was highly faithful to OS01 in summer. This group included species only collected at OS01 [*Equetus* (= *Pareques*) sp. nov., *C. sedentarius*] or which were more abundant at that station (*P. pagrus, Echiodon dawsoni, P. salmonicolor*). *Pagrus pagrus,* which was more frequent on the middle shelf in winter, was in a group that was highly faithful to OS01 in summer.

Several species co-occurred in the same depth zone in both winter and summer, whereas other species apparently moved inshore or offshore. For example, *L. rhomboides* and *O. chrysoptera* co-occurred in a species group which was faithful to inner shelf stations during both winter and summer. *Lutjanus campechanus* co-occurred in a group with *H. bermudensis* in both winter and summer, but these species were most frequent at middle shelf stations. Other species, such as *R. aurorubens* and *H. aurolineatum,* were ubiquitous across the shelf but were more abundant on the middle shelf and were in groups with higher constancy at middle shelf stations during both seasons. The associations and fidelity patterns of some species varied seasonally, perhaps due to migratory movement. *Pagrus pagrus,* for example, was most faithful to MS02 in winter but was included in a group which was highly faithful to OS01 in summer. *Ophidion beani* was more faithful to inner and middle shelf stations in winter, but was included with *P. pagrus* in the group faithful to OS01 in summer.

Fishes observed or collected with other gear

Approximately 40 species of fish were identified on the videotapes from television transects, and with the exception of *Sphyraena barracuda,* all species were caught by other removal gears. Underwater television abundance estimates of selected species that could be identified with certainty on videotapes were generally higher than trawl estimates (Table 5). Videotape analysis also showed differences in fish abundance among the three depth zones. Tomtate (*Haemulon aurolineatum*) was the most abundant species seen, with highest densities at middle shelf stations, especially MS01. Black sea bass (*Centropristis striata*) were also common in all three depth zones and were most abundant on the middle shelf. Red snapper (*Lutjanus campechanus*) were occasionally seen in all three depth zones, and gag (*Mycteroperca microlepis*), red porgy (*Pagrus pagrus*) and greater amberjack (*Seriola dumerili*) were commonly observed at middle and outer shelf stations.

Density estimates obtained from the television analysis indicated much lower fish densities in winter than in summer, except at the outer shelf. Differences noted between seasons were greatest at the inner shelf sites (Table 5). Within each season, however, density estimates often varied considerably between stations in a depth zone, particularly

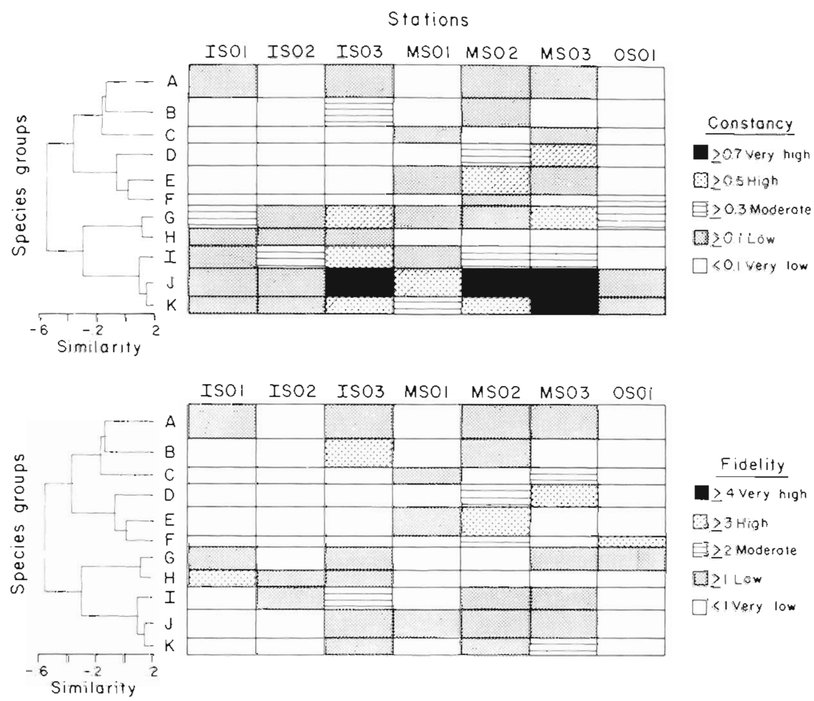

Fig. 6. Inverse classification hierarchies and nodal diagram showing constancy and fidelity of station – species group coincidence based on winter collections of demersal fishes.

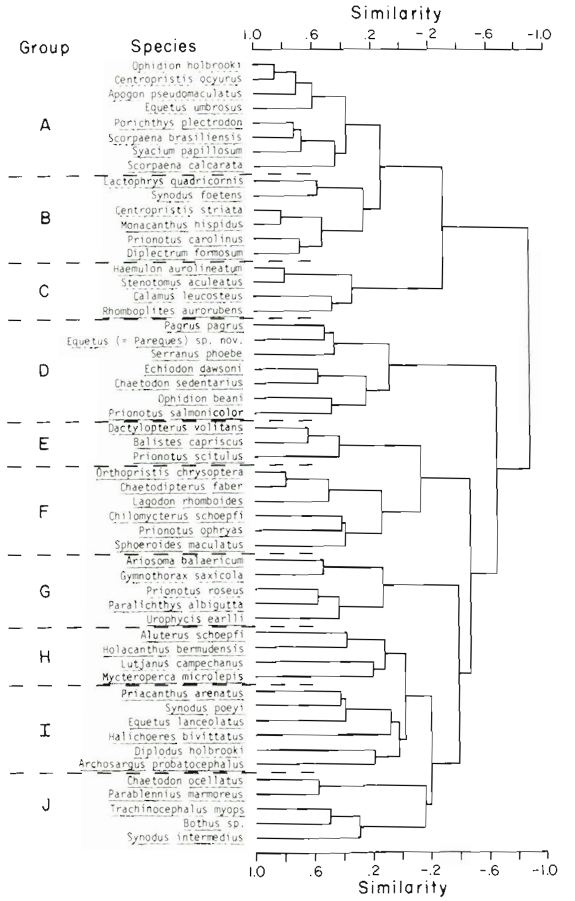

Fig. 7. Inverse cluster dendrogram of summer trawl collections of demersal fishes.

at middle shelf sites.

Although many fish observed on videotapes at OS02 and OS03 could not be identified, underwater television allowed us to compile a partial list of species present at those two outer shelf stations which could not be trawled. Based on comparisons with videotape observation of the middle and inner shelf stations, the two untrawlable outer shelf stations had greater numbers of *Centropristis ocyurus, Chromis enchrysurus,* large groupers (*Mycteroperca* spp., Serranidae), *Pagrus pagrus* and *Equetus* (= *Pareques*) sp. nov. (Table 6). These species were also frequently observed on transects or in trawl collections at OS01.

The large number of unidentified fishes observed on videotape transects at OS02 and OS03 were rapidly swimming schooling species. These unidentified fishes probably represent abundant schooling species such as *Rhomboplites aurorubens* which were commonly trawled at OS01. The number of individuals per hectare of television transect at OS02 and OS03 was generally higher than density estimates based on trawl collections at OS01 (Tables 3 and 6).

Baited fishing gears deployed at untrawlable stations confirmed the presence of fishes seen on videotapes (Table 7). Red porgy (*P. pagrus*) and *Centropristis ocyurus* were the dominant species collected.

Discussion

Species composition and abundance of demersal fishes varied seasonally, with the most striking seasonal differences occurring at inner and outer shelf stations. The results of cluster analysis indicate that the demersal fish fauna of hard bottom habitat on the continental shelf consists of an inshore component, a shelf break component and a middle shelf component composed of unique species plus species shared with the inner shelf and shelf break. The inner shelf is the most unstable thermally and was characterized by the greatest seasonal fluctuation in community composition and overall abundance. Many species found at inner shelf stations were not faithful during both seasons, and dominant species changed dramatically. This was particularly evident at the two northern-most inner shelf stations, which had the widest seasonal temperature differences (11.0° C at IS01 and 16.1° C at IS02). In winter, these stations were characterized by few fishes and by temperate species (e.g. *Urophycis regia*) which moved offshore to cooler water in summer. In summer, warm-temperate and subtropical species invaded these areas (e.g. *Haemulon aurolineatum, Apogon pseudomaculatus, Monacanthus hispidus*), and these two stations were similar in faunal composition to middle shelf stations. Station IS03 had fewer seasonal differences in species composition and abundance. This is probably due to its more southerly position and lower seasonal temperature range (8.8° C).

Table 5. Abundance estimates (number of individuals per ha) of selected species, and total number of demersal fishes, based on television and trawl analysis.

Species	Inner shelf				Middle shelf				Outer shelf			
	Winter		Summer		Winter		Summer		Winter		Summer	
	TV	Trawl	TV	Trawl	TV	Trawl	TV	Trawl	TV	Trawl	TV	Trawl
Archosargus probatocephalus	13.5	1.0	4.1	0.8	0.0	0.9	0.0	0.2	1.6	0.0	0.0	0.0
Centropristis striata	18.7	5.5	12.3	35.1	53.3	3.2	50.2	3.7	20.8	0.0	18.8	0.0
Holacanthus bermudensis	0.0	0.0	0.0	0.0	4.9	0.8	7.2	1.5	16.0	0.0	14.5	0.3
Lutjanus campechanus	0.4	0.0	0.0	0.2	0.0	1.6	0.8	0.5	0.0	0.0	3.0	0.3
Mycteroperca microlepis	0.0	0.0	0.0	0.0	5.9	0.1	10.2	0.2	17.6	0.2	15.9	0.0
Seriola dumerili	0.0	0.0	0.0	0.2	3.0	0.0	96.6	0.1	8.0	0.5	5.8	0.3
Haemulon aurolineatum	0.0	114.9	65.1	248.8	394.8	205.8	5300.4	116.0	0.0	0.0	4.4	0.0
Pagrus pagrus	0.0	0.0	0.0	0.0	13.3	2.1	3.0	1.1	11.7	15.2	5.1	3.8
Total demersal fishes	72.9	371.4	1154.4	1033.6	1586.3	1288.3	7682.0	1156.2	93.3	49.1	81.5	141.9

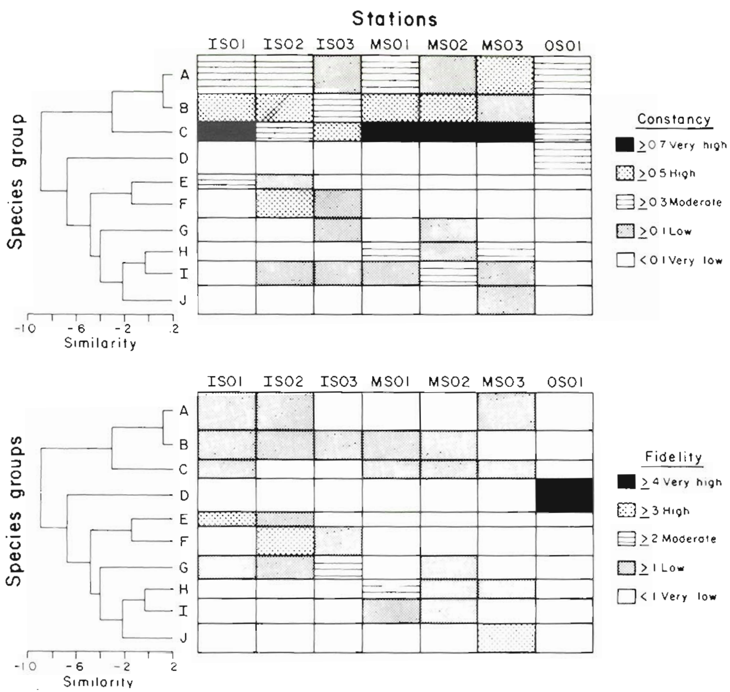

Fig. 8. Inverse classification hierarchies and nodal diagram showing constancy and fidelity of station – species group coincidence based on summer collections of demersal fishes.

Miller & Richards (1980) suggested that the middle shelf (19–55 m) in the South Atlantic Bight is the most thermally stable zone. They reported subtropical fish species in this zone with a center of distribution and maximum abundance of commercial species at 33–40 m. In the present study, fish abundance was also highest at middle shelf sites and did not vary as much between seasons as did inner shelf sites. Nodal analysis indicated a high affinity of dominant subtropical species (e.g. *Lutjanus campechanus, Equetus lanceolatus, Holacanthus bermudensis, Mycteroperca microlepis*) for middle shelf stations. With the exception of *Centropristis striata,* all commercially important spe-

Table 6. Abundance of fishes counted on videotape transects at outer shelf stations which could not be trawled during winter (w) and summer (s), 1980.

Species	Station			
	OS02		OS03	
	w	s	w	s
Dasyatis centroura		2		
Dasyatis sabina	1			
Dasyatis sp.	1			
Anguilliformes		3		1
Muraenidae				1
Fistularia sp.			2	
Serranidae (large groupers)	4	52	25	1
Centropristis ocyurus	9	1	2	6
Centropristis sp.			6	
Centropristis striata	8	10		2
Diplectrum formosum			1	
Mycteroperca microlepis	7	8	5	3
Mycteroperca sp.	1			
Serranus phoebe		1		1
Priacanthus sp.	1			
Seriola dumerili	2	3	3	1
Lutjanus campechanus		1	1	
Rhomboplites aurorubens	36		675	
Haemulon aurolineatum		18		1
Sparidae	5			
Archosargus probatocephalus	1			
Pagrus pagrus	5	18	46	1
Equetus sp.	29			
Equetus sp. now.	2	4	4	2
Chaetodon sedentarius				1
Chaetodon sp.	7	21		5
Holacanthus bermudensis	2	2	8	7
Chromis enchrysurus	3	103	125	57
Prionotus sp.		1		
Aluterus sp.	1			
Balistes capriscus	1		2	
Unidentified	497	1537	2874	232
Total:	624	1777	3779	323
Total length of transects (m):	5244	5580	5991	5112
Number of fish per 100 m of transect:	11.9	31.8	63.1	6.3
Number of fish per ha of transect:	350.0	936.6	1855.2	185.8

Table 7. Abundance of fish species caught by baited fishing gears at untrawlable stations during winter and summer 1980. n = number of sets which caught fish and N = number of sets deployed and recovered.

Species	Station											
	OS02						OS03					
	traps		longlines		snapper reels		traps		longlines		snapper reels	
	w	s	w	s	w	s	w	s	w	s	w	s
Rhizoprionodon terraenovae				1								
Opsanus pardus					1							
Corniger spinosus		1										
Centropristis ocyurus	9	2					8	17			7	
Centroptistis striata	2	3		2	1							
Epinephelus drummondhayi		1										
Seriola dumerili				1								
Rhomboplites aurorubens	1		1				2		1		1	
Pagrus pagrus	18	1		5	2		52	10	1		12	
n/N	3/4	2/4	1/6	4/8	3/6	0/6	3/4	1/1	2/8	0/2	4/6	0/3
Total number of fish	30	8	1	9	4	0	62	27	2	0	20	0
Catch per set (n)	10.0	4.0	1.0	2.2	1.3	0.0	20.7	27.0	1.0	0.0	5.0	0.0
Total soak time (hrs) of n sets	5.4	2.0	1.4	5.0	1.3	0.0	3.5	5.1	3.0	0.0	2.6	0.0
Catch per hr	5.5	3.9	0.7	1.8	3.2	0.0	17.6	5.3	0.7	0.0	7.7	0.0

cies were more abundant in trawl catches at middle shelf depths. Most species faithful to middle shelf stations were faithful in both winter and summer. Species that seasonally changed fidelity either moved to or from shallow or deeper water as suggested by Miller & Richards (1980). Thus *Pagrus pagrus,* which was in a species group highly faithful to MS02 in winter, belonged to a group highly faithful to OS01 in summer.

Outer shelf hard bottom areas are characterized by variable temperatures due to cold water intrusions (Miller & Richards 1980), and this is reflected in the seasonal instability of the fish community in our study. No species in the group faithful to OS01 in winter were included in the group faithful to that station in summer, indicating the community change at that station. Four major species assemblages were collected at the outer shelf station: (1) ubiquitous species that ranged across the shelf (e.g. *Rhomboplites aurorubens, Calamus leucosteus*); (2) temperate species that move up from the continental slope in winter (e.g. *Urophycis regia*) (Struhsaker 1969); (3) subtropical species that invade these depths from shallower water in summer (e.g. *Equetus umbrosus*); and (4) species which have their major abundances at these depths year-round [*Equetus* (= *Pareques*) sp. nov., *Serranus phoebe, Chaetodon aya, Chaetodon sedentarius*]. Miller & Richards (1980) noted similar results.

Overall fish abundance on hard bottom during winter and summer was much higher than that found in previous trawl surveys on sand bottom in the South Atlantic Bight (Wenner et al. 1980). Several species of demersal shelf fishes which dominated catches in the present study are also frequently taken on the open shelf; however, species such as *Stenotomus aculeatus, Haemulon aurolineatum* and *Calamus leucosteus,* which are ubiquitous species found in a wide range of habitats, are more abundant on and near hard bottom (Struhsaker 1969, Manooch & Barans 1982, Waltz et al. 1982). Total catch of *S. aculeatus* in six trawls at one of our live bottom areas, MS02, exceeded total catch in 40 trawls in similar depths and season over sand bottom on the continental shelf (Wenner et al. 1980). *Calamus leucosteus* was also much more abundant than reported from sand bottom trawls. The occurrence of *H. aurolineatum* over sand bottom (Wenner et al. 1980) may be related to feeding behavior, since many haemulids, including *H. aurolineatum,* are known to forage at night over sand flats, returning to the reef during the day (Randall 1963, Collette & Talbot 1972, Parrish & Zimmerman 1977). Other dominant species, such as *Rhomboplites aurorubens,* are very rare in trawl catches from sand bottom (Wenner et al. 1980) and are apparently much more dependent on hard bottom habitat.

Estimates from our trawl catches document much higher demersal fish biomass on hard bottom than has been previously observed on sand bottom shelf habitat in this region. Wenner et al. (1980) reported mean values of 3.070 kg ha^{-1} for demersal teleosts from 64 trawls over sand bottom in the South Atlantic Bight (9–366 m depth in summer). In contrast, mean biomass from summer trawls in the present study was 30.974 kg ha^{-1} for demersal teleosts. Powles & Barans (1980) and Wenner (1983) reported similar biomass estimates of demersal fish (27.3 kg ha^{-1} and 31.0 kg ha^{-1} respectively) on hard bottom, based on trawl catches. On the other hand, our fish biomass estimates are considerably less than the 446 to 6980 kg ha^{-1} estimated by others for natural and artificial tropical reefs in the western Atlantic (Bermuda) and central Pacific (Odum & Odum 1955, Bardach 1959, Stone et al. 1979). Bardach (1959) compared his reef fish biomass estimates to estimates from New England and the northeast Atlantic and concluded that higher temperatures and increased surface areas provided by reefs supported higher biomass. The decreased surface area because of lower relief, the cooler and more variable temperature, and the patchy nature of hard bottom reefs in the South Atlantic Bight could also explain the lower biomass estimates noted in the present study as compared to tropical reefs.

The significant differences in biomass between stations in winter were due to the very low biomass of demersal teleosts at IS01 and IS02 and the high biomass at MS02. As inshore waters warmed during summer, biomass at IS01 and IS02 increased as fishes apparently moved into these areas from warmer offshore waters, and there was no significant difference between stations in summer. Middle shelf hard bottom areas supported the greatest standing crop (kg ha^{-1}) of demersal teleosts. Miller & Richards (1970) noted similar conclusions and attributed the high productivity of these depths to increased seasonal temperature stability relative to inner and outer shelf depths.

Diversity values for demersal fishes were relatively low due to the numerical dominance of the community by a few species. Wenner et al. (1980) reported similar ranges of H′ trawl collections over sand bottom in the South Atlantic Bight in the same depths, with maximum values being higher at their inner and middle shelf sites but slighthly lower at outer shelf sites. Foell & Musick (1979) reported a lower range of diversity values for trawl collections at depths of 39–73 m in the Middle Atlantic Bight. The higher diversity of demersal shelf fishes in the South Atlantic Bight (versus the shelf north of Cape Hatteras) is due to increased species richness. Whereas Foell & Musick (1979) reported 41 species in 264 trawl collections over four seasons, the 83 collections over two seasons in the present study collected 128 species. Wenner et al. (1980) collected 152 demersal species in 64 trawls on the open shelf and slope in summer; however, their stations included a broader latitudinal and depth range in the South Atlantic Bight.

Normal cluster analysis resulted in grouping of stations by light phase within a depth zone. Separate grouping of day trawls from night trawls in normal analysis resulted from the capture of many species mainly during the night (e.g. *Apogon pseudomaculatus, Equetus umbrosus, Urophycis regia*). As pointed out by Wenner (1983) this is probably due to increased nocturnal activity of these species. Diurnal cryptic behavior of these species makes them unavailable to trawls during the day.

Species composition of the fish fauna as seen on the television transects differed from that captured by the trawl. One reason for this is the inability to accurately identify many fishes on the television monitor, whereas most fishes captured by trawl were identified to species. Many of the unidentified fishes on videotapes are probably species commonly caught in the trawl (e.g. *S. aculeatus, H. aurolineatum, R. aurorubens*). Another reason for the faunal differences in trawl collections versus television observations is that many fishes seen on videotapes, particularly large species, may avoid the trawl. Observed abundance of red snapper, groupers, sheepshead, black sea bass and greater amberjack was greater than trawl collections indicated. For example, *Seriola dumerili,* a large species, was rarely taken by trawl at any station, and only one was taken at middle shelf depths in the summer (<1 individual ha^{-1} of swept area). In contrast, videotape analysis indicated a density of 96.6 individuals ha^{-1} at the same stations. Differences in abundance estimates for these fishes between television and trawl collections are probably due to the ability of these large fishes to avoid the trawl or their attraction to the television camera. Overall estimates of fish abundance also differed between trawl samples and television transects, with abundance estimates based on underwater television being generally higher. Uzmann et al. (1977) and Powles & Barans (1980) also reported estimates of fish density obtained from underwater television that were generally higher than those obtained by trawl. Even so, comparisons of television data between depth zones suggests that fish densities were frequently highest at middle shelf sites and greatest seasonal variability was observed at inner stations. These results support our conclusions based on trawl data.

Baited fishing gear has only limited utility as a method of assessing fish abundance, but the present data provides useful comparisons with other studies. Vertical longlines deployed in the Virgin Islands caught a maximum of 0.04 fish per hook per minute (Olsen et al. 1974) while maximum catches in the present study were considerably lower, 0.004 fish per hook per minute. Powles & Barans (1980) reported catches in summer of from 3.0 (day) to 20.0 (night) fish per hour for Antillean S-traps on the South Atlantic Bight middle shelf. In the present study, summer catches at middle shelf stations were lower (1.2–8.6 fish per hour), although comparable catches were made in winter (2.7–21.2 fish per hour).

In summary, the hard bottom areas of the South Atlantic Bight continental shelf support a tropical and subtropical ichthyofauna, which consist of inner, middle and outer shelf assemblages. Middle shelf depths support the greatest numbers and biomass of demersal fishes available to trawls and appear to have the most seasonally stable community.

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