SPECIES ASSOCIATIONS AND DAY-NIGHT VARIABILITY OF TRAWL-CAUGHT FISHES FROM THE INSHORE SPONGE-CORAL HABITAT, SOUTH ATLANTIC BIGHT¹

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ABSTRACT

Biomass, species composition, diversity, and community structure of demersal fishes were studied during the spring of 1978 in the sponge-coral habitat of the South Atlantic Bight. These results were compared with sampling at an open-shelf site. Otter trawl catch rates were an order of magnitude higher in the sponge-coral habitat than at the open-shelf site. Density and biomass estimates in the sponge-coral habitat averaged 384 individuals/ha and 31.0 kg/ha, respectively, whereas at the open-shelf site they averaged 57 individuals/ha and 3.2 kg/ha. In sponge-coral habitat samples, 101 species of demersal teleosts were taken. The Sparidae accounted for the greatest number of species (9), as well as 59% of the total number and 48% of the weight of demersal teleosts. Species diversity was highest in night-trawl tows in the sponge-coral habitat. Species associations, described by numerical classification, showed major differences in faunal assemblages between reef and open-shelf sites and between day and night samples.

Struhsaker (1969) presented a generalized habitat classification based on substrate type and species composition in a summary of demersal fish resources off the southeastern United States (Fig. 1). The open-shelf habitat extends offshore from 18 m(10 fm(fathoms)) to about 55 m (30 fm) and is characterized by a sandy bottom and relatively stable hydrographic conditions due to the moderating influence of the Gulf Stream (Struhsaker 1969; Mathews and Pashuk 1977). The ichthyofauna of the open shelf are relatively diverse but have a low biomass (Wenner et al. 1979a, b, c). Abundant teleostean families are the Sparidae, Synodontidae, Serranidae, Bothidae, and Triglidae (Wenner et al. 1979a).

The sponge-coral habitat (= Struhsaker's [1969] "live bottom") is composed of isolated areas within the open-shelf habitat. These locales have a hard substrate composed of a carbonate, shell, and quartz sand conglomerate which is either exposed or covered with a thin veneer of sand to a depth of 8 cm or less (Powles and Barans 1980). This substrate provides suitable sites for the growth of dense stands of attached invertebrates (sponges, corals, echinoderms, tunicates, hydroids, and bryozoans) and algae. A recent classification divides the spongecoral habitat into estuarine and nearshore sites (<18 m [<10 fm]), intermediate sites (18-55 m [10-30 fm]), and offshore sites (55-183 m [30-100 fm]) (Miller and Richards 1979).

The most productive areas in the South Atlantic Bight, in terms of fish diversity and biomass, are the hard-bottom areas (Struhsaker 1969; Huntsman and Manooch 1978; Miller and Richards 1979; Powles and Barans 1980). The purposes of this report are to present distribution, relative abundance, and species composition of trawl-caught fishes from inshore and intermediate reefs sampled during the late spring of 1978 and to comment on the suitability of otter trawl gear for stock assessment of commercial finfish in this habitat.



FIGURE 1.—South Atlantic Bight habitat types as defined by Struhsaker (1969).

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MATERIALS AND METHODS

Sampling was conducted at seven sites (Fig. 2) from 18 June to 16 July 1978 from the 32.6 m RV Dolphin. White line recorder tracings and bottom observations made with a Hydro Products TC-125 SDA³ low light level underwater television system in conjunction with loran-C positions were used to produce maps of each site. The camera was suspended from the hydrographic wire (Fig. 3) and towed at low speed (~0.5 m/s; 1.0 kn) across each potential study area. The sponge-coral habitat was defined by the presence of attached invertebrate growth. In addition to the six sponge-coral habitat sites, an open-shelf (nonreef) area was studied to compare the species composition and biomass of both communities. Following habitat delineation, fishes were sampled by 10-min day and night trawl tows with a ¾ scale version of a Yankee No. 36 trawl (Wilk and Silverman 1976) at a speed of 6.5 km/h. The 16.5 m long footrope and the 11.9 m headrope of the net are attached to a 19 mm diameter ground cable by 12.7 mm diameter 11.6 m long leg lines. Each 17.7 m long ground cable attaches to a 226 kg wooden door. The footrope has about 1.000 rubber discs (114 mm diameter) attached to it which enable the net to bounce over small bottom irregularities. Day tows were made from 1 h after sunrise to 1 h before sunset, whereas night tows were made from 1 h after sunset to 1 h before sunrise.



FIGURE 2.—Reef sampling sites for the 1978 survey. OS = open-shelf study area.

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



FIGURE 3.— System for deployment of underwater television equipment used in habitat documentation.

Fishes caught in nets that were not damaged during trawling operations were identified, measured, and weighed.

Initial calculations showed that the variance of the number of individuals per tow and the weight per tow far exceeded the mean and approximated a negative binomial distribution. Therefore, data were transformed (ln [x + 1]) before analysis to standardize the variance and approximate the normal distribution (Taylor 1953; Elliott 1977). The number of species per tow was normally distributed and thus was not transformed. The Bliss (1967) approximation was used in retransforming the data from logarithmic to original units. Since occasional catches of large elasmobranchs and large catches of pelagic fishes contributed significantly to the variance, biomass estimates were made only for demersal teleosts. Density estimates were calculated by the swept area method (Rohr and Gutherz 1977), with the sweep of the net being 8.748 m (Azarovitz⁴) and 1.080 km distances covered during a 10-min tow. These density estimates should be viewed as minimum, since the effectiveness of the ³/₄ Yankee trawl in sampling reef fish populations is unknown.

Species diversity (H') and its components, evenness (J') and richness, were calculated for elasmobranchs and demersal teleosts in each trawl tow using the following formulae:

$$H' = -\sum_{i=1}^{S} (p_i) (\log_2 p_i)$$
 (Pielou 1969)

where H' = index of species diversity expressed in bits/individual

S = number of species

 $p_i =$ proportion of total sample belonging to *i*th species;

$$J' = H'/H'_{\text{max}} \quad (\text{Pielou 1969})$$

where J' = equitability or evenness H' = observed species diversity $H'_{max} = \log_2 S;$

Species richness $= S - 1/\ln N$ (Margalef 1968)

where S = number of species N = number of individuals.

Normal and inverse cluster analysis (Clifford and Stephenson 1975) were used to analyze trawl data. Prior to the analysis, data were edited to eliminate species occurring in only one trawl tow. These species have no discernible distribution pattern and, therefore, contribute no information to the analysis (Boesch 1977). Species abundance scores were then log_{10} transformed, thus reducing the dominance of species having high abundance. The Bray-Curtis similarity coefficient (Clifford and Stephenson 1975) (= the Czekanowski Quantitative Index of Bloom 1981) was used on the modified data set and is expressed by

⁴T. Azarovitz, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun., 1977.

$$S_{jk} = 2 \frac{\sum_{i} \min(X_{ij}, X_{ik})}{\sum_{i} (X_{ij} + X_{ik})}$$

where S_{jk} = similarity between entities j and k

- X_{ij} = value of the *i*th attribute for entity *j*
- X_{ik} = value of the *i*th attribute for entity k.

The Bray-Curtis similarity measure was chosen, since it most accurately reflects similarity in these types of analyses (Bloom 1981).

Normal analysis compared similarities among sites as indicated by the assemblages of fishes collected in trawl tows (entities are sites; attributes are the transformed species abundance scores). Inverse analysis compared similarities among the distribution patterns of species [entities are species, and attributes are the sites where they occur (Boesch 1977; Clifford and Stephenson 1975)]. The sorting strategy was flexible with $\beta = -0.25$ (see Clifford and Stephenson 1975 and Boesch 1977 for explanation).

Nodal analysis was used to examine the cooccurrence of species and site groups based on patterns of constancy and fidelity. Constancy, a measure of how consistently the members of a particular species group occur among the stations of a given site group, was calculated by the expression:

$$C_{ii} = a_{ii}/(n_i n_i) \qquad \text{(Boesch 1977)}$$

- where $C_{ij} = \text{constancy of species group } i$ in site group j
 - a_{ij} = actual number of individuals of species group *i* in site group *j*
 - $n_i n_j$ = number of entities in groups *i* and *j*, respectively.

Fidelity, the degree to which a given species group is

restricted to a particular site group was determined by

$$F_{ij} = (a_{ij} \sum_{i} n_j / n_j \sum_{i} a_{ij}) \qquad \text{(Boesch 1977)}$$

where F_{ij} = fidelity of species group *i* in site group *j*

 a_{ij} = actual number of individuals of species group *i* in collection group *j*

 n_j = number of entities in group j.

RESULTS

Biomass

Otter trawl catches from the sponge-coral habitat were highly variable, ranging from 6 to 2,976 individuals (1.6-244.8 kg) in a standard tow (Table 1). The means of the natural log-transformed values of the number of individuals per haul from all reef sites were not significantly different between day and night (t = 1.135, df = 55), whereas mean weight of fishes was significantly greater in day tows (t = 2.145, df = 55). Mean values and density estimates for all trawl tows within the sponge-coral and open-shelf habitats were

	Mean valu	ies/tow	Mean density h	y estimates'/ a	
Habitat	No.	Weight	No.	Weight	
	individuals	(kg)	individuals	(kg)	
Sponge-coral	363	29.3	384	31.0	
	²(268; 491)	²(24; 35.8)	²(284; 520)	²(25.4; 37.9)	
Open shelf	54	3.0	57	3.2	
	²(24; 121)	²(2.2; 4.0)	²(25; 128)	²(2.3; 4.2)	

'Using 0.95 ha as the swept area of a standard tow.

²Upper and lower 90% confidence limits.

TABLE 1.— Mean catch/tow of demersal teleosts, 90% lower and upper confidence limits (LCL and UCL), and ranges for ¾ Yankee trawl tows by site for the spring 1978 sponge-coral survey, South Atlantic Bight.

	Denth	Denth	No		No. of individuals				Weight (kg)			
Site	(m)	Time	of tows	LCL	ž	UCL	Range	LCL.	x	UCL	Range	
Open shelf	46	Day	5	3	6	10	2-10	0.3	1.4	2.3	0.0-3.6	
Open shelf	46	Night	6	55	. 75	101	42-101	3.1	4.4	6.2	1.9-6.2	
Reef 1	37	Day	6	86	257	766	39-1,376	17.0	34.7	70.0	12.3-116.7	
Reef 1	37	Night	5	105	172	280	64-248	12.9	16.7	21.7	11.2-24.0	
Reef 2	44	Day	4	48	361	2,670	6-247	9.3	40.9	169.7	2.5-42.3	
Reef 2	44	Night	4	103	164	260	87-214	13.7	19.1	26.5	11.7-25.6	
Reef 3	29	Day	6	678	3,518	18,233	32-2,976	54.0	206.1	778.8	2.9-244.8	
Reef 3	29	Night	6	125	188	284	66-307	14.1	19.8	27.6	8.1-27.8	
Reef 4	18	Day	6	344	1,325	5,094	47-2,853	16.1	44.2	125.4	1.6-132.6	
Reef 4	18	Night	7	148	220	328	64-413	8.5	13.8	23.0	2.6-27.6	
Reef 5	42	Day	4	198	599	1,812	108-847	14.7	23.9	35.7	14.6-37.3	
Reef 5	42	Night	1		45		_	_	12.0	—	· _	
Reef 6	27	Day	2		100		79-118		13.9	· ·	13.0-14.7	
Reef 6	27	Night	6	110	150	205	86-202	13.1	18.1	24.9	10.9-32.3	

Species Composition and Relative Abundance

Eleven trawl tows in the open-shelf habitat collected 470 individuals distributed among 26 species (16 families) with a total weight of 31.4 kg. Day catches (11 species, 8 families) accounted for only 6% of the number and 18% of the total weight of demersal teleosts taken at this site, and were not dominated by a single species. Night tows (22 species, 13 families) were dominated by planehead filefish, *Stephanolepis hispidus*, which accounted for 68% of the number and 46% of the weight of demersal teleosts at the open-shelf site (Table 2).

Trawl tows in the sponge-coral habitat (n = 57)collected 22,046 demersal teleosts belonging to 102 species (37 families) and having a total weight of 1,832 kg (Table 3). The Sparidae dominated the catches with the greatest number of species (9) and accounted for 59% of the total number and 48% of the total weight of demersal teleosts. The five most numerically abundant families comprised 92% and 77% of the total catch by numbers and weight. The 10most numerically abundant species accounted for 54% of the total abundance in all 57 trawl tows. Catches of the southern porgy, Stenotomus aculea*tus*, were an order of magnitude higher than those of other species (Table 4), contributing 57.3% of the total. This species also ranked first by weight, comprising 42.1% of the trawl-caught fish weight (Table 5).

Community Structure

One's perception of fish community structure in the South Atlantic Bight depends upon the habitat and time of sampling. Numerical classification indicated that four major divisions were present, consisting of 12 site groups (Fig. 4). The first major division contained, with one exception, otter trawl collections made during the day (site group 1) and night (site group 2) in the open-shelf area. A second division within the classificatory scheme included all trawl tows from reef 5 (site group 3). The two remaining broad divisions were composed of day tows (site groups 4 through 7) and night tows (site groups 8 through 12) from the five remaining reef sites. In general, major faunal distinctions were made, not only between collections from different habitats (open shelf vs. reef), but also between day and night samples taken at the same site.

The groundfish communities of the open-shelf and sponge-coral habitat formed 9 species groups containing from 5 to 11 species (Fig. 5). Each group was associated with specific spatial and temporal conditions. The five species of demersal fishes in group A showed a high frequency of occurrence and abundance at all reef sites, as reflected in the moderate to very high nodal constancy values (Fig. 6). The low and moderate constancy values for this species group in site groups 1 (5 open-shelf day tows, 1 day tow at reef 2) and 2 (6 open-shelf night tows) are a result of

TABLE 2 Demersal teleosts taken in ¾ Yankee trawl tows at the open-shelf study site,
South Atlantic Bight, spring 1978. $n =$ number of occurrences in 5 day or 6 night otter
trawl tows,

			Day			Night	
			weight			weigh	nť
Family	Species	No.	(kg)	n	No	o. (kg)	n
Muraenidae	Gymnothorax saxicola			_	4	0.37	3
Synodontidae	Synodus foetens	3	0.57	2		-	_
	Synodus intermedius	2	0.14	2	3	0.40	1
	Trachinocephalus myops				1	0.08	1
Ogcocephalidae	Ogcocephalus parvus	2	0.04	1	1	0.01	1
Ophidiidae	Ophidion beani			-	4	0.23	3
	Ophidion holbrooki				4	0.34	2
Serranidae	Centropristis ocyurus	3	0.09	1	17	1.02	6
	Diplectrum formosum	3	0.23	2	9	1.13	3
Priacanthidae	Pristigenys alta	-			1	0.03	1
Lutjanidae	Rhomboplites aurorubens				2	0.10	2
Haemulidae	Heemulon aurolineatum	-	-		69	6.20	з
Sciaenidae	Equetus lanceolatus		-		2	0.09	1
Mullidae	Mullus auratus		-	-	1	0.07	1
Labridae	Hemipteronotus novacula	2	0.13	1			-
Scorpaenidae	Scorpaena brasiliensis				1	0.19	1
Dactylopteridae	Dactylopterus volitans	2	2.3	1		-	-
Bothidae	Bothus ocellatus			_	1	0.02	1
	Cyclopsetta fimbriata		-	-	1	0.09	1
	Gastropsetta frontalis		<u> </u>	_	2	0.11	2
	Paralichthys dentatus		`	-	1	0.40	1
	Syacium papillosum	1	0.30	1	2	0.37	2
Balistidae	Aluterus heudeloti	2	1.60	1	1	0.05	1
	Monacanthus ciliatus		-	-	1	0.03	1
	Stephanolepis hispidus	4	0.14	3	315	14.30	6
Tetraodontidae	Sphoeroides dorselis	3	0.19	3		-	

TABLE 3.—Families and species of demersal fishes taken in 57 ¾ Yankee trawl tows in the sponge-coral habitat, South Atlantic Bight, during the spring of 1978. • = <0.1 kg.

Family	Species	No.	Weight (kg)	Family	Species	No.	Weight (kg)
Carcharhinidae	Rhizoprionodon terraenovae	1	1.3	Sciaenidae	Equetus lanceolatus	72	8.1
Rajidae	Raja eglanteria	11	6.6		Pareques acuminatus	1	•
Dasyatidae	Dasyatis americana	2	3.0		Pareques umbrosus	178	12.6
•	Dasyatis centroura	1	90.7	Mullidae	Mulius auratus	12	0.6
	Dasyatis sayi	1	0.1	Chaetodontidae	Chaetodon aya	4	0.3
Muraenidae	Anarchias yoshiaa	3	•		Chaetodon ocellatus	33	7.5
	Gymnothorax moringa	1	0.1		Chaetodon sedentarius	21	1.2
	Gymnothorax saxicola	6	0.9		Chaetodon striatus	1	0.1
	Muraena retifera	1	0.1	Pomacanthidae	Holacanthus isabelita	263	167.9
Congridae	Ariosoma balearicum	1	•		Holacanthus ciliaris	2	1.0
•	Conger oceanicus	4	0.2		Pomacanthus paru	2	0.2
Synodontidae	Saurida brasiliensis	1	•	Pomacentridae	Chromis enchrysurus	1,801	40.0
	Synodus foetens	19	2.5	Labridae	Halichoeres bathyphilus	1	0.1
	Synodus intermedius	17	1.5		Helichoeres bivittetus	8	0.4
	Synodus poeyi	24	0.1		Halichoeres caudalis	10	0.4
	Trachinocephalus myops	2	0.2		Hemipteronotus novacula	2	0.2
Batrachoididae	Opsanus c.f. pardus	7	0.1	Labridae unidentified		1	•
	Porichthys plectrodon	44	0.9	Scaridae	Nicholsina usta	1	•
Gobiesocidae	Gobiesox strumosus	1	•	Uranoscopidae	Kathetostoma albigutta	11	0.5
Antennariidae	Antennarius ocellatus	1	0.5	Clinidae	Starksia ocellata	8	•
Ogcocephalidae	Halieutichthys aculeatus	1	•	Blenniidae	Hypleurochilus geminatus	4	•
	Ogcocephalus corniger	2	0.2		Parablennius marmoreus	32	•
Gadidae	Urophycis earlli	19	3.0	Callionymidae	Callionymus pauciradiatus	1	•
	Urophycis regia	5	0.3	Gobiidae	Evermanichthys spongicola	1	•
Ophidiidae	Ophidion beani	11	0.7		logiossus calliurus	1	•
	Ophidian halbroaki	51	4.0	Scorpaenidae	Scorpaena brasiliensis	17	2.7
	Ophidion selenops	6	•		Scorpaena calcarata	16	0.7
	Otophidium osmostigmum	4	•		Scorpaena dispar	2	0.2
Carapidae	Carapus bermudensis	22	0.1		Scorpaenodes tredecimspinosus	1	•
Holocentridae	Holocentrus ascensionis	2	0.6	Triglidae	Prionotus carolinus	120	7.5
Syngnathidae	Hippocampus erectus	3	0.1		Prionotus ophryas	9	0.7
Serranidae	Centropristis ocyurus	158	6.9		Prionotus roseus	5	0.3
	Centropristis striata	435	61.6		Prionotus salmonicolor	1	0.2
	Diplectrum formosum	84	5.0		Prionotus scitulus	7	0.3
	Mycteroperca microlepis	5	24.2	Bothidae	Ancylopsetta quadrocallata	18	6.2
	Mycteroperca venenosa	1	0.1		Bothus ocellatus	11	0.4
	Serranus phoebe	37	5.0		Bothus robinsi	7	0.2
Priacanthidae	Priacanthus arenatus	5	1.9		Cyclopsetta fimbriata	5	0.5
	Pristigenys alta	31	4.7		Etropus microstomus	3	•
Apogonidae	Apogon pseudomaculatus	174	0.4		Paralichthys albigutta	2	1.0
Lutjanidae	Lutjanus campechanus	3	0.4		Paralichthys dentatus	19	5.4
	Rhomboplites aurorubens	384	33.7		Paralichthys lethostigma	1	0.6
Haemulidae	Haemulon aurolineatum	3,153	239.5		Syacium papillosum	24	2.7
	Haemulon plumieri	16	13.6	Balistidae	Aluterus heudeloti	7	3.3
	Orthopristis chrysoptera	1	0.2		Aluterus schoepfi	28	19.8
Sparidae	Archosargus probatocephalus	11	11.7		Balistes capriscus	20	25.7
	Calamus bajonado	2	9.3		Monacanthus ciliatus	3	0.1
	Calamus leucosteus	319	135.4		Stephanolepis hispidus	1,392	93.8
	Calamus nodosus	25	26.6	Ostraciidae	Acanthostracion polygonius	2	1.4
	Diplodus holbrooki	3	0.2		Acanthostracion quadricornis	53	21.5
	Lagodon rhomboides	2	0.2	Tetraodontidae	Spoeroides spengleri	6	0.4
	Pagrus pagrus	46	23.5	Diodontidae	Chilomycterus schoepfi	8	2.9
	Stenotomus aculeatus	12,630	771.2		Diodon holacanthus	4	1.0
	Stenotomus caprinus	1	•				

the infrequent occurrence of *Stephanolepis hispidus* and *Haemulon aurolineatum* in some of these tows. The widespread distribution pattern of this species group is apparent in the low nodal fidelity values (Fig. 7).

Species group B consisted of an assemblage of fishes that were widely distributed in night reef samples. Species showed very low to low constancy and negative fidelity to site groups 1 through 7. Group B species displayed moderate to high constancy in the remaining site groups which consisted entirely of night trawl tows. This wide distributional pattern among night samples was reflected in the low fidelity values for all site groups. Fishes of group C, although not very abundant, occurred almost exclusively in night trawl tows. Species in this group had low and high constancy, moderate and high fidelity to site groups 8 and 9, respectively, which were composed of night trawl tows from reefs 1 (38 m) and 2 (44 m). Synodus intermedius was the only species of this group that had a wide distribution in other site groups regardless of time of collection. Bothus robinsi and Prionotus roseus were found only in site groups 8 and 9, whereas the remaining species (Kathetostoma albigutta, Cyclopsetta fimbriata, Ophidion selenops, Otophidium omostigmum) occurred only in night tows of these and other site groups.

TABLE 4.—Ten most numerically abundant demersal teleosts taken spring 1978 in 57 sponge-coral habitat trawl tows, South Atlantic Bight.

Species	No. of individuals	% of total catch	Cumulative %	No. of occurrences
Stenotomus				
aculeatus	12.630	57.3		40
Haemulon		07.0		-0
aurolineatum	3 153	14 3	71.6	40
Chromis	0,.00	14.5	71.0	
enchrysurus	1 801		70.9	•
Stephanoleois		0.2	75.0	9
hispidus	1 302	6.2	06.1	50
Centropristis	1,552	0.3	60.1	52
striata	425	2.0	00.1	07
Rhombonlites	430	2.0	88.1	37
auroruhens	204			
Calamus	364	1.7	89.8	20
leucosteue	210			
Holacanthus	219	1.4	91.2	44
isabelite				
Pareoues	203	1.2	92.4	28
Umbrosue				
Apogon preudo	178	0.8	93.2	24
Maculatus				
	1/4	0.8	94.0	16

TABLE 5.—Ten most important demersal teleosts by weight in 57 sponge-coral habitat trawl tows taken spring 1978, South Atlantic Bight.

Species	Weight (kg)	% of catch	Cumulative %	No. of occurrences
Stenotomus				· · · · · · · · · · · · · · · · · · ·
aculeatus Haemulon	771.2	42.1		40
aurolineatum Holacanthus	239.5	13.1	55.2	49
isabelita Calamus	167.9	9.2	64.4	28
leucosteus Stephanolepis	135.4	7.4	71.8	44
hispidus Centropristis	93.8	5.1	76.9	52
striata Chromis	61.6	3.4	80.3	37
enchrysurus Rhomboplites	40.0	2.2	82.5	9
aurorubens Calamus	33.7	1.8	84.3	20
nodosus Balistes	26.6	1.4	85.7	11
capriscus	25.7	1.4	87.1	7

The five species of group D were rare in the trawl collections but had their greatest frequency of occurrence in night trawl tows from reef sites in depths >30 m. Members of group E were more abundant than group D and were collected primarily in night samples. They were not, however, restricted to reef sites, since five species (Synodus foetens, Aluterus heudeloti, Scorpaena brasiliensis, Syacium papil-losum, and Ophidion beani) cooccurred in site group 2 (night open-shelf collections). Generally, this group was rarely found in day trawl tows but was widely distributed and abundant in night samples from all sites.

Species group F occurred almost exclusively at night and was most frequently encountered and

abundant at site group 10 (6 night tows at reef 3; 1 night tow at reef 4). Low constancy values were observed for species at site groups 2, 7, 8, 9, and 12, whereas they exhibited high constancy and fidelity values for site group 10.

Group G had seven species that were relatively rare but most frequently found in daytime tows with maximum abundances in site group 7 (11 day samples from 4 reef areas). Group H also contained fishes that were widely distributed among site groups but not very abundant. Highest constancy and fidelity values were in site group 3 where species in group H had maximum abundance and frequency of occurrence.

Although members of species group I were found in several site groups, this assemblage was considered to be a regular component of the deeper reef sites where their greatest frequencies of occurrence and abundance were observed in day tows. Their affinity for deeper reefs is supported by high constancy and fidelity values in site groups 4 (3 day tows at reef 2, depth = 44 m), and moderate constancy and fidelity values in site groups 3 (4 day and 1 night tow at reef 5, depth = 42 m) and 5 (5 day tows at reef 1, depth = 37 m).

Diversity

More species were collected in night trawl tows in both open-shelf and reef habitats than in day tows. Comparisons of the mean number of species per tow in day and night samples at the open-shelf site showed night tows ($\bar{x} = 7.3$) had significantly more species than day tows ($\bar{x} = 3.6$) at the 95% probability level (t = 2.905, df = 9). The same trend was observed for samples from the sponge-coral habitat, pooled by time of collection. The 28 day tows had significantly fewer species ($\bar{x} = 10.8$) than night tows ($\bar{x} = 19.6$) at the 99% level (t = 7.777, df = 55).

Comparisons of the number of species per tow for each time period in the two habitat types showed that mean values for the open-shelf habitat were onethird to one-half the mean values for various reef sites. Night tows in the reef habitat had higher species diversity values than day tows. This was attributed to increased evenness and species richness (Table 6).

DISCUSSION

Standard otter trawl collections in the sponge-coral habitat (inshore and intermediate reefs of Miller and Richards 1979) yielded demersal teleost biomass estimates that were an order of magnitude higher than those of the open shelf (Table 7). Although these



 $\label{eq:FIGURE 4.-Normal analysis (station cluster) of 1978 late spring sponge-coral habitat survey. OS = open shelf; D = day; N = night. Area refers to collection location; see Figure 2.$

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FIGURE 6.—Nodal constancy for station and species groups as defined by cluster analysis for the 1978 late spring sponge-coral habitat survey.

FIGURE 7.—Nodal fidelity for station and species groups as defined by cluster analysis for the 1978 late spring sponge-coral habitat survey.

TABLE 6.—Number of species/tow, diversity, evenness and species richness values for demersal fishes taken spring 1978 in $\frac{3}{4}$ Yankee trawl tows in the open shelf and sponge-coral habitat, South Atlantic Bight, LCL and UCL = lower and upper 90% confidence limits.

	No. of species				Diversity (bits/individuals)	Evenness	Species richness	
Site	Time	LCL	x	UCL	Range	range	range	range
Open shelf	Day	1.9	3.6	5.3	2-7	0.918-2.646	0.918-1.000	0-1.242
Open shelf	Night	5.5	7.3	9.1	4-10	0.443-1.947	0.221-0.586	0.779-2.140
Reef 1	Day	9.0	13.3	17.6	6-22	1.697-3.185	0.380-0.920	1.364-3.143
Reef 1	Night	17.2	20.0	22.8	16-24	2.102-3.667	0.525-0.863	2.867-4.312
Reef 2	Day	3.8	9.2	14.7	5-15	0.383-2.251	0.148-0.394	0.911-2.541
Reef 2	Night	17.4	23.8	30.2	16-28	3.108-3.408	0.677-0.819	3.350-5.175
Reef 3	Day	7.0	9.2	11.4	6-13	0.311-2.119	0.093-0.706	0.894-1.849
Reef 3	Night	18.1	21.8	25.7	16-27	1.494-3.727	0.373-0.817	2.619-4.990
Reef 4	Day	9.1	10.0	10.9	9-12	0.621-2.621	0.196-0.789	1.131-2.324
Reef 4	Night	12.5	15.4	18.3	9-21	2.227-3.171	0.559-0.746	1.923-3.336
Reef 5	Day	6.9	12.5	18.1	8-18	0.131-1.037	0.041-0.345	1.212
Reef 5	Night	_	18.0	_		3.758	0.901	4.465
Reef 6	Day		10.5	_	8-13	1.654-2.515	0.551-0.697	1.467-2.746
Reef 6	Night	16.9	19.5	22.1	15-22	3.063-3.575	0.714-0.827	3.065-4.265

compared closely with values for a reef at a depth of 37 m off the South Carolina coast (Powles and Barans 1980), they were one to two orders of magnitude lower than tropical reef systems (Table 7), with the exception of an estimate of 40.4 kg/ha based on five visual transects at Rabbit Island in Hawaii (Brock 1954). This latter value, however, was indicative of marginal reef habitat, since the estimate was derived from counts taken largely over sandy bottom with an occasional rocky ledge or coral head. Edwards (1968) provided a rationale for obtaining biomass estimates from otter trawl catches for resource surveys in the western North Atlantic. Catches are adjusted on a species-by-species basis using a correction factor which is derived from the individual species' availability and vulnerability to the survey gear. In addition, areal and seasonal changes in the species' distribution pattern are figured into the adjustment. Correction factors are determined from long-term distribution and relative

Area	kg/ha	Citation	Comments
South Atlantic Bight sponge-coral	27.3	Powles and Barans 1980	
South Atlantic Bight sponge-coral	31.0	Present study	
South Atlantic Bight open-shelf	5.6	Wenner et al. 1979a	fail, 1973
South Atlantic Bight open-shelf	5.0	Wenner et al. 1979b	spring, 1974
South Atlantic Bight open-shelf	2.9	Wenner et al. 1979c	summer, 1974
South Atlantic Bight open-shelf	3.2	Wenner et al. 1979d	winter-early spring, 1975
South Atlantic Bight open-shelf	3.2	Present study	
Keahole Point, Hawaii	1,856	Brock 1954	rock, boulders and coral
Waiane, Hawaii	417	Brock 1954	rock, coral and small sand patches
Hilo, Hawaii	214	Brock 1954	rock and coral
Waikiki, Hawaii	195	Brock 1954	some rock and coral, mostly thin sand over rock
Kealekekua Bay, Hawaii	145	Brock 1954	rock and coral with sand
Kumakahi Puna, Hawaii	144	Brock 1954	rock and sand, little coral
Hanauma Bay, Hawaii	154	Brock 1954	sand, rock and coral
Rabbit Island, Hawaii	40	Brock 1954	largely sand; occasional rocky ledge or coral head
Bermuda	490	Bardach 1959	-
Virgin Islands	1,600	Randall 1963	

TABLE 7.—Summary of biomass estimates from South Atlantic Bight sponge-coral and open-shelf habitats and selected tropical reefs.

abundance data, observations from submersibles, underwater television observations of fish and their reactions to trawls, and comparative gear observations. Since we lack the necessary data to compile these values for South Atlantic Bight reef species and, hence, to judge trawl efficiency in sampling this habitat, the estimates of the present study should be considered minimum values. However, some qualitative gear efficiency observations can be made.

Since the ³/₄ Yankee otter trawl net has an average vertical mouth opening of only 1.25 m at a towing speed of 6.5 km/h, it is inefficient in sampling many of the commercially important lutianids and sparids. Although Pagrus pagrus, the most commercially important sparid in the South Atlantic Bight (Ulrich et al. 1976), is a generalized benthic feeder (Manooch 1977), it frequently forms aggregations 2 m off the bottom on intermediate depth reefs. Vermilion, Rhomboplites aurorubens, and red snapper, Lutianus campechanus, often show the same behavior. Although these species are represented in trap collections from various reef sites and are taken with hook-and-line gear, their low relative abundance (with the exception of small R. aurorubens in day trawl tows) can be explained by their unavailability to the net due to their position in the water column.

Comparisons of the dominant species from spongecoral and open-shelf habitat studies in the South Atlantic Bight show that, with one exception, the sparid *Stenotomus aculeatus* is the most numerous trawl-caught demersal teleost. Powles and Barans (1980) cited tomtate, *Haemulon aurolineatum*, as the most abundant fish taken with the ¾ Yankee trawl at a sponge-coral site at a depth of 37 m. *Stenotomus aculeatus* taken in stratified-random otter trawl sampling in the open-shelf habitat were most abundant in depths <28 m (Wenner et al. 1979a, b, c, d). The means of the natural logarithmic values of the number of *S. aculeatus* per tow for each of the sponge-coral habitat sites are negatively correlated with the depth of the site (r = -0.89, n = 7). The numerical dominance of tomtate in the previous trawl study (Powles and Barans 1980) is a reflection of the greater site depth.

The most apparent feature of the species diversity and community analysis is the marked difference between day and night tows. The increased species diversity for night collections is attributed to a greater number of species and a more even distribution of individuals among species. Hoese et al. (1968) reported more species taken in night than day trawl tows in Texas coastal waters and attributed the differences to changes in species availability (movement from the sampling area; vertical movement above the headrope; burrowing into the substrate) or vulnerability (increased daytime net avoidance due to trawl visibility).

Most reef studies using visual census techniques have shown the diversity of fish species to be higher during the day than at night (Collette and Talbot 1972; Goldman and Talbot 1976; Helfman 1978). The results of the present study indicate the opposite to be true. Day trawl tows in the sponge-coral habitat had a lower diversity because these areas lack many of the diurnal species of labrids, scarids, pomacentrids, and acanthurids found in tropical systems. In addition, where night trawl samples contained fish that may be diurnal, the lack of hiding places associated with the luxuriant coral growth in the tropics increased the vulnerability of these fish to night trawl tows, despite the fact they were not actively moving about and feeding. In the present study, certain families were collected more frequently in, or were restricted to, night trawl tows (Table 8). Ophidiids (4 species), sciaenids (3 species), and gadids (2 species) occurred only in night tows. Seven of the 15 most abundant species were taken significantly more frequently in night collections (Table 9). The explanation for these patterns varies according to the species.

The significantly greater frequency of occurrence in night catches of black sea bass, *Centropristis striata*, was caused by this species' increased vulnerability to night trawl tows. Trap and handline collections, as well as underwater television observations, have shown *C. striata* to be much more abundant than was indicated by our otter trawl tows. This supports the findings of Powles and Barans (1980).

Ophidioid fishes of the sponge-coral habitat are nocturnal species that were unavailable to day trawl tows. Starck and Davis (1966) indicated that although cusk eels were abundant in rotenone collections, they were never visually observed moving about reef systems during the day. These investigators found, however, that *Ophidion holbrooki* was active over the sandy portion of a Florida reef at night. When this species was disturbed with lights, it

TABLE 8.—Families of fishes taken primarily in night otter trawl tows in the sponge-coral habitat of the South Atlantic Bight.

	Di	Night		
Family	Present	Absent	Present	Absent
Ophidiidae	0	28	24	5
Scorpaenidae	2	26	16	13
Triglidae	1	27	23	6
Synodontidae	4	24	17	12
Bothidae	5	23	26	3
Sciaenidae	0	28	27	2
Gadidae	0	28	13	16
Batrachoididae	1	27	12	17

TABLE 9.—Comparison of frequency of occurrence of the 15 most numerically abundant species in day and night trawl tows in the sponge-coral habitat, South Atlantic Bight. * = significant at the 95% probability level.

	Daγ	tows	Nig		
Species	Pres- ent	Absent	Pres- ent	Absent	X²
Stenotomus aculeatus	17	11	23	6	1.54
Haemulon aurolineatum	20	8	28	1	5.00°
Chromis enchrysurus	7	21	2	27	0.07
Stephenolepis hispidus	23	5	' 28	1	1.79
Centropristis striate	13	15	24	5	6.73*
Rhomboplites aurorubens	12	16	6	23	2.29
Calamus leucosteus	22	6	22	7	0.01
Holacanthus isabelita	17	11	11	18	1.38
Peregues umbrosus	0	28	11	18	10.83*
Apogon pseudomaculatus	0	28	16	13	18.83*
Prionotus carolinus	0	28	17	12	20.67*
Acanthostracion quadricornis	13	15	13	16	0.00
Ophidion holbrooki	0	28	22	7	31.46*
Porichthys plectrodon	0	28	11	18	10.83*
Chaetodon ocellatus	8	20	6	23	0.07

burrowed tail-first into the sand. Another species (O. selenops) was seen by Starck and Davis (1966) swimming near bottom in night dives at deeper water reef sites. The four species (O. holbrooki, O. beani, O. selenops, Otophidium omostigmum) collected during the present study were taken only in night trawl tows indicating that because of their daytime burrowing behavior, cusk eels are unavailable to day collections.

Atlantic midshipman, *Porichthys plectrodon*, is another nocturnal species that burrows into the sediment during daylight thus making itself unavailable to day trawl tows (Lane 1967). In laboratory tests (Lane 1967), *P. plectrodon* emerged from the substrate 45 min after sunset and burrowed about 45 min to 1 h before sunrise. Nocturnal feeding on nearbottom crustacean plankton was shown (Lane 1967).

Sciaenids (Pareques umbrosus, Equetus lanceolatus, P. acuminatus) were absent from all day samples but occurred in 27 of 29 night tows. Their absence from day collections can more likely be attributed to their unavailability rather than their decreased vulnerability to day trawl tows. Unlike the burrowing ophidioids and Porichthys plectrodon, these secretive sciaenids (Parker et al. 1979) seem to hide around or under available structures. Starck and Davis (1966) reported that Pareques acuminatus hides under rocks on the reef during the day and ventures out to feed at night. Hobson (1965) indicated that the closely related P. viola is a nocturnal foraging fish that hides under ledges and rocks during the day.

The daytime residence of Apogon pseudomaculatus in caves and crevices on the reef (Starck and Davis 1966) effectively excluded this species from the sampling capability of the trawl. The emergence of A. *pseudomaculatus* and other apogonids at night to forage on midwater plankton over the reef (Collette and Talbot 1972) explains the occurrence of this species only in night tows.

Triglids (Prionotus carolinus, P. ophryas, P. scitulus, P. roseus, P. salmonicolor) were found in only a single day tow but were in 23 of 29 night tows. The dominant northern searobin, P. carolinus, is a nocturnal species, however, which would seem to suggest that its greater frequency of occurrence in night trawl tows cannot readily be explained by a concomitant increase in its vulnerability to the gear. Prionotus carolinus is a common member of the South Atlantic Bight open-shelf ichthyofauna in depths from 9 to 55 m (Wenner et al. 1979a). Analysis of stratified, random ¾ Yankee trawl collections from summer 1974 and 1975 and fall 1973 showed that although this species was encountered in more night (53%) than day tows (12%), the frequency of occurrence was not significantly different ($x^2 = 0.18$, df = 108). Based on the percent of fish with stomach contents, Ross (1977) found that peak feeding activity for eight species of searobins (P. carolinus not included) was in the morning. He indicated, however, that these triglids had some food items in the stomach at all times. Bigelow and Schroeder (1953) noted that P. carolinus burrows with only the eyes and head showing, and Bardach and Case (1965) confirmed that this species buries itself in the substrate. The available evidence, then, indicates that P. carolinus is a nocturnally active species that either buries itself in the sandy portions of the sponge-coral habitat during the day or makes nocturnal feeding forays into this habitat from the surrounding sandy areas where it resides during the day. Conclusive evidence can only be obtained from analysis of its food habits as determined from specimens collected in the spongecoral habitat.

Haemulon aurolineatum were taken in significantly more night tows because dense day-resting schools dissociate at night when this species disperses to feed. It is well documented that grunts form resting schools on various reefs during the day (Starck and Davis 1966; Collette and Talbot 1972; Hobson 1973; Ebeling and Bray 1976; Ogden and Ehrlich 1977). At dusk, members of the school become active and undertake feeding migrations into areas near the reef which may have sandy bottom or algal cover. The dispersal of H. aurolineatum from dense daytime schools is reflected in the present study by changes in Morisita's index of dispersion (Elliott 1977) for day and night trawl tows. The index equals 1 for a random distribution, >1 for a contagious distribution, and <1 for a regular distribution (Elliott 1977). Day trawl tows had an index of dispersion of 5.51 which indicates a highly significant contagious distribution of H. aurolineatum. Night collections also had a significant contagious distribution, but the value of the index was much lower (1.44). By comparing both Morisita's index and the frequency of occurrence of H. aurolineatum in day and night tows, it can be inferred that tomtate disperse over the habitat during the night hours. In addition, the occurrence of tomtate in three of six night tows in the open-shelf study area provided evidence that the species leaves the sponge-coral habitat at night.

Although Stenotomus aculeatus occurred more frequently in night tows (79%) than in day tows (39%), the results were not significantly different. Southern porgy are daytime feeders (Harris 1979) which, as indicated by trawl results, form relatively large schools. The index of dispersion showed significant contagion in both day ($I_{\delta} = 4.14$) and night tows ($I_{\delta} = 2.43$); however, the lower night values indicate that the cohesiveness of the schools decreases at night. As a result of the greater nocturnal dispersal of this species throughout the sponge-coral habitat, the frequency of its occurrence in trawl tows increases. This accounts for the more consistent but lower catch rate at night, in comparison with day catches.

Stephanolepis hispidus showed the same pattern as Stenotomus aculeatus in its distribution and abundance in sponge-coral habitat tows. Planehead filefish were more aggregated during the day $(I_{\delta} =$ 3.99) than at night $(I_{\delta} = 1.96)$ and had a slightly higher frequency of occurrence in night trawl tows (97%) than in day collections, although the difference was statistically insignificant.

In addition to the species discussed above, several other less abundant fishes showed increased availability to night trawl tows in the sponge-coral habitat. The gadid Urophycis earlli was found only in night collections. Parker et al. (1979) reported U. earlli to be a secretive species that hid in and under artificial reef structures off the South Carolina coast. Daytime observations in winter revealed hundreds of Carolina hake under reef material (see Parker et al. 1979, fig. 10). Data from historical surveys indicate that U. earlli is a nocturnal species since almost all specimens collected by traps, handlines, and trawls were taken at night in the sponge-coral habitat or the rugged areas of the shelf-break (Wenner, unpubl. data). During the day, U. earlli probably hides under small ledges where it is unavailable to the trawl gear.

Carapus bermudensis is a nocturnal species that was unavailable to day otter trawl tows. This species spends its day residing in the respiratory tree of several species of holothurians and emerges at night to feed on near-bottom plankton (Starck and Davis 1966; Smith et al. 1981). Most bothids were encountered in night tows, probably due to these species' increased vulnerability at night.

In summary, day otter trawl catches were more variable in numerical abundance but frequently weighed more than night catches. This was due to the dense schools formed during daylight by species such as *Haemulon aurolineatum* and *Stenotomus aculeatus*. Night tows had more species because of the nocturnal availability of such species as *Apogon pseudo*maculatus, Carapus bermudensis, the ophidioids, etc., as well as the increased vulnerability of diurnal species such as *Holacanthus isabilita* and *Chromis* enchrysurus.

Comments on Use of Otter Trawl Nets in Sponge-Coral Habitat Surveys

Demersal trawl surveys are conducted in the northeast region of the United States to determine the species composition, distribution, and relative abundance of finfish, squids, and decapod crustaceans (Grosslein 1969). This survey has been designed so that the investigators can use some aspect of the catch per unit effort from research vessels to obtain an index of relative abundance for some groundfish stocks. This index, with appropriate adjustments, can be used (see Clark and Brown 1977) to derive regional stock-size estimates independent of the commercial catch. These, in turn, can be utilized for management decisions. In addition, some indication of the abundance of prerecruits can be obtained from the juveniles retained in the small mesh cod end liner of most research survey nets.

Although trawl gear can determine the size and relative abundance of many species that are available and vulnerable to the gear, its use to assess commercially harvested species of the sponge-coral habitat is suspect for the following reasons. First, as previously indicated, most commercially important lutjanids, sparids, and serranids are adept at avoiding the survey gear. High rise nets (otter trawls with greater vertical mouth openings) are more efficient in obtaining representative samples of these fishes, but sweptarea estimates of the density of these species are unreliable. Most sponge-coral habitats have sections of small rock outcroppings and ledges where epinepheline serranids, lutjanids, and sparids aggregate. Because of possible gear destruction due to the high relief, these areas are untrawlable and catches in the remainder of the habitat show these species to be either absent or of minor importance. Trap and handline collections in untrawlable areas of this habitat document the localized abundance of these animals and indicate the importance of these species to the fish community.

Second, even with cod end liners, the ¾ Yankee and high-rise roller trawl nets fail to give indications of the abundance of prerecruits (Wenner unpubl. data). Available data indicate that the juveniles of epinepheline serranids are either spatially separated from the adults (*Mycteroperca microplepis*) or are cryptic forms which hide in cracks and crevices in this habitat (Johnson⁵). Juvenile *Rhomboplites auro*- *rubens* are available and vulnerable to the gear during late summer months on 30-40 m sampling sites. This is the only species of the commercially important complex that is taken with any regularity.

Thus, otter trawl gear is neither effective in predicting recruitment of most commercially important species, nor reliable in providing accurate abundance estimates of these species. In addition, the physical habitat may sustain considerable damage caused by the bottom trawl net.

The ¾ Yankee trawl net effectively covers a much wider area of the bottom than the measured sweep (8.7 m) due to the configuration of the otter doors, ground cables, and bottom leg lines. Although this arrangement cannot increase the actual spread of the net beyond the headrope length, the passage of these cables over the substrate creates a disturbance that serves to herd fish in the path of the net (Baranov 1969). This net does, however, damage the spongecoral habitat by shearing off sponges, soft corals, bryozoans, and other attached invertebrates. The 56 trawl tows made in the sponge-coral habitat for this study collected 2,351 kg of attached invertebrates (including sponges, soft corals, tunicates, bryozoans. and hydroids) yielding an average 42 kg/tow. This is only the amount of bottom material actually removed from the habitat. An estimate of the total amount of bottom destroyed by the doors, ground cables, and leg lines cannot be ascertained from the current study.

Personal observations and interviews with commercial fishermen attest to the productivity of the sponge-coral habitat. Most studies indicate the importance of habitat availability and space in determining the abundance and diversity of reef fishes (Emery 1978). With this in mind, and given the knowledge that 1) the use of the ¾ Yankee trawl net reduces the amount of attached invertebrate growth (the amount damaged by doors and ground cables is presently not quantifiable); 2) the places where the invertebrates had been attached may be sanded over and rendered unsuitable for recolonization; and 3) the removal of these attached invertebrates reduces refugees for decapods, polychaetes, etc., that are food items for Centropristis striata and other benthic feeders, one must conclude that the continued use of this trawl net reduces the amount of productive fish habitat. For these reasons, in addition to the ineffectiveness of the gear in sampling commercially important species, alternate nondestructive methods, such as direct observations or the use of mark-recapture techniques with trap catches, should be employed in assessment surveys of the commercially important species of this habitat.

³G. David Johnson, South Carolina Wildlife and Marine Resources Dept., P.O. Box 12559, Charleston, SC 29412, pers. commun., 1981.

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LITERATURE CITED

BARANOV, F. I.

- 1969. Selected works on fishing gear. In P. Greenberg (editor), Commercial fishing techniques, Vol. I, p. 1-631. Israel Program for Scientific Translations; (translated from Russian by E. Vilim).
- BARDACH, J. E.
 - 1959. The summer standing crop of fish on a shallow Bermuda reef. Limnol, Oceanogr. 4:77-85.
- BARDACH, J. E., AND J. CASE.
 - 1965. Sensory capabilities of the modified fins of squirrel hake (Urophycis chuss) and searobins (Prionotus carolinus and P. evolans). Copeia 1965:194-206.

BIGELOW, H. B., AND W. C. SCHROEDER.

1953. Fishes of the Gulf of Maine. U.S. Fish and Wildl. Serv., Fish. Bull. 53, 577 p.

BLISS, C. I.

1967. Statistics in biology. Statistical methods for research in the natural sciences, Vol. I. McGraw-Hill, N.Y., 558 p.

BLOOM, S. A.

1981. Similarity indices in community studies: Potential pitfalls. Mar. Ecol. Prog. Ser. 5:125-128.

BOESCH, D. F.

1977. Application of numerical classification in ecological investigations of water pollution. Ecological Research Series, EPA-600/3-77-033, Corvallis, Oreg., 114 p.

BROCK, V. E.

1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:297-308.

CLARK, S. H., AND B. E. BROWN.

1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish. Bull., U.S. 75:1-21.

CLIFFORD, H. T., AND W. STEPHENSON.

1975. An introduction to numerical classification. Acad. Press, N.Y., 229 p.

COLLETTE, B. B., AND F. H. TALBOT.

1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. In B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 98-124. Nat. Hist. Mus., Los. Ang. Cty. Sci. Bull. 14.

EBELING, A. W., AND R. N. BRAY.

1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull., U.S. 74:703-717.

- EDWARDS, R. L.
 - 1968. Fishery resources of the North Atlantic area. In D. Gilbert (editor), The future of the fishing industry of the United States, p. 52-60. Univ. Wash. Publ. Fish, New Ser. 4.

Elliott, J. M.

1977. Some methods for the statistical analysis of samples of benthic invertebrates. 2d ed. Freshw. Biol. Assoc., Sci. Publ. 25, 160 p.

EMERY, A. R.

1978. The basis of fish community structure: marine and freshwater comparisons. Environ. Biol. Fishes 3:33-47. GOLDMAN, B., AND F. H. TALBOT.

1976. Aspects of the ecology of coral reef fishes. In O. A. Jones and R. Endean (editors), Biology and geology of coral reefs, Vol. 3 (Biol 2), p. 125-154. Acad. Press, N.Y.

GROSSLEIN, M. D.

1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

HARRIS, C. A.

- 1979. Resource partitioning in four species of reef fishes in Onslow Bay, North Carolina. M.S. Thesis, East Carolina University, Greenville, N.C., 35 p.
- HELFMAN, G. S.

1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fishes 3:129-148.

- HOBSON, E. S.
 - 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
 - 1973. Diel feeding migrations in tropical reef fishes. Helgol. wiss. Meeresunters. 24:361-370.
- HOESE, H. D., B. J. COPELAND, F. N. MOSELEY, AND E. D. LANE. 1968. Fauna of the Aransas Pass Inlet, Texas. III. Diel and seasonal variations in trawlable organisms of the adjacent area. Tex. J. Sci. 20:33-60.

HUNTSMAN, G. R., AND C. S. MANOOCH, III.

1978. Coastal pelagic and reef fishes in the South Atlantic Bight. In H. Clepper (editor), Marine recreational fisheries, No. 3, p. 97-106. Proc. 2d Ann. Mar. Rec. Fish. Symp., Norfolk, Va., Sport Fish Inst., Wash., D.C.

LANE, E. D.

1967. A study of the Atlantic midshipmen, *Porichthys* porosissimus, in the vicinity of Port Aransas, Texas. Contrib. Mar. Sci. 12:1-53.

MANOOCH, C. S., III.

1977. Foods of the red porgy, Pagrus pagrus Linnaeus (Pisces: Sparidae), from North Carolina and South Carolina. Bull. Mar. Sci. 27:776-787.

MARGALEF, R.

1968. Perspectives in ecological theory. Univ. Chicago Press, Chicago, 111 p.

MATHEWS, T. D., AND O. PASHUK.

1977. A description of oceanographic conditions off the southeastern United States during 1973. S.C. Mar. Resour. Cent. Tech. Rep. 19, 112 p.

- MILLER, G. C., AND W. J. RICHARDS.
 - 1979. Reef fish habitat, faunal assemblages and factors determining distributions in the South Atlantic Bight.

Proc. Gulf Caribb. Fish. Inst. 32:114-130.

- OGDEN, J. C., AND P. R. EHRLICH.
 - 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar. Biol. (Berl.) 42:273-280.
- PARKER, R. O., JR., R. B. STONE, AND C. C. BUCHANAN.
 - 1979. Artificial reefs off Murrells Inlet, South Carolina. Mar. Fish. Rev. 41(9):12-24.
- PIELOU, E. C.
 - 1969. An introduction to mathematical ecology. Wiley-Interscience, N.Y., 286 p.
- POWLES, H., AND C. A. BARANS.
- 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42(5):21-35.
- RANDALL, J. E.
 - 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3:31-47.
- ROHR, B. A., AND E. J. GUTHERZ.
 - 1977. Biology of the offshore hake, *Merluccius albidus*, in the Gulf of Mexico. Fish. Bull, U.S. 75:147-158.
- Ross, S. T.
 - 1977. Patterns of resource partitioning in searobins (Pisces: Triglidae). Copeia 1977:561-571.
- SMITH, C. L., J. C. TYLER, AND M. N. FEINBERG.
 - 1981. Population ecology and biology of the pearlfish (*Carapus bermudensis*) in the lagoon at Bimini, Bahamas. Bull. Mar. Sci. 31:876-902.
- STARCK, W. A., II, AND W. P. DAVIS.
 - 1966. Night habits of fishes of Alligator Reef, Florida. Ichthyol. Aquarium J. 38:313-356.

STRUHSAKER, P.

- 1969. Demersal fish resources: Composition, distribution, and commercial potential of the continental shelf stocks off southeastern United States. U.S. Fish. Wildl. Serv., Fish. Ind. Res. 4:261-300.
- Taylor, C. C.
 - 1953. Nature of variability in trawl catches. U.S. Fish Wildl. Serv., Fish. Bull. 54:145-166.

ULRICH, G. F., R. J. RHODES, AND K. J. ROBERTS.

- 1976. Status report on the commercial snapper-grouper fisheries off South Carolina. Gulf Caribb. Fish. Inst., Proc. 29th Annu. Sess., p. 102-125.
- WENNER, C. A., C. A. BARANS, B. W. STENDER, AND F. H. BERRY. 1979a. Results of MARMAP otter trawl investigations in the South Atlantic Bight. I. Fall, 1973. S.C. Mar. Resour. Cent. Tech. Rep. 33, 79 p.
 - 1979b. Results of MARMAP otter trawl investigations in the South Atlantic Bight. II. Spring, 1974. S.C. Mar. Resour. Cent. Tech. Rep. 40, 78 p.
 - 1979c. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. S.C. Mar. Resour. Cent. Tech. Rep. 41, 62 p.
 - 1979d. Results of MARMAP otter trawl investigations in the South Atlantic Bight. IV. Winter-early spring, 1975. S.C. Mar. Resour. Cent. Tech. Rep. 44, 59 p.
- WILK, S. J., AND M. J. SILVERMAN.
 - 1976. Fish and hydrographic collections made by the research vessels *Dolphin* and *Delaware II* during 1968-72 from New York to Florida. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-697, 159 p.