

Abstract.—Videotapes of the sea floor were taken from a submersible during dives at two areas on the continental slope off Cape Hatteras and Cape Lookout, North Carolina, in September 1989. We counted demersal nekton, epifauna, and environmental features for 1-minute intervals from video transects. Common morphospecies of demersal nekton were identified, and multivariate analyses were performed to find environmental features that related to habitat use by these forms. In both areas, the ocean floor was extensively sculptured with holes and mounds, and both small and large sea anemones were commonly observed. Crinoids were seen in Cape Hatteras dives. Small sea anemones were much more abundant off Cape Hatteras, whereas holes and mounds were more densely distributed off Cape Lookout. Rattails, hake, and sergestid shrimp were common at both locations. Eels were extremely abundant at the Cape Lookout site, whereas eelpouts, flounder, and lizardfish were found only at the Cape Hatteras location. At both locations, analyses of nekton habitat choices showed that habitat selection was related to density of the holes and mounds made by infauna and to density of the epifauna, such as crinoids and the different types of anemones. Hake, squid, sergestid shrimp, and lizardfish showed the strongest evidence of habitat selection. Analysis of videotapes, originally recorded for other purposes, is a cost-effective means for preliminary examination of the problems that may only be addressed by in situ observations.

Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles

James D. Felley

Office of Information Resource Management, Room 2310
A&I Building, Smithsonian Institution, Washington, D.C. 20560

Michael Vecchione

National Marine Fisheries Service Systematics Laboratory
National Museum of Natural History, Washington, D.C. 20560

Understanding of the ecology of the deep ocean floor has improved substantially since underwater cameras have begun recording life at depths beyond which divers may penetrate. Recently, nekton communities on the shelf and slope have been studied by means of underwater cameras carried by remotely operated vehicles (ROV's) and occupied submersibles. Such studies have included analyses of environmental features (Hecker, 1990b; Levin et al., 1991), spatial distribution of individual species (Vecchione and Gaston, 1986; Wenner and Barans, 1990; Schneider and Haedrich, 1991), and patterns of habitat use by species assemblages (Richards, 1986; Felley et al., 1989; Auster et al., 1991; Carey et al., 1990). Underwater cameras have allowed questions to be addressed that are intractable to conventional sampling methods (Haedrich and Gagnon, 1991). Though problems with accurate identification of species and habitat variables are inherent to these studies, such studies open an important window to poorly known ecosystems.

We used archived videotapes recorded by the submersible *Johnson Sea-Link* to investigate patterns of habitat use by demersal and benthopelagic nekton on the continental slope off Cape Hatteras and Cape Lookout, North Carolina. From the

videotapes, we identified and counted nekton species, and quantified selected environmental variables discernible from video images. Using these environmental variables, we identified the habitat where each species was most likely to be found. We used factor analysis to identify patterns of habitat use among the species (Felley and Felley, 1987; Felley et al., 1989) and to determine which environmental variables seemed most important in structuring the nekton assemblage of the continental slope off North Carolina. We then compared distributional variances of environment and species occurrence to identify those species selecting subsets of available habitats.

Materials and methods

Video recording

Video transects were recorded during dives by the *Johnson Sea-Link II* submersible from the RV *Edwin Link*. Table 1 summarizes latitudes and longitudes, dates, and dive times. These data and videotapes are from NOAA's National Undersea Research Center at the University of North Carolina at Wilmington. Time starting and time ending are the beginning and ending points of the videotape section that we

Table 1

Information on dives at Cape Hatteras and Cape Lookout, North Carolina, from which videotapes were used for analysis of demersal nekton habitat use. "Dive no." is the identification number we used to request the tapes. "Start time" and "End time" are the beginning and ending points on the videotape section used in the analyses (not the launch and recovery times of the dives). Depths are in m.

Dive no.	Date 1989	Latitude °N	Longitude °W	Start time (HH:MM)	End time (HH:MM)	Start depth	End depth
Cape Hatteras							
2623	14 Oct	35°23'	74°50'	15:37	18:11	853	853
2627	16 Oct	35°38'	74°48'	8:52	10:01	782	573
2629	17 Oct	35°23'	74°51'	7:29	8:24	610	549
2630	17 Oct	35°29'	74°48'	13:16	13:43	511	420
Cape Lookout							
2619	12 Oct	34°15'	75°45'	13:40	14:47	903	853
2620	13 Oct	34°14'	75°45'	9:00	9:07	945	843
2621	13 Oct	34°14'	75°46'	16:31	18:28	793	843

used in the analyses (not the launch and recovery times of the dives). The videotapes were recorded as the submersible cruised along the bottom, generally at a speed of 0.5–1 knot (ca. 25–50 cm/sec). The camera faced forward and down and was not panned or moved during the recording of videotape sections used for analysis. At times the submersible stopped to deploy experiments or pick up samples and at other times moved away from the bottom. We recorded data from video images only during periods when the submersible was moving and the bottom was clearly visible. During these periods, we quantified environmental variables and counted individuals of nekton species during 1-minute intervals. If the submersible stopped or moved away from the bottom during an interval, that interval was discarded. We did not start measuring again until the submersible began moving steadily and the bottom was clearly visible. The bottom topography at the Cape Hatteras site was extremely complex, with gullies, walls, and flat expanses. Only videotapes of flat areas were used for the analysis. The videotapes of Cape Lookout dives included only broad expanses of flat slope.

Environmental variables recorded are listed in Table 2 and included holes, mounds, and tubes. Holes and mounds are indicators of infaunal activity. Holes were generally 1–3 cm in diameter and mounds generally >10 cm in diameter. Tubes were 5–10 cm in length and most often curved, sometimes with both ends touching the substrate. Objects classified as tubes were identified (Schaff¹) as those of polycha-

etes and foraminifera (*Bathysiphon* spp.). Further characterization of sediment samples from these dives can be found in Levin (1991) and Gooday et al. (1992). Holes, mounds, and tubes were coded as follows: 0 = none visible during the whole interval; 1 = no more than a total of 1 or 2 visible during the whole interval; 2 = 1 or 2 visible at all times during the interval; 3 = several always visible at any time in the interval, but countable; 4 = too many to count in the interval. Category 4 coded those situations where the environmental feature was so densely distributed that individual features were obscured by others nearer the camera. Other coded variables were gastropod/echinoderm tracks (grooves in the substrate), sea grass detritus/*Hyalinoecia* tubes, and sargassum detritus. These were coded 1 or 0 for presence or absence in the interval; e.g. a value of 1 was assigned to the interval whenever one or more tracks were observed. Long thin dark objects that appeared to be bits of sea grass detritus might also include tubes of the polychaete *Hyalinoecia* (Schaff²). Such objects are referred to as "grass detritus" in this study. Finally, we counted raw numbers of small anemones, large anemones, gastropods, and crinoids. Small anemones probably represented *Actinauge verrilli* and large anemones may be *Bolocera* sp. (Levin³). Gage and Tyler (1991) give excellent descriptions of epifaunal and infaunal organisms and benthic features similar to those listed above.

¹ Schaff, T. Natl. Mar. Fish. Serv., Silver Spring, MD. Personal commun., 1992.

² Schaff, T. Natl. Mar. Fish. Serv., Silver Spring, MD. Personal commun., 1993.

³ Levin, L. Scripps Institution of Oceanography, La Jolla, CA. Personal commun., 1992.

Numbers of individuals of selected demersal nekton species were also recorded for each 1-minute interval. This provided a consistent estimate of relative abundance. Nekton included fishes, cephalopods, and macrocrustacea. As no voucher specimens were collected, identifications were made visually with the assistance of specialists familiar with the groups (noted below in the Results section). Most of these forms could be confidently identified only to genus from the videotapes.

Data analysis

Data from dives at Cape Hatteras and at Cape Lookout were analyzed separately. Cape Hatteras dives spanned a depth range that included two faunal zones (upper and middle slope) identified by Haedrich et al. (1980) and Wenner and Boesch (1979). In general, these authors found differences between continental slope communities above 700 meters and those below. Thus, Cape Hatteras dives 2629 and 2630 (Table 1) were conducted on the upper slope, whereas dive 2623 was conducted on the middle slope. Dive 2627 crossed the boundary identified by Haedrich et al. (1980). All Cape Lookout dives were conducted on the middle slope. Depth was not included as a variable in the statistical analyses detailed below, because it was not recorded for each 1-minute videotape segment. Potential effects of biotic zonation were investigated separately by comparison of species distribution with dive depth.

Statistical analysis of habitat choice by the identified nekton followed Felley and Felley (1986, 1987) and Felley et al. (1989). All statistical analyses were conducted with the SAS program (SAS Institute, 1988). The steps in the analysis were as follows: 1) calculation of species' mean abundances for environmental variables; 2) calculation of a correlation matrix among species' mean abundances; 3) factor analysis of the correlation matrix; 4) comparison of variances of sampling units and of numbers of individuals of a species on the artificial variables (factors) generated by the factor analysis. These steps were accomplished as follows.

First, we calculated means of environmental variables for each species as each variable's mean over 1-minute intervals, weighted by the number of individuals of that species seen in each interval. Thus, a species' mean abundance for a variable represented the value of that environmental variable in intervals where the species was most likely to be found. The species' mean abundance was considered the species "preference" for the variable, assuming that these nektonic species select their habitat.

Second, species' mean abundances for the environmental variables were used to construct a correla-

tion matrix among the variables. Note that this correlation matrix implies standardizing each variable using a "mean of means" and a "standard deviation of means." A high correlation between two variables is seen when species tend to occur in habitats with contrasting values for both of these variables. For example, an analysis might include some species found typically in shallow gravel areas and some preferring deep sandy areas. This analysis would generate a high correlation between such environmental variables as depth and substrate particle size. Thus, patterns of habitat use by species are reflected in patterns of interrelations among the variables. This is an analysis of species associations with particular environments, and the data contain no information about why a particular species is occurring more often in one habitat type than another.

Third, factor analysis (principal component analysis with Varimax rotation, Mulaik, 1972) was performed on the correlation matrix. Factor analysis resolves patterns of interrelationships among variables into a smaller set of composite variables (factors) to which observed variables (species mean abundances) are correlated. Sets of interrelated variables correlating highly with a factor are variables reflecting similar patterns of habitat use among the species. Each factor represents a particular trend in habitat use, an axis differentiating among sets of species that are likely to be found in habitats with contrasting conditions for the variables that define the factor. The example above might produce a factor defined by depth and substrate particle size.

Species' values, or scores, for a factor can be calculated by using a factor scoring function. Species with contrasting scores are those found most often in contrasting environments relative to that factor. To continue the example, species more likely to be found in deep water over sandy substrate would have factor scores that contrasted with those of species more often found in shallow water over coarse substrates (i.e. positive vs. negative scores on the factor). Species with intermediate scores may be characteristic of intermediate environments on that factor, or they may be found over the entire range of environments reflected by a factor (because the species' score is the weighted mean of scores of intervals where it was found).

Note that only a subset of the species analyzed in the example may in fact select habitat based on environmental variables related to depth and substrate. Though a trend in habitat use may be identified for a species assemblage, not all species in the assemblage may select habitat according to that trend. Further analysis is required to determine which species show evidence of active selection according to a particular habitat trend.

Fourth, we investigated habitat selection by individual species by comparing species' variances on each factor with variance of the environment. Environmental variance on a factor was determined by calculating factor scores for each 1-minute interval. First, the value for each environmental variable in a 1-minute interval was standardized by using the appropriate "mean of means" and "standard deviation of means" noted above. Then the scoring function was applied to each 1-minute sampling unit. Environmental variance was then determined as the variance of sampling unit scores. The score of a 1-minute interval was assigned to all individuals of all species seen in the interval. A species' variance was then calculated for each species as the variance of these scores. The procedure of investigating both species and locality scores on multivariate axes corresponds to Rotenberry and Wiens⁴ "synthetic approach" to the study of communities.

We compared a species' variance with environmental variance for each factor by using Levene's test (Levene, 1960; Van Valen, 1978). Bonferroni corrections for multiple statistical tests were made by using Rice's (1989) method for investigating tables of statistical test results. Rice's method is a correction for inflated type-I error in situations where several

different tests of significance are made for a particular null hypothesis. Such a series of tests constitute a "table of statistical tests." In this study, a "table" was considered to be all significance tests made relative to a factor, the corresponding null hypothesis being "species variances are not significantly different from environmental variance with respect to this factor." Active habitat selection by a species was inferred when a species' variance was significantly smaller than the observed environmental variance (1-tailed test). This implies that the species was actively selecting a subset of the available environment with respect to that factor. See Felley and Felley (1987) and Felley et al. (1989) for more details.

Results

Environments and biota

Cape Hatteras—Table 2 presents means of environmental variables for flat areas traversed by dives on the slope off Cape Hatteras. Holes and mounds were common environmental features: one to several holes and mounds were in view at almost all times. In general, intervals where holes were dense also had a large number of mounds. Tubes were variable in occurrence. Many were seen in dive 2627 but relatively few were seen in dives 2629 and 2630. Grass detritus was very common in dives 2627, 2629, and 2630, occurring in almost every interval. Sargassum detritus was infrequent in upper slope intervals (dives

⁴ Rotenberry, J. T., and J. A. Wiens. 1981. A synthetic approach to principal component analysis of bird/habitat relationships. In D. E. Capen (ed.), *The use of multivariate statistics in studies of wildlife habitat*, p. 197-208. USDA Forest Serv. Gen. Tech. Rep. RM-87, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Table 2

Environmental variables measured on each interval, with means and standard deviations (in parentheses) for each dive at Cape Hatteras and Cape Lookout, North Carolina. Holes, mounds, and tubes were coded as follows: 0=none in the interval; 1=no more than 1 or 2 seen in an interval; 2=always 1 or 2 visible throughout an interval; 3=several always visible, but countable; and 4=too many visible to count. Gastropod/echinoderm tracks, and grass and sargassum detritus were coded 1/0 for presence/absence in the interval (only percentages are reported for these variables). Number of individuals were counted for small anemones, large anemones, gastropods, and crinoids.

	N	Environmental variables									
		Holes	Mounds	Tubes	Tracks	Grass detritus	Sargassum detritus	Small anemones	Large anemones	Crinoids	Gastropods
Cape Hatteras											
2623	61	1.75 (0.830)	1.36 (0.484)	2.41 (1.321)	100.0	47.5	18.0	6.87 (6.711)	0.03 (0.180)	5.90 (15.367)	0.31 (0.564)
2627	35	2.63 (0.490)	1.66 (0.482)	2.23 (0.942)	45.7	88.6	8.6	25.80 (19.954)	0.17 (0.382)	0.00 (—)	0.40 (0.976)
2629	41	2.51 (0.506)	1.78 (0.571)	0.73 (0.633)	85.4	82.9	4.9	1.37 (1.577)	4.63 (3.006)	4.66 (13.190)	0.27 (0.449)
2630	7	2.29 (0.756)	1.14 (0.378)	0.57 (0.535)	14.3	100.0	0.0	0.00 (—)	0.00 (—)	0.00 (—)	0.00 (—)
Cape Lookout											
2619	36	3.36 (0.529)	2.22 (0.485)	0.25 (0.439)	16.7	69.4	38.9	0.33 (0.676)	0.53 (0.629)	0.00 (—)	0.03 (0.167)
2620	7	3.28 (0.488)	2.14 (0.378)	0.00 (—)	28.6	14.3	28.6	0.14 (0.378)	0.43 (0.534)	0.00 (—)	0.00 (—)
2621	32	3.25 (0.440)	2.25 (0.508)	0.25 (0.440)	53.1	62.5	40.6	0.41 (0.560)	0.44 (0.619)	0.00 (—)	0.00 (—)

2627, 2629, 2630), but was more common at the middle slope site (dive 2623).

Anemones, echinoderms, gastropods, and invertebrate tracks were common. Epifaunal forms tended to occur in patches. Coefficients of dispersion (CD, Sokal and Rohlf, 1981) were calculated for small anemones, large anemones, crinoids, and gastropods (data in Table 2). Coefficients of dispersion much greater than 1 (indicating clumped distribution patterns) were found for small anemones in all Cape Hatteras dives where they were observed. Small anemones were very abundant in dive 2627. For 15 minutes, the submersible traversed a dense aggregation where numbers ranged from 30 to 80 individuals per interval. Small anemones were also common (though not as densely distributed) in dive 2629. Large anemones were seen regularly and were relatively dense in dive 2629 (up to 12 in an interval). Large anemones had a clumped distribution in this dive, indicated by a high CD value. Coefficients of dispersion were very high for crinoids. A dense patch of crinoids appeared in dive 2629, with 4 to 62 individuals per interval for 6 consecutive intervals. Another area of dense crinoids appeared in dive 2623, with 7–70 individuals per interval in 10 consecutive intervals. In dive 2630, an extremely dense patch of ophiuroids appeared over 4 consecutive intervals (ophiuroids were not included in the statistical analysis as they were seen in so few intervals).

Cape Lookout—Holes and mounds were very dense; holes were, in fact, too dense to count during some portions of dives 2619 and 2621. As at Cape Hatteras,

intervals with high numbers of holes also had large numbers of mounds. Tubes were rarely observed and were not seen in dive 2620. Grass detritus was commonly seen but was not as frequent as at Cape Hatteras. Conversely, sargassum detritus was quite frequent, occurring in 39–41% of Cape Lookout intervals. Epifaunal species were not abundant and were not patchily distributed. Small anemones were not common (fewer than one per interval) and were less abundant than large anemones. No crinoids were seen in the Cape Lookout dives.

Demersal nekton species

Many nektonic species were observed on the tapes, but only a few appeared in abundance. These were the species included in analysis of habitat preferences. As no voucher specimens were obtained, identifications were assigned on the basis of species known to be common in the area, after consultations with taxonomic experts (listed in the Acknowledgments section). Table 3 lists the species included in analyses of habitat choice and their mean numbers in particular dives.

The eel (*Synaphobranchus* sp.; Smith⁵), though rare at Cape Hatteras, was the most abundant form at Cape Lookout. This genus forms an important part of the middle-slope fauna (Markle and Musick, 1974; Haedrich et al., 1980; Sulak⁶). Eels were always ob-

⁵ Smith, D. G. National Museum of Natural History, Washington, D.C. Personal commun., 1992.

⁶ Sulak, K. Atlantic Reference Centre, Huntsman Marine Science Centre, New Brunswick, Canada. Personal commun., 1990.

Table 3

Common demersal nekton species identified in upper slope and middle slope dives, North Carolina, and average numbers of individuals per 1-minute interval seen in each dive (number of intervals are given in Table 2). See text for discussion of the probable identities of these forms and scientific names.

Species	Cape Hatteras dives				Cape Lookout dives		
	2627	2629	2630	2623	2619	2620	2621
Eel	—	0.02	—	0.10	2.17	2.71	1.75
Rattail	2.60	1.12	0.29	1.69	0.61	0.57	0.78
Longfin hake	0.43	0.66	0.57	0.54	0.22	0.14	0.25
Scorpaenid	4.26	0.07	0.57	1.20	—	—	0.03
Lizardfish	0.03	0.34	—	0.02	—	—	—
Eelpout	12.43	5.83	1.43	5.43	—	—	—
Flounder	2.14	1.90	0.86	1.25	—	—	—
Species A	—	0.15	—	—	—	—	—
Sergestid shrimp	0.17	0.59	0.86	0.25	0.11	0.29	0.72
Shrimp	0.09	0.02	—	0.07	0.03	—	0.03
Red deepsea crab	—	—	—	0.02	0.06	0.14	0.16
Cancroid crab	—	0.07	0.56	—	0.03	0.14	0.03
Shortfin squid	0.06	0.20	—	0.56	—	—	0.22
Octopod	0.03	0.05	—	0.03	—	—	0.06

served swimming slowly slightly above the bottom, maintaining position with low amplitude tail-beats.

Individuals identified as rattails represented either *Nezumia bairdi*, *N. aequalis* (Sulak⁶), or *Coryphaenoides rupestris*, the three species most commonly encountered in the depth range of these dives (Markle and Musick, 1974; Haedrich et al., 1980; Middleton and Musick, 1986). Rattails were common in all dives and were seen both lying on the bottom and maintaining position off the bottom by swimming slowly (with low amplitude tail-beats).

The hake commonly observed in the tapes was the longfin hake, *Urophycis chesteri*, a common species on the continental slope of the western North Atlantic (Markle and Musick, 1974; Haedrich et al., 1980; Wenner, 1983; Sulak⁶). Hakes were observed in every dive, normally lying on the bottom. Quite often they were found in depressions, their bodies in a circular or semicircular posture.

Scorpaenids were observed in all Cape Hatteras dives but only in dive 2621 at Cape Lookout. The species represented may be *Helicolenus dactylopterus* (Sulak⁶). At Cape Hatteras, they were abundant in both the upper slope (e.g. dive 2627) and the middle slope (dive 2623). When seen, they were always lying on the bottom, their bodies often in a semicircular posture.

Lizardfish were seen only on the upper slope, most notably in dive 2629, where 14 individuals were observed. These may represent *Saurida brasiliensis* or *S. normani* (Sulak⁶).

Several different eelpouts were likely present on these tapes, including *Lycenchelys verrillii* and *Lycodes atlanticus* (Sulak⁶). *Lycenchelys paxillus* is a more northerly species (Markle and Musick, 1974) but may occur on the North Carolina slope. Eelpouts were the most abundant fish at Cape Hatteras, in all dives, but were not seen at Cape Lookout. Individuals tended to be small (<15 cm), with dark blotches, and lay in sinusoidal posture, usually near objects on the bottom (most often small anemones).

Small flounders were seen in all dives at Cape Hatteras but were not found at Cape Lookout. There were most likely several species represented, including *Glyptocephalus cynoglossus*. This species is an important component of the slope fauna (Markle and Musick, 1974; Haedrich et al., 1980; Sulak⁶).

A fish occurring commonly only in dive 2629 was designated as Species A. This may have been the offshore hake, *Merluccius albidus* (Sulak⁶). It was light-colored with dark dorsal blotches, of moderate size (<20 cm), had a terete shape, and a relatively large

head. It was always observed lying on the bottom, its body straight. Most individuals swam away before the submersible got close enough for adequate observation. The eel and the shortfin squid, *Illex illecebrosus* (see below), also tended to move away from the submersible.

Several decapod crustaceans were also observed. Sergestid shrimp were seen in every dive, always off the bottom. Another decapod seen regularly at both Cape Hatteras and Cape Lookout may have been the shrimp *Glyphocrangon* sp. (Williams⁷). Wenner and Boesch (1979) found *G. sculpta* and *G. longirostris* at depths greater than 1,000 m. These shrimp were most abundant in dives 2623 and 2627. Individuals were seen walking on the open bottom, where their dark coloration and highly reflective eyes made sighting these easy.

The red deepsea crab, *Geryon quinquedens*, was not seen in the upper slope dives but was observed in all middle slope dives, walking on the open bottom. It was included in analysis of Cape Lookout species but was too rare to be included in the analysis of Cape Hatteras species. Wenner and Boesch (1979) found this species throughout the depth range included here.

Cancroid crabs were seen at Cape Hatteras and Cape Lookout, in both upper and middle slope dives and likely represent two species. Wenner and Boesch (1979) found *Cancer borealis* and *C. irroratus* on the slope of the Middle Atlantic Bight and *C. borealis* farther downslope than *C. irroratus*. Several cancroid crabs were seen in dive 2630, where they occurred in association with an extremely dense patch of ophiuroids.

The shortfin squid was observed at both Cape Hatteras and Cape Lookout, in both upper and middle slope dives. Individuals were usually lying on the bottom but rose off the bottom when disturbed by the submersible. Occasionally schools were seen off the bottom.

Small octopods were seen at both Cape Hatteras and Cape Lookout in both upper and middle slope dives. Individuals were small and most often associated with objects on the bottom, including sea anemones, crinoids, and gastropod shells. The species had short arms and was probably *Bathypolypus arcticus*.

Galatheid crabs were very common on the bottom, especially in areas where holes were dense. We did not include them in the analysis, because we found that estimates of their numbers were biased depending on whether the submersible travelled up or down the slope. When travelling upslope, only individuals walking on the bottom were seen. When travelling downslope, the camera was able to look down into holes. Viewed in this way, many (if not most) of the holes were occupied by galatheid crabs.

⁷ Williams, A. Natl. Mar. Fish. Serv. Systematics Laboratory, Washington, D.C. Personal commun., 1992.

Analysis of habitat preferences

Cape Hatteras—Analysis of species' habitat preferences produced three factors (Table 4). Factor 1 was related to species preferences for different types of epifaunal assemblages. Factor 2 was related to different amounts of mounds and crinoids and presence or absence of sargassum detritus. Factor 3 was related to density of holes and presence of grass detritus.

Factor 1 had high positive loadings for numbers of small anemones, tubes, and gastropods, and a negative loading for numbers of large anemones. This factor differentiated nekton species found more often in intervals with large numbers of small anemones, gastropods, and tubes, from forms more common in areas with few small anemones, tubes, and gastropods (but where large anemones might be found). Species' scores showed that the scorpaenid, rattail, and shrimp were characteristic of areas with large numbers of small anemones and tubes, whereas cancrivora crabs, lizardfish, and Species A were not usually found in such areas (Fig. 1).

Factor 2 had high positive loadings for density of mounds and number of crinoids. Sargassum detritus had a high negative loading on this factor. This factor differentiated between forms found in association with crinoids and mounds, and forms found away from such areas, more in association with sargassum detritus. Species found more in areas with crinoids and mounds included the eel and lizardfish. Forms found in areas with few crinoids and mounds (but with sargassum detritus) included Species A, squid, octopod, and scorpaenid (Fig. 1).

Factor 3 had high loadings for density of holes and presence of grass detritus. Gastropods and crinoids also contributed positively to this factor. Species found more in areas where holes were dense included the lizardfish, flounder, and scorpaenid, while species not characteristic of such areas included the squid, cancrivora crab, and shrimp (Fig. 1).

We compared species' and location variances on each of the three factors to determine which species appeared to be selecting subsets of the environment represented by each factor. Figure 2 illustrates the distributions on factor 1 of location scores, squids (a significant variance comparison), and scorpaenids (variance comparison not significant).

Habitat selection according to type of epifaunal assemblage (factor 1) was shown for the squid, which preferred areas where neither small anemones nor large anemones were found (Fig. 2). Habitat selection related to mounds and crinoids (factor 2) was demonstrated for the hake. Hakes tended to be found in areas with many mounds and crinoids. Habitat selection with respect to density of holes and grass

detritus (factor 3) was demonstrated for the hake, sergestid shrimp, and lizardfish. These three forms all tended to be seen in areas with intermediate numbers of holes.

Cape Lookout—Only five species were observed in enough intervals to include in a factor analysis of their means. These included the rattail, eel, hake, sergestid shrimp, and red deepsea crab. Factor analysis of these species produced two factors (Table 4). Factor 1 related to density of holes and mounds, and factor 2 related to types of epifaunal assemblages.

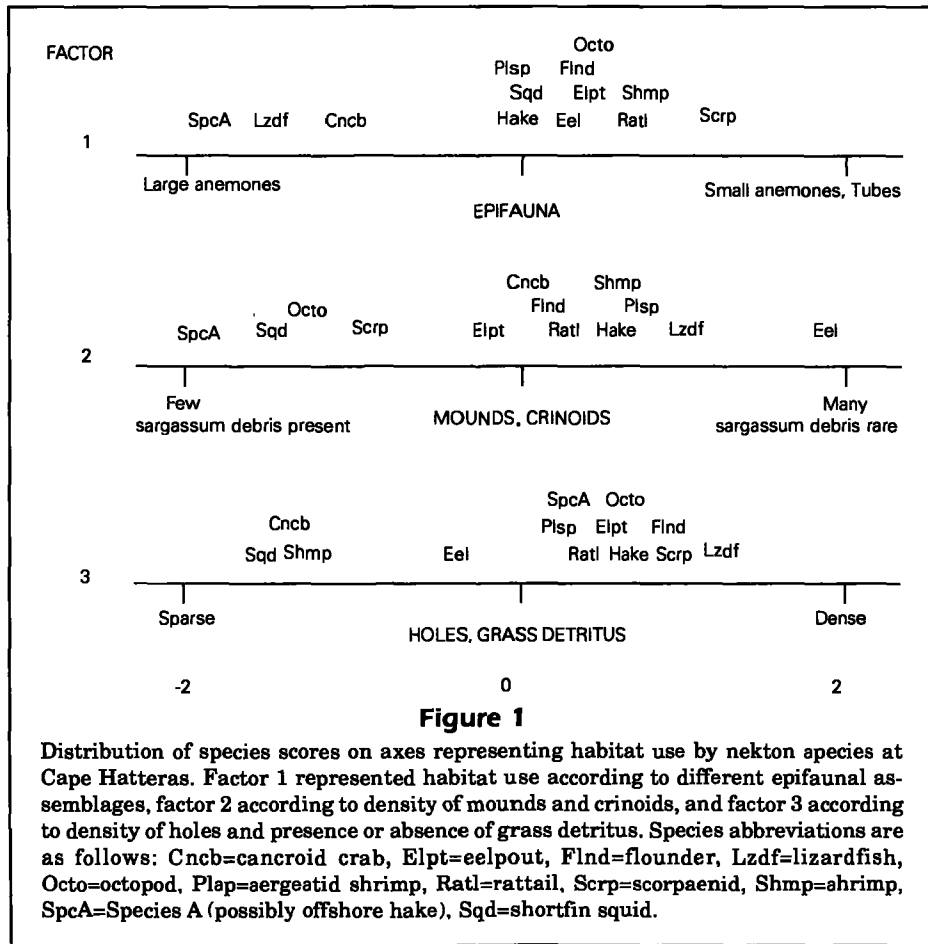
Factor 1 had high positive loadings for density of holes, mounds, and tubes. Numbers of gastropods, presence of invertebrate tracks, and presence of sargassum debris contributed negatively to this factor. This factor differentiated between species found more often in areas with many holes and mounds and species not usually found in such areas. The hake and the red deepsea crab were characteristic of areas with many holes, whereas the sergestid shrimp tended to be found where holes, mounds, and tubes were less densely distributed. None of the comparisons between environmental and species variances were significant.

Factor 2 had high positive loadings for number of small anemones and number of large anemones, and for presence of detritus (both grass and sargassum). The hake was the species most characteristic of areas with many anemones and much detritus, whereas the red deepsea crab was most characteristic of areas devoid of epifauna and detritus. None of the comparisons between environmental and species variances was significant.

Discussion

Mobile species respond to environmental variables, seeking certain conditions and avoiding others. The assumption that individuals select their environment is central to this analysis, as it is to multivariate analyses of habitat selection in general (James and McCulloch, 1990). Environmental variables affecting an individual's habitat choice may include abiotic variables, the presence and density of other species, and the presence and density of members of its own species. The individual's response to a variable of importance may be negative (avoidance) or positive (attraction). Together, the habitat choices of all individuals in an area produce the distributional patterns observed by the investigator.

We used patterns of species distribution and associations between species and environmental variables as a guide to understanding the structure of a



poorly known deep-ocean nekton assemblage. Accepting the assumption discussed above, we confronted the following methodological questions: 1) which species to analyze, 2) which environmental variables to measure, and 3) at what scale to sample. Our answers to these questions were pragmatic. We quantified those forms we felt could be recognized easily and consistently and were consistently visible on the videotape. We measured as many variables as we could quantify visually in an accurate and repeatable fashion and also included those variables that seemed to be dominant in the environment (e.g. small anemones, holes). We sampled at a spatial scale assumed to approximate the area monitored by species of the assemblage. Although the area viewed in one minute of submersible cruising (a distance of ca. 15–30 m) is doubtless greater than the area monitored by an individual at any particular moment, we felt this to be the smallest manageable sampling unit. Shorter intervals (e.g. 30 seconds) required an inordinate amount of videotape stopping and starting. Preliminary analyses suggested that increasing the size of sampling units would create problems, includ-

ing 1) a much smaller number of samples for the analysis, 2) loss of information in 1/0 coded variables, as these tended to become 1 (environmental attribute present) in all intervals, and 3) loss of information in variables whose scale of change was smaller than the sampling unit. In each case, increasing the size of sampling units tended to decrease the measurable association between a species and particular environmental variables (see also Schneider et al., 1987).

Correlations between species occurrence and particular environmental variables were subjected to multivariate analysis to find the patterns of habitat use in this species assemblage. In accordance with James and McCulloch's (1990) caveats, we recognize and stress the correlational aspect of this study. Our analysis produced artificial axes that only reflect real trends. These artificial axes provided the data for all further statistical tests. However, our interpretations are strictly tied to the real variables represented by the artificial axes. When a factor had high loadings for holes and small anemones, we inferred that one of these variables, or some other variable strongly related to them, was in fact affecting distri-

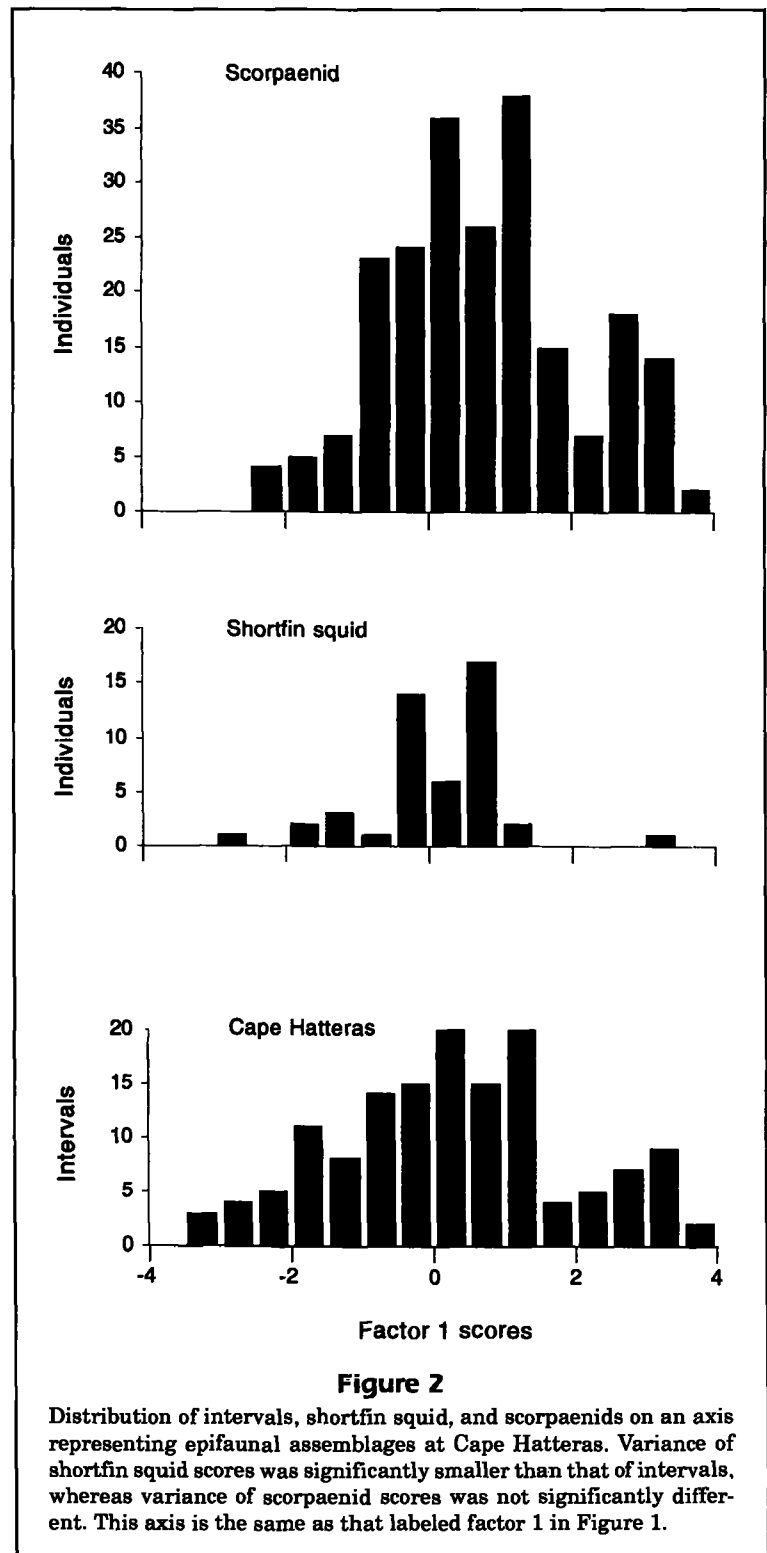
bution of some species in the assemblage. In this way, we attempted to move from our view of the environment to a view more concordant with that of the species that live there.

Our view was molded by the environmental variables we measured and the species distributions we observed. These highlighted differences between the Cape Hatteras and Cape Lookout sites, as well as differences between dives at a site. In all dives, the benthic environments included in this analysis had soft substrate, with visible epifauna and evidence of infauna (holes, mounds). Differences between the two dive sites were seen in the species composition and in the spatial distribution of these species. There were some depth-related patterns in species occurrence at the Cape Hatteras location (Cape Lookout dives were all at similar depths).

Density of organisms differed greatly between Cape Hatteras and Cape Lookout. Biota was much more dense at Cape Hatteras. Summing all demersal nekton, anemones, gastropods, and crinoids in each interval, we found that Cape Hatteras dives had a mean of 29.0 organisms per interval, whereas Cape Lookout dives had a mean of 4.6 organisms per interval. At Cape Hatteras, dives 2623, 2627, 2629, and 2630 averaged 24.3, 48.7, 23.0, and 5.1 organisms per interval, respectively. At Cape Lookout, dives 2619, 2620, and 2621 averaged 4.2, 4.9, and 5.0 organisms per interval, respectively. Schaff et al. (1992) found density of biota at the Cape Hatteras site to be much higher than at other slope localities, including the Cape Lookout site. They related the high density of biota at Cape Hatteras to nutrient enrichment due to an interaction between the complex topography of the area and upwelling currents.

Distribution patterns of sessile epifauna differed at the two sites. At Cape Hatteras, ophiuroids, crinoids, and small anemones showed evidence of clumped distributions. Large anemones showed a clumped distribution in dive 2629. There was no evidence of clumped distributions for any sessile organisms at Cape Lookout.

At Cape Hatteras, some species were restricted to particular depths. Zonation by depth has been documented for slope megafauna (Gardiner and Haedrich, 1978; Rowe and Haedrich, 1979; Hecker, 1990a). The eel and the red deepsea crab were found



almost exclusively at middle slope dives (2623 and 2627, Table 3), whereas the lizardfish and Species A were found mostly in the upper slope dives. Most species included in the analysis were found in a range of depths.

Table 4

Factor loadings of environmental means for benthic megafauna from the slope at Cape Hatteras and Cape Lookout, North Carolina. The representations below are of principal components rotated to simple structure. Only factor loadings >0.50 are shown.

Analysis	Factors					
	1		2		3	
Cape Hatteras	Large anemones	-0.91	Mounds	0.94	Holes	0.94
	Small anemones	0.83	Crinoids	0.73	Grass detritus	0.65
	Tubes	0.88	Sargassum detritus	-0.88	Gastropods	0.54
	Gastropods	0.54			Crinoids	0.50
Cape Lookout	Holes	0.92	Grass detritus	0.89		
	Mounds	0.93	Large anemones	0.88		
	Tracks	-0.72	Small anemones	0.91		
	Tubes	0.93	Sargassum detritus	0.82		
	Gastropods	-0.96				
	Sargassum detritus	-0.52				

Although the various areas appeared qualitatively different, analyses of species' habitat preferences showed us that species in both areas were distributed in relation to similar types of benthic features. Some forms were typically seen in areas with dense aggregations of holes and mounds; others were seen in areas with fewer holes and mounds. Thus, at both localities, nekton distributions were related to particular types of infaunal assemblages. Associations with particular epifaunal assemblages were demonstrated by those species found most often in dense patches of small anemones and (at Cape Hatteras) in areas with dense patches of large anemones or crinoids. Analysis of species preferences suggested that in different areas on the continental slope, nekton species respond to similar sets of environmental variables.

While analysis of species preferences identified broad patterns of habitat selection for a group of species, analysis of species variances allowed identification of habitat selection by individual species. Active habitat selection (occurrence of a species in a subset of available environments) was demonstrated for 4 of the 13 species included in the Cape Hatteras analysis. While habitat selection according to factors 1 and 2 was shown for only one species each, habitat selection according to density of mounds and grass detritus (factor 3) was shown for three species (hake, lizardfish, sergestid shrimp). Note that sergestid shrimp distribution was related to benthic features, although shrimp were always seen hovering 1 to 2 m above the bottom. Such a seemingly counterintuitive result (a species selecting habitat according to a variable that it does not seem to monitor) suggests the need for more study in this environment.

For most species at Cape Lookout and for several at Cape Hatteras, small sample sizes made tests of variance equality quite weak. An uncommon species restricted to a particular habitat might be sampled in numbers too low to allow a statistically significant test. Examples abound in this study. Our analyses identified various environmental gradients. Locations with scores at the extremes of the gradients were sampled in low numbers (e.g. Fig. 2). Forms characteristic of these extreme environments were sampled in correspondingly low numbers, unless they happened to be extremely abundant in a few intervals. Thus, we found it most difficult to show statistically significant habitat selection for those species that were tightly clustered in specific habitat types.

Some examples of uncommon forms found in specific habitat types came from dive 2629 (Table 3). The lizardfish was most abundant in this dive, and Species A and the only eels observed on the upper slope were visible during this dive. The dive area had a high diversity of habitats. The submersible passed over areas with many holes and few anemones or other epifauna, areas dense with small anemones, a dense patch of crinoids (from 5 to 50 individuals per interval over 8 intervals), and an aggregation of large anemones (from 4 to 12 individuals over 18 intervals). The extreme scores of Species A, cancroid crab, and lizardfish were strongly affected by their high densities in particular habitats seen in dive 2629. Detailed studies of such heterogeneous areas could clarify the environmental variables used by slope species to select their habitats.

In this study, we saw patterns of habitat choice by nekton at different scales, from differences along the slope, to species preferences for different habitats

within a dive. Most species were found across the range of habitat types identified by the analysis, though they might be most abundant in one specific habitat. Active habitat selection (species variances smaller than environmental variance) was not seen for such species. Other species were found in numbers too small to allow a powerful test of active habitat selection. Despite these qualifications, this study demonstrated trends in habitat selection by slope nekton and suggested hypotheses for further work.

At both sites, habitat selection by demersal nekton was related to numbers and types of sessile invertebrates and to infaunal organisms that created holes and mounds. These are also two of the trends seen by Felley et al. (1989). They found that habitat selection by demersal nekton of a sandy-bottom shelf environment of the Gulf of Mexico was related to presence or absence of large sessile invertebrates (sponges, cnidarians, and small corals) and to presence or absence of holes and mounds. Habitat selection in that study was also related to amount of algal cover.

Both this study and that of Felley et al. (1989) were based on analysis of videotapes originally recorded for other purposes. There may be problems with using such videotapes. The submersible tracks were not arranged as transects; therefore, we had to remain aware of potential sampling problems (e.g. the submersible crossing and recrossing a particular area, which did not occur on these videotapes). Sampling bias might result from the conditions under which we collected data. We had to stop collecting data when the submersible stopped, when it moved away from the substrate, or when it traversed areas of gullies or ridges. Thus our results can be generalized to only the habitat we did sample—flat areas. Despite such qualifications, archived videotapes are an inexpensive source of data for exploration of questions relating to distribution patterns in deep-sea organisms. Such patterns are difficult to study in the deep sea (Gage and Tyler, 1991). By using archived videotapes, hypotheses can be developed, utility of specific sampling systems assessed, and improvements in methods recommended. We feel that consistent collection and archiving of video transects is important for extending the usefulness of submersible missions.

Acknowledgments

We would like to thank L. Levin, T. Schaff, K. Sulak, and A. N. Shepard for their comments on the manuscript, insights into the dives, and identifications of several invertebrate species. K. Sulak at the Atlan-

tic Reference Centre, Huntsman Marine Science Centre, New Brunswick, Canada, examined still photos of several species taken during these dives, and his identifications form the basis of much of our demersal nekton species section. A. B. Williams identified a number of decapod crustaceans, and identifications of particular fish species were provided by J. Williams, D. G. Smith, and B. B. Collette.

Literature cited

- Auster, P. J., R. J. Malatesta, S. C. LaRosa, R. A. Cooper, and L. L. Stewart.**
1991. Microhabitat utilization by the megafaunal assemblage at a low relief outer continental shelf site—Middle Atlantic Bight, USA. *J. Northwest Atl. Fish. Sci.* 11:59–69.
- Carey, A. G., Jr., D. L. Stein, and P. L. Rona.**
1990. Benthos of the Gorda Ridge axial valley (NE Pacific Ocean): taxonomic composition and trends in distribution. *Prog. Oceanogr.* 24:47–57.
- Felley, J. D., and S. M. Felley.**
1986. Habitat partitioning of fishes in an urban, estuarine bayou. *Estuaries* 9:208–218.
1987. Relationships between habitat selection by individuals of a species and patterns of habitat segregation among species: fishes of the Calcasieu drainage. *In* W. J. Matthews and D. C. Heins (eds.), *Community and evolutionary ecology of North American stream fishes*, p. 61–68. Oklahoma Univ. Press, Norman, Oklahoma.
- Felley, J. D., M. Vecchione, G. R. Gaston, and S. M. Felley.**
1989. Habitat selection by demersal nekton: analysis of videotape data. *Northeast Gulf Sci.* 10:69–84.
- Gage, J. D., and P. A. Tyler.**
1991. *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge Univ. Press, New York, NY, xvi+504 p.
- Gardiner, F. P., and R. L. Haedrich.**
1978. Zonation in the deep benthic megafauna. *Oecologia* 31:311–317.
- Gooday, A. J., L. A. Levin, C. L. Thomas, and B. Hecker.**
1992. The distribution and ecology of *Bathysiphon filiformis* Sars and *B. major* de Folin (Protista, Foraminiferida) on the continental slope off North Carolina. *J. Foraminiferal Res.* 22:129–146.
- Haedrich, R. L., and J.-M. Gagnon.**
1991. Rock wall fauna in a deep Newfoundland fiord. *Continental Shelf Res.* 11:1199–1207.
- Haedrich, R. L., G. T. Rowe, and P. T. Pollard.**
1980. The megabenthic fauna in the deep sea south of New England, USA. *Mar. Biol.* 57:165–179.
- Hecker, B.**
1990a. Variation in megafaunal assemblages on the continental margin south of New England. *Deep-Sea Res.* 37:37–57.
1990b. Photographic evidence for the rapid flux of particles to the sea floor and their transport down the continental slope. *Deep-Sea Res.* 37:1773–1782.
- James, F. C., and C. E. McCulloch.**
1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Ann. Rev. Ecol. Syst.* 21:129–166.
- Levene, H.**
1960. Robust test for equality of variances. *In* I. Olkin, S. G. Ghurye, W. Hoeffding, W. D. Madow, and H. G. Mann

- (eds.), Contributions to probability and statistics, p. 278–292. Stanford Univ. Press.
- Levin, L. A.**
1991. Interactions between metazoans and large, agglutinating protozoans: implications for the community structure of deep-sea benthos. *Am. Zool.* 31:886–900.
- Levin, L. A., C. L. Huggett, and K. F. Wishner.**
1991. Control of deep-sea community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. *J. Mar. Res.* 49:763–800.
- Markle, D. F., and J. A. Musick.**
1974. Benthic-slope fishes found at 900 m depth along a transect in the western N. Atlantic Ocean. *Mar. Biol.* 26:225–233.
- Middleton, R. W., and J. A. Musick.**
1986. The abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfolk Canyon area. *Fish. Bull.* 84:35–62.
- Mulaik, S. A.**
1972. The foundations of factor analysis. McGraw-Hill, Inc., New York, NY.
- Rice, W. R.**
1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Richards, L. J.**
1986. Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia; observations from the submersible *Pisces IV*. *Environ. Biol. Fishes* 17:13–21.
- Rowe, G. T., and R. L. Haedrich.**
1979. The biota and biological processes of the continental slope. *Society of Economic Paleontologists and Mineralogists Spec. Pub.* 27:49–59.
- SAS Institute.**
1988. SAS Language guide for personal computers, release 6.04 edition. SAS Institute, Inc., Cary, NC, 558 p.
- Schaff, T., L. Levin, N. Blair, D. Demaster, R. Pope, and S. Boehme.**
1992. Spatial heterogeneity of benthos on the Carolina continental slope: large (100 km)-scale variation. *Mar. Ecol. Progr. Ser.* 88:143–160.
- Schneider, D. C., and R. L. Haedrich.**
1991. Post-mortem erosion of fine-scale spatial structure of epibenthic megafauna on the outer Grand Banks of Newfoundland. *Continental Shelf Res.* 11:1223–1236.
- Schneider, D. C., J.-M. Gagnon, and K. D. Gilkinson.**
1987. Patchiness of epibenthic megafauna on the outer Grand Banks of Newfoundland. *Mar. Ecol. Progr. Ser.* 39:1–13.
- Sokal, R. R., and F. J. Rohlf.**
1981. Biometry. W. J. Freeman and Co., San Francisco, CA.
- Van Valen, L.**
1978. The statistics of variation. *Evol. Theory* 4:33–43.
- Vecchione, M., and G. R. Gaston.**
1986. In situ observations on the small-scale distribution of juvenile squid (Cephalopoda; Loliginidae) on the Northwest Florida shelf. *Vie et Milieu* 35:231–235.
- Wenner, C. A.**
1983. Biology of the longfin hake, *Phycis chesteri*, in the western North Atlantic. *Biol. Oceanogr.* 3:41–75.
- Wenner, E. L., and C. A. Barans.**
1990. In situ estimates of density of golden crab, *Chaceon fenneri*, from habitats on the continental slope, southeastern U.S. *Bull. Mar. Sci.* 46:723–734.
- Wenner, E. L., and D. F. Boesch.**
1979. Distribution patterns of epibenthic decapod crustacea along the shelf-slope coenocline, middle Atlantic Bight. *Bull. Biol. Soc. Wash.* 3:106–133.