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HABITAT SELECTION BY DEMERSAL NEKTON: ANALYSIS OF VIDEOTAPE DATA

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ABSTRACT: In the past, analysis of habitat choice by marine nekton has been hampered by limited access to its environment. We suggest a method to facilitate study of habitat choice, using data gathered from videotapes. The aims of this study were (a) to identify members of a particular nekton assemblage, and (b) to identify environmental variables important to the assemblage as a whole. Data on species and environmental variables came from videotapes of a sandy-bottom shelf area (60 m depth) in the Gulf of Mexico off Pensacola, Florida, taken by a remote-controlled submersible travelling along defined transects. We analyzed these videotapes to derive information on habitat use of several species of fishes and large invertebrates. We divided the transects into sections which were homogeneous for bottom type and algal coverage, and in each section measured habitat variables and abundances of the most common and reliably identifiable species of demersal nekton. Factor analysis of species' means for environmental variables identified patterns of habitat use among these species. The analysis identified these patterns by generating axes that represented environmental gradients. The patterns of habitat use by these species related to their preferences for different amounts of three-dimensional structure, algae, and infaunal and epifaunal organisms. We compared species distributions and habitat distributions on these axes to find which environmental gradients were of most importance in habitat selection by these species. We found that more species selected habitats on the basis of particular amounts of structure, fewer selected on the basis of algal coverage and infaunal organisms. Only one species seemed to select habitats on the basis of types or abundances of epifaunal organisms. Thus, amount of three-dimensional structure seemed an important variable to the sandy-bottom assemblage overall, followed by amount of algal coverage and types of infaunal organisms.

Understanding patterns of habitat use by marine nekton has obvious commercial and research value, but the vast majority of marine environments it inhabits remain understudied. Detailed analyses of patterns of habitat use by marine nekton have been largely restricted to easily accessible communities, such as coral reefs (Helfman 1978), rocky intertidal areas (Grossman 1982) and kelp beds (Quast 1968, Ebeling *et al.* 1980). These well-studied communities occur in shallow water (allowing easy access by divers or surface observers). Thus, these communities have been the target of intensive studies of habitat selection by fishes and large invertebrates. Ross (1986) reviewed the literature on resource partitioning by fishes of these and other communities.

Nekton communities in open water, in very deep water, and in other apparently featureless areas have received little attention. These types of habitats are not amenable to study by divers due to time-at-depth limitations. In fact, Ross (1986) pointed out that data from such regions have come mostly from trawl surveys, yielding information on species composition rather than on habitat use or preference. Recently developed equipment offers better access to these poorly studied areas. Manned submersibles have recently been used to study marine

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fish communities (Grimes *et al.* 1986, Parker and Ross 1986, Shipp *et al.* 1986). Richards (1986) investigated habitat use of rockfishes using observations from a manned submersible. Remote-controlled submersibles also allow study of characteristic biological and geomorphological forms, without the limitations of SCUBA. Videotapes taken from submersibles provide, in addition, a record of essential information on habitat choice by nekton.

We illustrate a method for investigating habitat selection by members of demersal nekton assemblages (large invertebrates and fishes) using data gathered from videotapes and a statistical procedure outlined by Felley and Felley (1986, 1987). Videotapes of a sandy-bottom shelf area (60m depth) in the Gulf of Mexico off Pensacola, Florida, were taken by remote-controlled camera. From these videotapes, we identified species of the sandy-bottom nekton assemblage. Using a number of environmental variables measured from the tapes, we characterized the areas where individuals of these species were most likely to be found. The central assumption of this type of analysis is that the individual chooses the habitat in which it occurs, and thus environments where a species is most likely to be found represent the species' environmental preference. We used factor analysis to identify patterns of habitat use among these species (Felley and Felley 1986, 1987). This analysis generated axes on which we plotted distributions of species and habitat types. We then compared species' distributions with distributions of habitats to find which environmental variables influenced habitat selection by members of this assemblage.

MATERIALS AND METHODS

Videotapes of the bottom

Videotapes were recorded from a remote-controlled submersible (owned and operated by John Chance and Associates, Lafayette, Louisiana) to identify patches of "live bottom" off the northwest coast of Florida ("Destin Dome", 29° 50′ N, 86° 05′ W) during September 1984. The tethered, unmanned, 20 hp submersible (International Submarine Engineering Type 2-20) was equipped with 360 degree scanning sonar, black and white and color video, 35 mm still camera, four 500 watt variable-intensity floodlights and a five-function manipulator. The submersible was navigated at ca. 1.9 km hr-1, controlled from a surface console aboard the host vessel. Position of the host vessel was established by a high-precision radiopositioning system (ARGO), while position of the submersible was monitored relative to the host vessel by an acoustic reference system (SIMRAD HPR-209). The two positioning systems were integrated by an on-board computer to establish the absolute position of the submersible. Real-time positioning coordinates of the submersible, its heading, and the time of day were then superimposed on the color video display.

The study area averaged 60 m depth, with primarily sand and sand/shell substrate. Coralline algae covered much of the sand bottom, but there were also small areas of emergent rocks of relic coral with "live-bottom" sponge-coral assemblages established upon them.

The submersible travelled along the bottom on transect lines (Fig. 1) pre-established by John Chance and Associates (to survey the area for future oil exploration). Navigation fixes were recorded every 152 m, and these are represented by points along the transect

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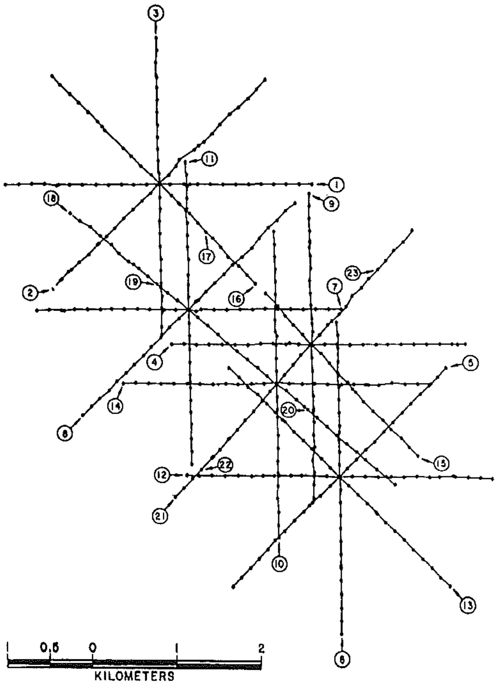

Figure 1. Path navigated by the remote-controlled submersible. Dots indicate high-resolution navigation fixes. Numbers designate start points for numbered transects.

lines. Two points very close together indicate that the videotape film was changed at that location. Videotapes were recorded continuously during the 38-hr. period of operation. Floodlights were only used at night.

Identification of habitat variables and species

After completion of the cruise, we reviewed 38 hrs. of videotapes recorded along the entire survey route and identified species of nekton, benthic cnidarians, echinoderms, sponges and algae. Transect lines were divided into contiguous sections, each section defined both by navigation fixes and by a particular substrate type (sand, sand and shell, rubble, or hard bottom) and amount of algal coverage, estimated visually (low $\leqslant 30\%$ coverage, high $> 30\%$ coverage). Thus, the distance between navigational fixes might be subdivided into several substrate/algal coverage subsections. Sections did not exceed the 152 m between fixes. Even if substrate and algal coverage were homogeneous over several such fixes, species and environmental variables were recorded separately between each pair of fixes.

Within each section, we recorded substrate type, estimation of algal coverage, any particular substrate features, and numbers of individuals of target animal species. Substrate types were coded (1 = sand, 2 = sand and shell, 3 = rubble, 4 = hard bottom), as were algal coverage types ($0 \leqslant 30\%$ coverage, $1 > 30\%$ coverage). Substrate features were identified and counted in each section, including craters (depressions over 1 m in width), holes, tracks (of plowed sand, possibly created by sea cucumbers or other echinoderms), and small mounds (< 10 cm high). We interpreted these features as evidence of different infaunal and epifaunal species. Sessile invertebrates were also counted along each section; these included several types of sponges (round, basket, finger, encrusting, and clump sponges), cnidarians (anemones, corals and sea whips), and echinoderms (stout-spined and spiny sea urchins, sea cucumbers, sea stars and brittle stars). Finally, individual fishes and large demersal invertebrates were identified to species or lowest taxon possible and counted along each section. Appendix 1 lists all taxa identified from the videotapes.

We analyzed the habitat choices of thirteen species of demersal nekton. We included in the analysis only those forms that were relatively abundant (seen in at least 10 different sections), and reliably identifiable. These included the following forms (each given with its likely species identification): skate (*Raja eglanteria*), moray (*Gymnothorax nigromarginatus*), lizardfish (*Synodus intermedius*), batfish

(*Ogcocephalus* sp.), cuskeel (*Ophidion holbrooki*), sandperch (*Diplectrum formosum*), bigeye (*Pristigenys alta*), snapper (*Rhomboplites aurorubens*), croaker (*Micropogonias undulatus*), razorfish (*Hemipteronotus novacula*), filefish (*Monacanthus* sp.), flame-box crab (*Calappa flammea*), and squid (*Loligo* sp.). Of these taxa, three (*Ogcocephalus*, *Loligo* and *Monacanthus*) have sympatric and phenotypically-similar congeners in this area, making confident identification (at the species level) difficult. However, we assumed that only one species of each genus was important in the study area (those species found by Darcy and Gutherz 1984 and Smith 1976).

A number of abundant species were excluded from consideration for study. We did not include pelagic fishes in this analysis, as they tended to school around the submersible. We also eliminated species that were differentially visible in different habitats. For example, we excluded scorpaenid fishes, as they tended to remain immobile in heavy algae and were easily overlooked in such habitats. We also excluded sets of species that were not visually distinguishable but that might have different habitat preferences. Thus, we excluded flatfishes and searobins (Ross 1977 discussed habitat differences among searobins of the Gulf coast).

Analysis of habitat preferences

Studies of fish habitat often address the occurrence of various species along some environmental gradient. Generally, the investigator chooses those environmental variables over which habitat use will be studied. For example, Richards (1986) investigated habitat use of rockfish (*Sebastes*) on the predefined environmental variables of depth and bottom topography. However, when the environmental gradients to be studied are predefined, trends in habitat choice associated with other, unmeasured, environmental variables may be overlooked. These other gradients may become apparent upon observation of the species and their interactions with the environment, necessitating a second study to investigate habitat choice along the newly recognized environmental gradients. Thus, to identify all important environmental variables, the same question must be addressed twice. Felley and Hill (1983) and Felley and Felley (1986, 1987) illustrated a method of identifying important environmental gradients which (ideally) allows the question to be addressed once. An individual is sampled (observed) from a discrete habitat — a small area of the environment that is homogeneous for some (predefined) environmental variables. A number of variables (including the predefined ones) are measured from the habitat where the individual was sampled. After sampling a number of individuals of various species (and their associated environmental variables), species are characterized by their means for each variable. Analysis of these means identifies sets of variables that reflect trends in habitat use. The investigator is still limited by the variables chosen for measurement. However, measurement of a large number of environmental variables ensures that most variables of importance to the species group will be included.

We used a modification of this method to investigate habitat selection in fishes of the sandy-bottom community. Rather than sampling an individual physically, it was observed on videotape. For purposes of this analysis, we considered each section or subsection of a transect to be a "habitat" — an area of the bottom with one particular type of substrate and algal coverage. We considered substrate type and substrate structures, algal coverage, and types of sponges, cnidarians and echinoderms to be "environmental variables" (Table 1). In each section, substrate characteristics, cnidarians and sponges were all coded as 1/0 for presence/absence, while the actual numbers of seastars and stout-spined sea urchins were used.

We calculated the means of these environmental variables for each of the 13 species included in the analysis. A species mean is a weighted mean, a mean where some observations are accorded greater weight or importance than others (Sokal and Rohlf, 1981). We weighted the value of a variable in a section by the number of individuals of the species sighted in that section. Sections where no individuals were seen made no contribution (since they had a weight of 0), whereas sections where the species was abundant made a heavy contribution to the species' mean. Therefore, a species' mean for a variable represented the state of that variable in habitats (sections) where the species was most likely to be found. For example, with environmental variables coded 1/0 (as were many in this study), the species mean represented the proportion of all individuals found in sections where that variable was coded "1". Given that these nektonic species are free to select the habitat in which they appear (within certain constraints), we call the species' mean for a variable its' "preference." The constraints which might limit a species' appearance in a habitat include the lack of such habitat in its environment, or the presence of other species which exclude it from that habitat. We calculated species means separately for sections viewed during the day and at night, to account for diel variability in habitat use. Sections viewed at twilight and at dawn were excluded from analysis.

Table 1. Environmental variables measured along sections and subsections of the submersible survey path. Variables measured as "present/absent" were coded "1" if they appeared at least once along a section or subsection, "0" if they did not. Substrate type was a coded variable.

Variable	Measurement
Substrate type	1 = sand, 2 = sand shell, 3 = rubble, 4 = hard bottom
Algal coverage	0 ⩽ 30% coverage, 1 > 30% coverage
Craters	present/absent
Holes	present/absent
Tracks	present/absent
Mounds	present/absent
Small corals	present/absent
Cnidarians	present/absent
Round sponges	present/absent
Basket sponges	present/absent
Finger sponges	present/absent
Encrusting sponges	present/absent
Clumps of sponges	present/absent
Stout-spined sea urchins	Number of individuals
Sea stars	Number of individuals

Species' means were used in a factor analysis that identified trends in habitat choices of the species. Day and night data were analyzed separately. For analysis of a data set, a correlation matrix was generated from all species' means for the measured environmental variables. This was thus a matrix of correlations between environmental variables (as measured by species means). Factor analysis (principal components analysis with Varimax rotation, Mulaik 1972) was then used to identify sets of interrelated variables. This procedure produces orthogonal, rotated factors. Only those factors with eigenvalues greater than 1.0 were rotated.

Factor analysis allows identification of sets of interrelated variables. Factors are composite variables, or axes, that are generated by the analysis and to which the observed variables (species' means) are variously correlated. Sets of interrelated variables (variables that tend to covary highly) are identified by their high correlations ("loadings") with a particular factor. The variables of such a set have some common basis that accounts for their covariation. In our analysis, patterns of covariation among species' means reflect underlying patterns of habitat use among species. Consider a situation where some species are found in shallow rocky areas with vegetation, and others in deep, sandy areas with no vegetation. Factor analysis of the species' means for depth, substrate type and vegetation would show the common relationship of the three variables to a single habitat gradient important to these species. Analysis of species that occur in contrasting types of habitats (as reflected by these species' means for particular environmental variables) produces factors that identify these differences in habitat use. We interpret each factor as a representation of a range of contrasting types of habitat use among the species. As these factors also define axes, we can plot observations (species) on these axes to identify those with contrasting or similar habitat use.

Factor-scoring functions were used to plot the species on the axes generated by analysis of nighttime or daytime data. On each axis, those species with high positive scores and those with high negative scores were associated with contrasting types of habitat. The scoring functions were also used to compute the score of each section on these axes. This allowed us to compare species distributions and section distributions on each axis. This procedure corresponds to Rotenberry and Weins' (1981) "synthetic approach" of comparing species and location distributions on the same multivariate axes. Assigning a section's score to individuals of a species seen in that section allowed us to calculate species' variances on these axes. On each axis, we compared species distributions and section distributions by testing each species' distributional variance against the variance of all sections, using Levene's test (Levene 1960, Van Valen 1978). If a particular axis reflects an environmental variable important for habitat choice by that species, the species will select a subset of the available environments relative to that axis. In this case, the species' variance will be significantly less than the variance of available environments (i.e., sections). If the axis does not reflect any habitat variable of importance to that species, we would expect no significant difference between species variance and section variance. Felley and Hill (1983) and Felley and Felley (1986, 1987) discussed this type of analysis in detail.

We were limited to comparisons of variances rather than means or overall distributions of species and section scores. We analyzed species distributions on axes that were produced from a statistic derived from these same distributions. Patterns of species' means defined the axes on which species and section scores were plotted, and a species' means for environmental variables defined its mean score on an axis. Any test which incorporated a species' mean or mean score in a comparison with section scores would be biased towards finding a significant difference between the species and sections. Such comparisons would therefore be somewhat circular. Thus, we did not conduct t-tests of species and section means on these axes, nor did we conduct goodness-of-fit tests of section and species scores on an axis. This argument does not hold for studies involving predefined environmental variables, where t-tests or goodness-of-fit tests are quite appropriate. For example, Richards (1986) used such tests to demonstrate

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habitat selection in rockfishes.

RESULTS

Species' means for the 13 species analyzed and means of environmental variables for sections during night and day are given in Table 2 (111 daytime and 323 nighttime sections were surveyed). The substrate was primarily sand and shell, mounds were seen on almost all sections, and thick algal cover was found in ¼ to ⅓ of the sections. We found it necessary to do separate analyses of daytime and nighttime data, for the following reasons: (a) Target species had different behaviors during day vs. night. Several of the thirteen species were never seen during the day (skate, lizardfish, batfish, snapper and crab). The cuskeel, bigeye, croaker, and squid were seen only occasionally and with much less frequency than at night. Only the razorfish was seen more often during the day than at night. Seastars (an "environmental variable") were seen with greater frequency at night; they were likely buried in the substrate during the day. (b) Because of the layout of the transects, more hard-bottom habitat was covered during the day. (c) Detectability of some things varied between day and night. Because visibility was better during the day, the submersible cruised at higher elevations over the substrate, therefore viewing a larger area. The added area allowed more stout-spined sea urchins to be recorded in daytime sections. Conversely, small corals were more easily seen at night, as their whiteness was more apparent in the submersible's floodlights. Some variables had different means in day and night section as a consequence of these reasons (Table 2).

Analysis of daytime data

Factor analysis of species' means from daytime sections showed three trends which differentiated the 13 species (Table 3). The first trend (Factor 1) contrasted those species found more often in areas of hard substrate and much three-dimensional structure with those that were not often found in such

Table 2. Species means for environmental variables during day (D) and night (N). Also given are location means for each variables, total number of habitats (sections and subsections) surveyed, and total numbers of each species and the number of habitats in which they appeared. Notice that not all species were seen during the day.

												Sponges					Stout-spined Sea	
Species	Time	Number	Sections	Substrate	Algae	Craters	Holes	Tracks	Mounds	Small Corals	Cnidarians	Round	Basket	Finger	Encrust.	Clumps	urchins	Seastars
Skate	N	25	23	1.96	.04	.52	.40	.72	.92	.48	.12	.28	.04	0.00	.04	.92	11.76	.28
Moray	D	11	10	2.00	.27	.54	.18	.64	.91	.36	0.00	.36	.27	0.00	.09	1.00	23.00	0.00
	N	304	168	1.99	.15	.45	.33	.69	.93	.47	.07	.31	.04	.02	.09	.88	9.19	.26
Lizardfish	N	47	41	2.02	.21	.47	.32	.62	.92	.47	.02	.36	.08	.06	.08	.83	10.53	.36
Batfish	N	11	10	2.09	.36	.82	.09	.54	.91	.36	.09	.27	0.00	0.00	.27	.64	9.27	.18
Cuskeel	D	4	4	2.00	1.00	.25	0.00	.50	1.00	.25	0.00	.25	0.00	0.00	0.00	1.00	13.75	0.00
	N	208	140	2.02	.17	.45	.41	.63	.98	.42	.09	23	.08	.01	.05	.89	8.55	.36
Sandperch	D	19	16	2.00	.16	.10	.68	.68	1.00	.21	0.00	.32	0.00	0.00	0.00	.95	20.79	0.00
	N	51	45	2.00	.12	.39	.65	.71	.96	.47	.08	.20	.04	0.00	.06	.92	9.47	.33
Bigeye	D	6	1	4.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00
	N	35	17	2.20	.42	.73	.20	.37	.86	.89	.46	.71	.54	.37	.43	.94	2.43	.20
Snapper	N	25	12	2.25	.60	.44	.32	.12	.84	.86	.12	.44	.32	.28	.32	.56	1.20	.16
Croaker	D	3	1	2.00	0.00	1.00	0.00	1.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	22.00	0.00
	N	70	10	2.00	0.00	.93	.51	.17	.98	.70	0.00	.23	.11	.01	0.00	.99	6.04	.86
Razorfish	D	13	11	2.00	.15	.46	.38	.38	1.00	.23	0.00	.08	0.00	0.00	0.00	1.00	14.54	0.00
	N	3	2	2.00	.67	0.00	1.00	1.00	1.00	.33	0.00	0.00	0.00	0.00	0.00	1.00	10.33	0.00
Filefish	D	8	7	2.00	.12	.38	.62	.75	.87	.25	0.00	.12	.12	0.00	0.00	1.00	17.75	0.00
	N	117	82	2.00	.05	.44	.54	.73	.92	.44	.08	.32	.04	.03	.13	.91	8.35	.27
Crab	N	10	9	1.90	.10	.10	.60	.90	1.00	.70	.20	.10	0.00	0.00	0.00	.90	13.90	.50
Squid	D	3	3	2.00	1.00	.33	0.00	.33	1.00	0.00	0.00	0.00	0.00	0.00	.33	1.00	10.33	0.00
	N	1817	235	2.01	.10	.44	.34	.68	.95	.45	.12	.25	.03	.01	.04	.91	9.79	.30
Locations	D		111	2.03	.30	.37	.36	.54	.95	.19	.04	.19	.14	.01	.02	.96	16.95	.02
	N		323	2.01	22	.43	.35	.58	.90	.47	.10	.27	.07	.04	.08	.34	7.90	23

areas. Variables that loaded on this factor included substrate type, soft-bottom features, and presence or absence of corals and various sponges. On the basis of their scores on this axis, species that were found more often on soft bottom with little structure included the filefish, moray and croaker while the species most characteristic of areas with much structure was the bigeye. Factor 2 contrasted species preferring areas with thick algal cover (and few basket sponges) with species preferring the converse. Squid, cuskeel and razorfish had scores reflecting preferences for dense-algae sections; filefish, bigeye and croaker had scores reflecting preferences for clearer areas with basket sponges. Factor 3 contrasted species found more often in areas with many holes (including the sandperch and filefish) with species found in areas with few holes (squid and croaker).

Analysis of nightime data

Factor analysis showed four trends in nighttime habitat selection among species (Table 3). Factor 1 contrasted species preferring areas with much structure (with hard substrate, corals, cnidarians and different types of sponges) with species found less often in such areas. The razorfish and batfish had scores indicating their preferences for areas with little structure (Fig. 2). As in the daytime analysis, the bigeye was the species most characteristic of areas with much structure. Factor 2 differentiated between species characteristic of areas with many holes and mounds (razorfish and crab, as well as sandperch and croaker) and those found more often in areas with clump sponges and craters (batfish, primarily) (Fig. 2). Factor 3 contrasted species (crab and skate) found more often in sections with evidence of echinoderm epifauna, with species not characteristic of such habitats (snapper, croaker). Finally factor 4 contrasted species preferring areas high in algae and with few seastars (razorfish, snapper), with those found in areas with low

Table 3. Factor loadings of environmental means for demersal species during day and at night. The representations below are of principal components rotated to simple structure. Only factor loadings > 0.50 are shown.

Time	Factors							
	1		2		3		4	
Day	Substrate	.96	Algae	-.91	Holes	-.95		
	Craters	-.73	Basket sp.	.72	Basket sp.	.56		
	Tracks	-.84						
	Mounds	-.95						
	Small coral	.94						
	Round sponge	.92						
	Finger sp.	.96						
	Encrust. sp.	.92						
	Clumps of sp.	-.96						
	Urchins	-.86						
Night	Substrate	.53	Craters	-.64	Tracks	-.85	Algae	-.89
	Small coral	.78	Holes	.92	Urchin	-.78	Seastars	.92
	Cnidarians	.95	Mounds	.68				
	Round sponge	.74	Encrust. sp.	-.58				
	Basket sp.	.83						
	Finger sp.	.78						
	Encrust. sp.	.60						

algal coverage, where more seastars were visible (skate, crab, croaker).

Analysis of species and section distributions

Comparisons of species variances with section variances on each axis were only performed on the nighttime data. Sample sizes for most species in daytime were too small to allow statistically meaningful tests. A species' variance significantly smaller than section variances was the criterion for identifying habitat selection by that species ($p<.05$, 1-tailed test). Levene's test of variance equality showed that six species selected subsets of available environments based on amounts of three-dimensional structure (Table 4), while four species selected environments based on different types of infauna (reflected by substrate features). The sandperch, filefish and squid all selected subsets of the algal coverage axis. Only the sandperch had a distributional variance significantly smaller than that of the sections on the epifauna axis. The sandperch was most selective of habitats overall. Its distribution on all four axes had a significantly smaller variance than that of sections. Of the abundant species, the moray seemed least selective (only showing evidence of habitat selection on the basis of three-dimensional structure). In general, Levene's test was not significant for species with low sample sizes (fewer than 50 individuals recorded), perhaps due to the conservative nature of the test in such cases.

Figures 3-6 illustrate the distributions of sections and the distributions of

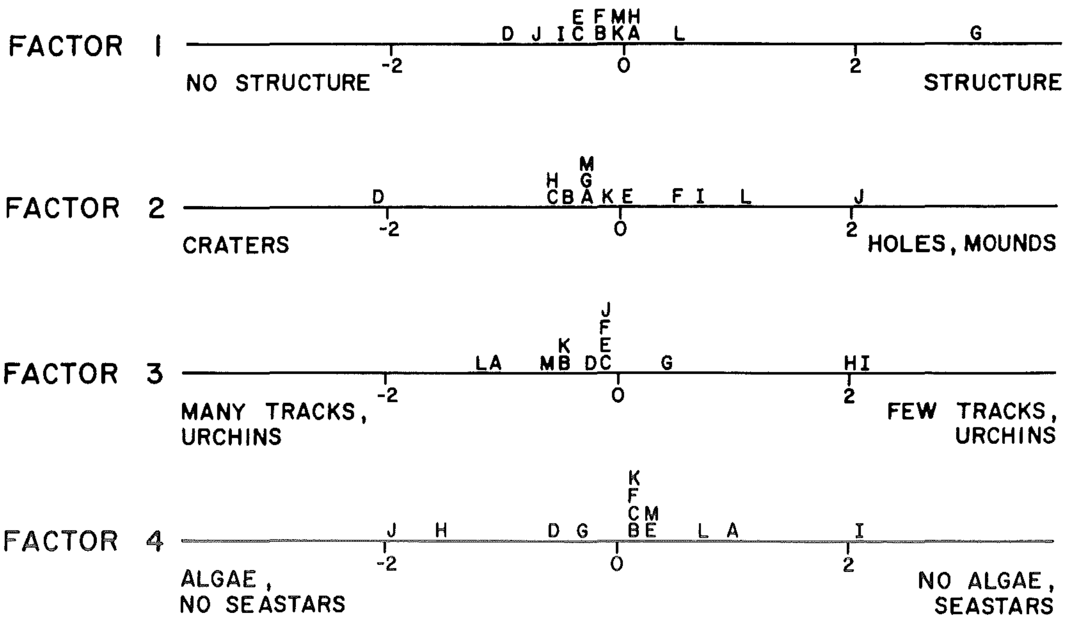

Figure 2. Distribution of species scores on axes representing habitat use at night by species of demersal nekton. Factor 1 represented habitat use according to different amounts of three-dimensional structure, Factor 2 different types of infauna, Factor 3 different types of epifauna, Factor 4 different amounts of algae and seastars. Species are coded as follows: A = Skate, B = Moray, C = Lizardfish, D = Batfish, E = Cuskeel, F = Sandperch, G = Bigeye, H = Snapper, I = Croaker, J = Razorfish, K = Filefish, L = Crab, M = Squid. Species codes placed above another indicate that the species had very similar scores.

Table 4. Distribution tests of individuals of different species on factors describing habitat use by demersal forms at night. Levene's test of variance equality was used to compare species variances with variance of sections and subsections on each factor. An asterick (*) indicates a species variance significantly smaller than location variance (implying that the species uses a subset of available conditions relative to that factor). Razorfish was not included in this analysis.

Species	Factor			
	Structure	Infauna	Epifauna	Algae
Skate				
Moray	*			
Lizardfish				
Batfish				
Cuskeel	*	*		
Sandperch	*	*	*	*
Bigeye				
Snapper				
Croaker	*	*		
Filefish	*			*
Crab				
Squid	*	*		*

some selected species on axes reflecting habitat use by nekton at night. Figure 3 shows the distributions of sections and bigeye individuals according to their scores on the structure axis (factor 1). Most of the area covered had intermediate amounts of three-dimensional structure, as indicated by the large number of sections with intermediate scores on the structure axis. In both day and night, bigeyes were found more in areas with much structure. However, at night they were not limited to such habitats and occurred widely across a range of habitat types. As a result of their occurrence in habitats with varying amounts of three-dimensional structure, the variance of bigeyes on the structure axis was not significantly less than that of sections. Filefish, on the other hand, did select a subset of habitats relative to structure (Table 4). Figure 4 shows that they tended to select habitats with intermediate amounts of structure, being uncommon in habitats with either very high or very low amounts of structure. As reflected in Fig. 5 , cuskeels were not abundant in areas toward the "crater" end of the infauna axis (factor 2), but were more abundant than expected in sections near the "holes and mounds" end of the axis. This accounted for the significant variance comparison associated with the cuskeel (Table 4). Finally, Table 4 and Fig. 6 show habitat selection by squid relative to the algal coverage-seastar axis; squids were found more commonly in low algae, high seastar sections.

DISCUSSION

This study presents an exploratory investigation designed to identify members of a particular assemblage and to determine which environmental variables contributed to habitat partitioning among the assemblage members. Videotape data allowed us to census species and measure variables in an environment that would otherwise be very difficult to sample. Using the method of Felley and Hill (1983) and Felley and Felley (1986, 1987) we analyzed species' "mean" ("preferred') habitats to identify patterns of habitat use among nekton species of sand-bottom community. Axes generated by factor analysis showed that habitat selection by the common species was related to three environmental gradients, reflecting differences in amount of three-dimensional structure, in types of infaunal organisms, and in amounts of algal coverage. These three trends were apparant in analyses of both day and night data. A separate analysis was needed to demonstrate which of these environmental gradients were actually of importance to habitat selection by individual species (since any one gradient might not actually be relevant to habitat selection by a species). A species' distribution on axes that

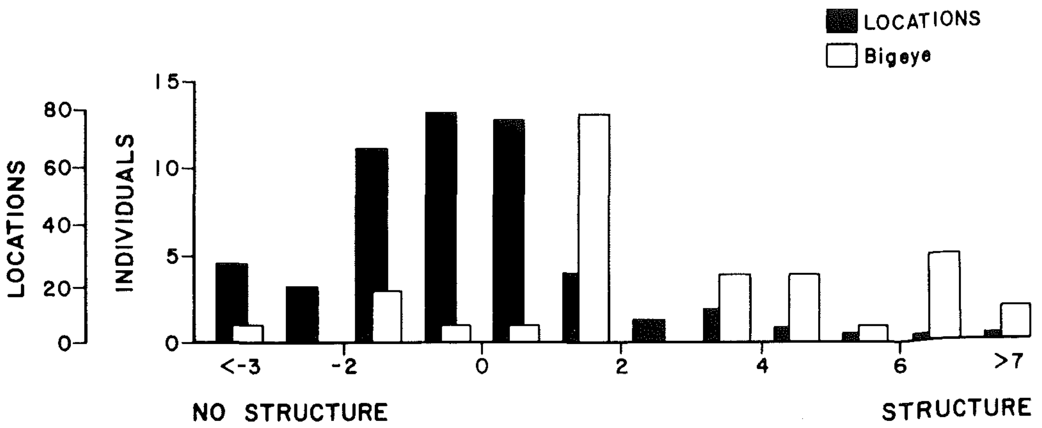

Figure 3. Distribution of short bigeyes and sections on an axis representing nighttime habitat use by species, on the basis of amounts of three-dimensional structure in the environment. This axis is the same as that labelled Factor 1 in Figure 2.

represented these gradients allowed us to identify the gradients of importance to habitat selection. Finally, we ranked the importance of these gradients to the entire community.

To identify the relative importance of these gradients, we compared the number of species that were found in subsets of available habitats on axes representing those gradients. Amount of stucture was judged most important to the sand-bottom community as a whole, since (of those species that could be shown to select some aspect of the habitat) most species selected some subset of the structure axis. By the same measure, type of infauna was next in importance, followed by amount of algal coverage. An axis separating species according to their associations with epifauna was not judged to reflect a gradient of importance to species of the sandy-bottom community, since only one species (sandperch) was found in a subset of this axis, and only at night.

Our criterion for demonstrating "habitat selection" was very conservative, and forced us to ignore some obvious examples of habitat selection. For example, bigeyes definitely preferred areas with much three-dimensional structure (Fig. 3), even though the variance test showed no significant difference between bigeye and section

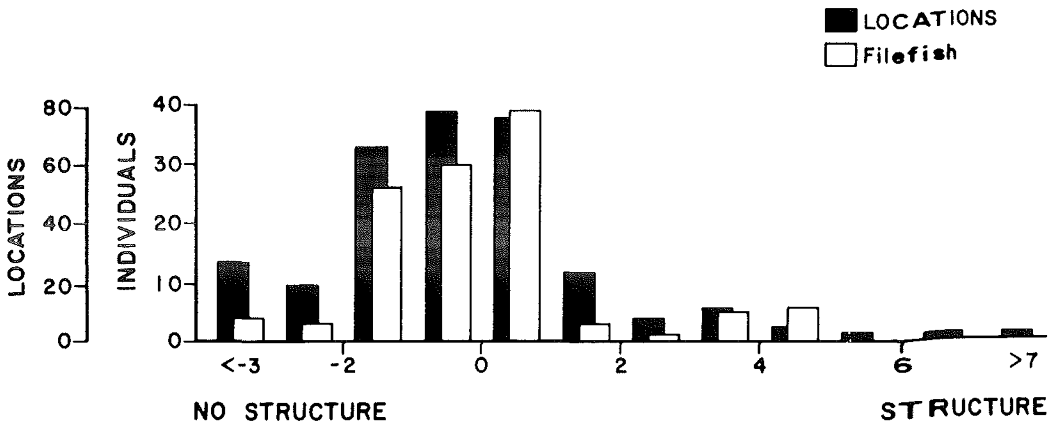

Figure 4. Distribution of filefish and sections on an axis representing nighttime habitat use by species, on the basis of three-dimensional structure. This is the same axis as that labelled Factor 1 in Figure 2.

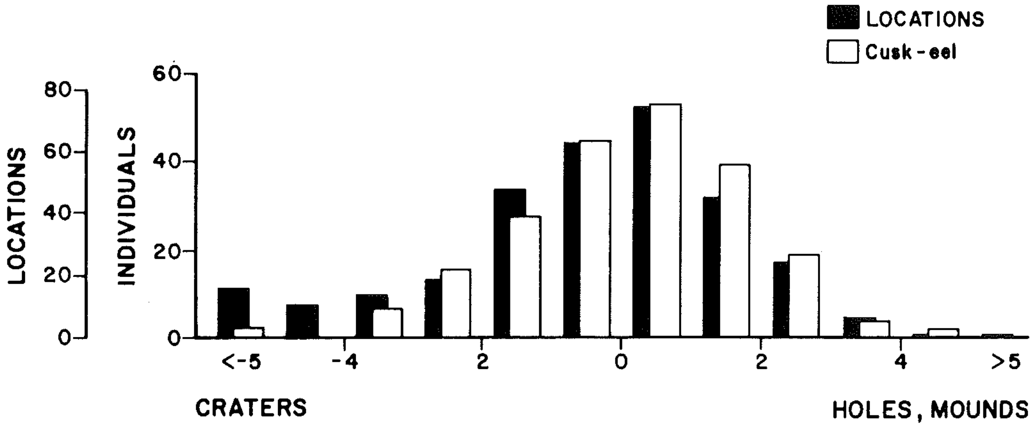

Figure 5. Distribution of cuskeels and sections on an axis representing nighttime habitat use by species, on the basis of different bottom features. We interpret these different bottom featues as representing different types of infaunae. This is the same axis as that labelled Factor 2 in Figure 2.

scores. We note this species' preference here, but since tests of section and species means were biased in this study, we present no statistical evidence of habitat selection by bigeyes.

It is likely that we did not encompass all variables of importance to all members of the sandy-bottom community. An apparent lack of habitat selection by some species suggests that we did not measure environmental variables of importance to them. Additional work on these species, using videotape data, might allow us to find which environmental variables should be measured. Furthermore, a species' habitat selection (as we define it) must be understood in the proper context. Any particular individual may not have been found in its "ideal" habitat. Such habitat might not be available in the area surveyed, or may have been available but occupied by a competitor or predator (conditions which could not be addressed in this study). We assumed that within such constraints, individuals of a species selected the habitats in which they were found, and that such selection was based on particular environmental features. This study was primarily involved with iden-

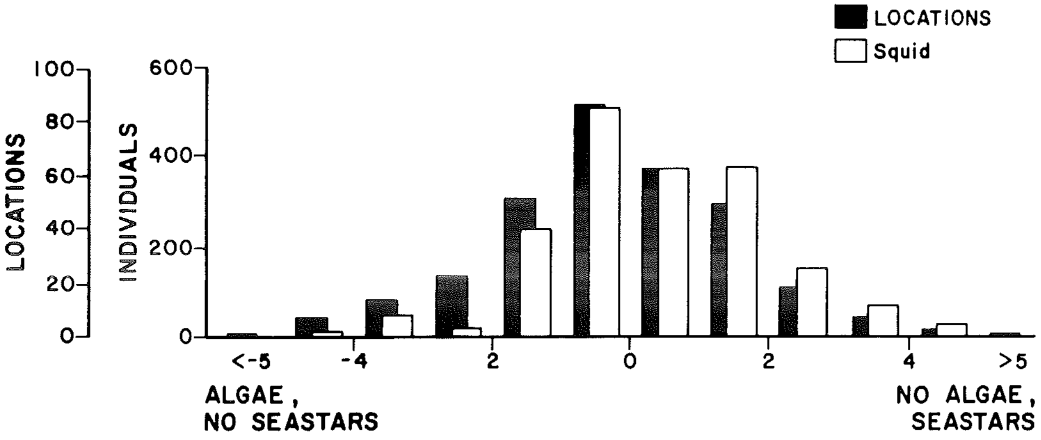

Figure 6. Distribution of squids and sections on an axis representing nighttime habitat use by species, on the basis of differing amounts of seastars and algal coverage. This is the same axis as that labelled Factor 4 in Figure 2.

tifiying those features that species of the sandy-bottom assemblage used to select their "preferred" habitats.

Though the operation of the submersible precluded intensive observations of individuals, there were several striking differences in particular species' distributions and habits in daytime and nighttime. The most dramatic difference was in the number of individuals seen. Some species were not observed at all in daylight. Of these, the skate, moray, lizardfish, and cuskeel were likely buried in the substrate during daytime. Cuskeels and morays were seen emerging from the substrate at twilight. Others (snapper, croaker) may have been schooling in areas not sampled during the day. The bigeye demonstrated a pronounced shift between day and night. Only 6 individuals were seen (in only one section of hard bottom, with many sponges and corals) during the day. At night, the bigeye was relatively abundant and was seen in all types of habitats (though it was still mostly associated with high-structure areas). We hypothesize that the short bigeye spends daylight hours in holes associated with hard substrate, but moves out over the bottom at night to feed. Squids also showed diel changes in abundance. Only 3 individuals were seen during the day, and only in areas with much algal cover. At night, most squids seen were juveniles (Vecchione and Gaston 1986) and were scattered over the bottom, apparently avoiding areas high in structure or algae.

Vecchione and Gaston (1986) discussed the disadvantages of using submersibles for biological work, including (a) the inability to measure animal size, (b) problems with schooling fishes and squids that were attracted to the submersible's lights at night, and (c) lack of standardization of submersible operations among different operators (this was why the submersible cruised higher off the substrate during the day than at night). This study suffers from some of these disadvantages, as well as some specific to this study, as follows: First, only a few taxa could be unambiguously identified to species level. For purposes of this analysis, however, identification to species was not critical. It was important that two species (with different habitat preferences) not be confused and analyzed as a single species. Such confusion would result in incorrect estimates of the "species'" preferred environment, and an overestimate of the "species'" variance on an axis. Second, some types of habitats were poorly sampled because transects were established without reference to any particular habitat gradients. Figures 3-6 demonstrate this: extreme environments on each axis (e.g., reef environments, dense algae environments) were rarely sampled. Many of the characteristic species of these extreme environments were sampled too rarely to include in the analysis (Appendix 1 lists many characteristic reef species (Smith, 1976) that were only seen in one or two sections). Other species characteristic of extreme environments were included in the analysis, but small samples resulted in weak variance tests that often failed to indicate habitat selection by these species. The skate and batfish may have been examples of such species — the batfish was found most often in habitat with little structure, the skate typically in areas devoid of algae. Statistically, neither species could be shown to select a subset of available habitats.

As with any multivariate study of habitat use, our representation of habitat is based on multivariate axes. Species do not select their environments on the basis of scoring functions. However, each factor (and its scoring function) may include habitat variables of importance to a particular species. By comparing species distributions with section distributions, we can defend our argument that these axes represent environmental variables of importance to habitat selection.

The "hypothesis-generating" role of multivariate studies (Nabholz and Richardson, 1975) may be the most valuable part of analyses such as these. Several variables may correlate highly with a factor, but not all of these variables are of equal importance to habitat selection by a species. Each factor embodies hypotheses that one or more of these habitat variables are actually the ones by which a species selects its habitat. A test of such a hypothesis would center on specific species and on explicitly-defined environmental variables, measured in some way comparable to the way the individual species might assess them. If the structure axis is to be investigated, density of items contributing to structure might be defined as the relevant variable. From videotape data (preferably from different transects than those used to identify patterns of habitat use), the distribution of the structure variable and the distribution of the species could be assessed and compared, using goodness-of-fit tests.

Multivariate analyses of species' means for environmental variables allowed us to identify patterns of species distributions, and to clarify aspects of the distributions of individual species. In turn, these results suggested new, testable hypotheses regarding habitat selection by nektonic species of the sandy-bottom community. This analysis, and tests of hypotheses herein generated, depended on the use of data from videotapes recorded from a submersible. The particular advantage of the submersible was that it allowed monitoring of large amounts of the bottom (necessary with the widely-dispersed fauna of the sandy-bottom). Videotapes provided a record of these environments from which we identified habitat features of importance to species and from which we were able to estimate the availability of these habitat features.

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APPENDIX 1.
Species Sightings From Videotape

Fishes

Raja eglanteria	clearnose skate
Gymnothorax nigromarginatus	blackedge moray
Ophichthus ocellatus	spotted snake eel
Synodus intermedius	sand diver
Arius felis	hardhead catfish

Porichthys plectrodon	midshipman
Ogcocephalus sp.	batfish
Ophidion holbrooki	bank cuskeel
Aulostomus maculatus	trumpetfish
Diplectrum formosum	sand perch
unident. serranid	grouper
Rypticus saponaceus	greater soapfish
Pristigenys alta	short bigeye
Echeneis naucrates	sharksucker
Seriola dumerili	greater amberjack
Decapterus punctatus?	scad (round?)
Caranx bartholomaei	yellow jack
Rhomboplites aurorubens	vermillion snapper
Haemulon aurolineatum	tomtate
Conodon nobilis	barred grunt
Stenotomus caprinus	longspine porgy
Micropogonias undulatus	Atlantic croaker
Equetus lanceolatus	jackknife fish
Mulloidichthys martinicus	yellow goatfish
Holacanthus bermudensis	blue angelfish
Chaetodon ocellatus	spotfin butterflyfish
C. aya	bank butterflyfish
Pomacentrus variabilis	cocoa damselfish
Hemipteronotus novacula	pearly razorfish
Thalassoma bifasciatum	bluehead wrasse
Halichoeres bivittatus	slippery dick
H. garnoti	yellowhead wrasse
unident. uranoscopid	stargazer
unident. gobiid	goby
unident. triglid	sea robin
Dactylopterus volitans	flying gurnard
unident. bothid	flounder
Achirus lineatus	lined sole
Symphurus sp.	tongue sole
Balistes capriscus	grey triggerfish
Monacanthus sp.	filefish
Aluterus schoepfi	orange filefish
Lactophrys quadricornis	scrawled cowfish
Sphoeroides sp.	puffer
Diodon hystrix	porcupine fish
unident. teleosts	many

Decapods

unident. penaeid	commercial shrimp
Panulirus argus	spiny lobster
unident. scyllarid	spanish lobster
unident. pagurid	hermit crab
Persephona sp.	purse crab
Calappa flammea	flame-box crab
unident. portunid	swimming crab
Libinia sp.	spider crab
Stenorynchus seticornis	arrow crab

Echinoderms

Luidia clathrata	slender seastar
Astropecten cingulatus	margined seastar
Goniaster tesselatus	biscuit seastar
Oreaster reticulatus	cushion seastar
unident. asteroid	"striped seastar"
Astrophyton muricatum	basket star
unident. ophiuroid	brittle star
Euchidaris tribuloides	stout-spined urchin
Diadema antillarum	spiny urchin
Clypeaster sp.	biscuit urchin
Aspidochirotida sp.	sea cucumber

Molluscs

Pecten ravenelli	scallop
Unident. gastropod	sea snails
Vermicularia spirata	common worm shell
Cassis flammea	flame helmet
Busycon sp.	whelk
Fasciolaria hunteria	banded tulip shell
Scaphella junonia	junonia
Conus floridanus	Florida cone
Aplysia morio	black sea hare
Loligo sp. (*pealei?*)	long-finned squid
Octopus sp (*defilipi?*)	lilliput longarm octopus
O. sp. (*zonatus?*)	Atlantic banded octopus

Miscellaneous Taxa

Ircinias campana	vase sponge
Axinella polycapella	tall branching sponge
Cinachyra allocalada	clump sponge
Geodia neptuni (?)	round sponge
unident. demospongians	sponges
unident. hydrozoans	colonial hydroids
Millipora alcicornis	fire coral
Gorgonia ventalina	sea fan
Plexaurella sp.	sea whip
Oculina sp.	coral
unident. ceriantharian	tube anemone
unident. antipatharian	sea whip
Spirobranchus gigantea	Christmas-tree worm
Lithophyllum sp.	calcareous alga
Lithothamnion sp.	calcareous alga
Caulerpa sp.	green algae
Halimeda sp.	green algae
Udotea sp.	green alga