

Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope

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ABSTRACT: Video transects from occupied submersibles were used to define associations of mobile megafauna (primarily demersal fishes and crustaceans) with microhabitat features including shell, burrow, biogenic depression, biogenic depression with adjacent burrow, sand wave crest, boulder, and burrowed clay outcrop. Sites were located on low-relief bottoms across the southern New England (USA) continental shelf and slope at depths of 55, 240, and 712 m. No significant diel differences in abundance were found for the 8 taxa censused at the 55 m (inner shelf) site. Non-random distributions and associations with specific microhabitats were found for the 8 taxa from diurnal transects and 6 taxa had non-random distributions from nocturnal transects. Silver hake *Merluccius bilinearis* and little skate *Raja erinacea* were associated with particular microhabitats during the day but were randomly distributed at night. These shifts in pattern are attributed to diel differences in feeding behavior. Three of 6 taxa at a 240 m (outer shelf) site and 5 of 6 taxa at a 712 m (slope) site showed non-random distributions and associations with specific microhabitats from diurnal transects. Observations with an ROV (remotely operated vehicle) at inner shelf sites (33 to 55 m) identified a distinction between species which produce biogenic depressions and species which later occupy abandoned depressions. We posit that associations with microhabitat features enhance individual fitness possibly by reducing contact with potential predators and enhancing the ability to capture prey. Use of microhabitat features occurs in assemblages where predators of focal organisms are abundant and possibly where prey density allows ambush predator tactics.

KEY WORDS: Submersible · ROV · Transect · Predator avoidance · Prey capture

INTRODUCTION

Habitat has been defined as 'the structural component of the environment that attracts organisms and serves as a center of biological activity' (Peters & Cross 1992). The environmental characteristics which define the habitats of megafaunal organisms, fishes and crustaceans in particular, can be found at a variety of spatial and temporal scales (Langton et al. 1995). At the regional scale, Murawski (1993) found that seasonal and annual variations in seawater temperature explained the annual variation in the distribution for 17 of 36 species of fish and squid on the northeast United

States continental shelf and slope. Within this region, temporally stable associations of species have been found and tend to follow isotherms and isobaths (Colvocoresses & Musick 1984, Overholtz & Tyler 1985, Phoel 1986, Gabriel 1992). Nearshore and mid-shelf species were primarily influenced by variations in temperature while outer-shelf and slope species were more affected by depth. Species groups were seasonal and often split or showed changes in composition that correlated with temperature patterns. In the Middle Atlantic Bight, no mesoscale correlations with sediment type have been found (Colvocoresses & Musick 1984, Phoel 1986).

Nested within regional scale patterns, small-scale variations in abundance and distribution can be partially attributed to variation in topographic structure.

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Wigley & Theroux (1970) recognized that the microtopography at photographic stations on Georges Bank (NW Atlantic) was greatly influenced by the feeding and shelter-seeking activities of demersal fishes. Other studies (Wigley & Theroux 1971, Uzmann et al. 1978, Valentine et al. 1980) have described relationships of fishes and crustaceans with certain microtopographic (= microhabitat) features (e.g. depressions, burrows, sessile fauna) but these observations were generally ancillary components of other studies. Cooper & Uzmann (1980) developed a general classification scheme of habitat types and associated fauna for northeast U.S. continental shelf, slope and submarine canyon habitats. This scheme was based on direct observation of faunal-habitat relationships and provided a framework to determine changes in the density of organisms between habitat types (e.g. Cooper et al. 1987). Subsequent studies of low topography continental shelf habitats have shown statistically significant associations of megafaunal species with specific microhabitat features (Auster et al. 1991, 1994, Malatesta et al. 1992).

Our ultimate goal is to discern the role that physical habitat plays in the dynamic aspects of distribution and abundance of mobile species in temperate and boreal marine systems. In particular, we wish to determine if associations with particular habitat features increase the fitness of individuals. While studies have been conducted which focus on the ecological role of particular species associations with particular habitat features, little work has been done which discerns the pattern and frequency of use of habitat features by assemblages of megafaunal species (but see Able et al. 1982, Grimes et al. 1986, Cooper et al. 1988, Felley & Vecchione 1995). Herein we describe associations of mobile fauna with particular microhabitats at a series of stations across the continental shelf and slope of the Middle Atlantic Bight. The present question is: Are associations of mobile fauna with various microhabitats a common behavioral attribute of species in cold temperate marine assemblages?

METHODS

Video transects were conducted at a series of stations across the Middle Atlantic Bight at 55, 240, and 712 m sites using DSVs 'Delta' and 'NR-1' (Fig. 1). The

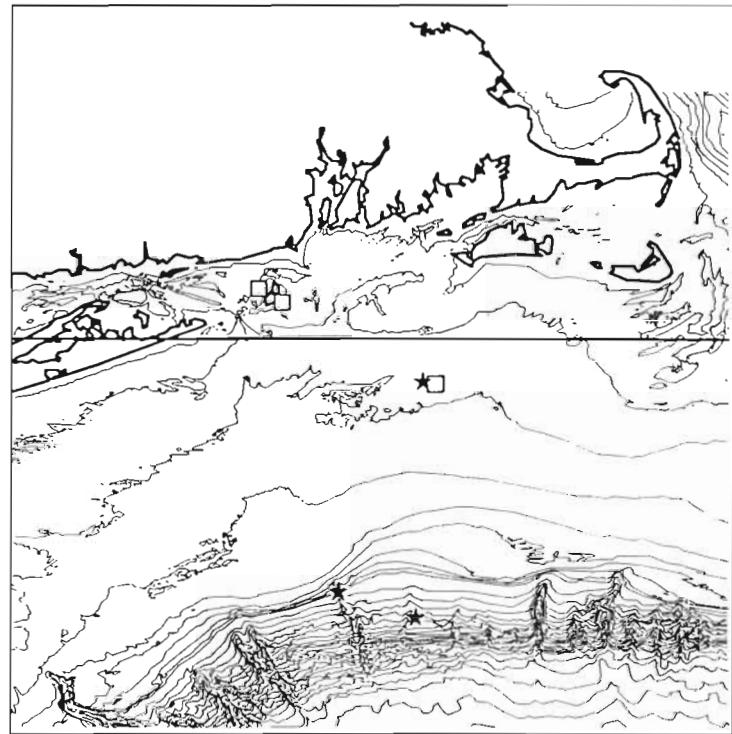


Fig. 1 Location of submersible and ROV dive stations in the Middle Atlantic Bight. Latitude line through chart is 41° N. Stars are locations of transect dives. Boxes are locations of supplemental ROV dives

'NURP 1' remotely operated vehicle (ROV) was used to make additional behavioral observations. Table 1 summarizes the use of each dive system and the sites which were visited. All transects were conducted during the summer. Due to the unique design of each vehicle and limitations on camera placement, area-of-coverage of individual video frames and transect lengths were different. The video camera was mounted obliquely to the bottom for dives at the 55 and 240 m sites with areas-of-coverage of 1.54 and 2.10 m² respectively. Cameras were calibrated by measuring a quadrat placed on the bottom in the cameras' field of view. The video camera was perpendicular to the bottom during transects at the 712 m

Table 1. Summary of dive locations off of southern New England, USA

Year	Dive system	Depth (m)	Temp. (°C)	Location
1989	'Delta'	55	11.6	40° 50.3' N, 70° 55.6' W
1990	'NR-1'	712	4.3–5.1	39° 54.0' N, 71° 00.0' W
1991	'Delta'	240	10.3–11.4	40° 00.5' N, 71° 19.3' W
	'NURP 1'	33–55	10.4	41° 00.8' N, 71° 32.6' W
			14.9	41° 12.7' N, 71° 37.9' W
			11.4	40° 50.3' N, 70° 55.6' W

site and the field of view was 2.50 m². This camera was calibrated using vehicle speed to determine the distance an object traveled across the field of view. Speed was determined using a doppler speed log mounted on the hull of the submersible. Substrate type varied between the 55, 240, and 712 m sites and was previously classified as sand and shell, silty-sand, and silt respectively (Wigley & Theroux 1981, Auster et al. 1991).

TriPLICATE transects were conducted at the 55 m site both day and night to assess diel variation in the abundance of mobile fauna and microhabitat use. To determine if there were diel differences in abundance, individual transects were treated as strips and abundances standardized to number per hectare. Video path width was 0.53 m and distance along the transect was determined using Loran-C coordinates (range 0.65 to 0.97 km). A Mann-Whitney *U*-test was used to determine significant differences in abundance for individual taxa. Single transects were conducted at the other 2 sites to determine patterns in microhabitat use only. Transect lengths were 1.8 km at the 240 m site and 23.2 km at the 712 m site.

The data extracted from all video transects to determine patterns in microhabitat use included species-microhabitat associations as well as the relative abundance of each microhabitat resource. Associations were attributed to individuals if they were within 1 body length of a microhabitat feature. Otherwise the individual was associated with the background habitat (e.g. flat sand-silt). The relative frequency of microhabitats was determined for the 55 and 240 m sites by stopping the video tape at 60 s intervals along the transect and attributing the feature in the field of view to a microhabitat category. A different method was used to determine the relative frequency of microhabitats from the 712 m transect because multiple features were seen in single video frames. The tape was stopped at 120 s intervals and an acetate overlay with 10 randomly marked dots was overlaid on the video image. The microhabitat feature under each dot was assigned to a particular microhabitat type. A chi-square test of homogeneity of distribution, with expected frequencies weighted by the percent frequency of occurrence of each microhabitat, was used to determine if distributions of taxa were non-random. The percent difference between observed and expected values from the chi-square computation was used as a measure of association of a taxon with a particular microhabitat.

A list of taxa observed during all dives is presented in Table 2. Names of fishes follow Robins et al. (1991) and of crustaceans follow Austin et al. (1989).

Table 2. Species observed at each location across the continental shelf and slope. Common names are listed and used throughout the text

Inner shelf	
<i>Cancer irroratus</i>	Atlantic rock crab
<i>Homarus americanus</i>	American lobster
<i>Loligo pealei</i>	Longfinned squid
<i>Macrozoarces americana</i>	Ocean pout
<i>Merluccius bilinearis</i>	Silver hake
<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin
<i>Pagurus</i> spp.	Hermit crab
<i>Pep Iris tricanthus</i>	Butterfish
<i>Pleuronectiformes</i>	Flounder
<i>Pomatomus saltatrix</i>	Bluefish
<i>Raja erinacea</i>	Little skate
<i>Stenotomus chrysops</i>	Scup
<i>Urophycis chuss</i>	Red hake
Outer shelf	
<i>Cancer borealis</i>	Jonah crab
<i>Conger oceanicus</i> (?)	Conger eel
<i>Helicolenus dactylopterus</i>	Blackbelled rosefish
<i>Pleuronectiformes</i>	Flounder
<i>Urophycis tenuis</i>	White hake
Slope	
<i>Geryon quinquedens</i>	Red deep-sea crab
<i>Coryphaenoides rupestris</i> and <i>Nezumia bairdii</i>	Grenadier
<i>Glyptocephalus cynoglossus</i>	Witch flounder
<i>Munida</i> spp.	Galatheid crab
<i>Synaphobranchus kaupi</i>	Northern cutthroat eel
<i>Urophycis chesteri</i>	Longfinned hake

RESULTS

55 m site

Microhabitats included biogenic depressions, sand wave crests, and surficial shell produced by the ocean quahog *Arctica islandica*. No significant diel differences in abundance were found for any of the 8 taxa censused (Table 3). Non-random distributions and associations with specific microhabitats (Fig. 2) were found for all 8 taxa from diurnal transects and 6 taxa from nocturnal transects (Table 4). While silver hake and little skate were associated with particular microhabitat features during the day, they were randomly distributed at night. Ocean pout, longhorn sculpin, and Atlantic rock crab used shell and biogenic depressions both day and night. Red hake used both types of microhabitats more than expected during the day but used shell less than expected at night. Flounders used biogenic depressions more than expected both day and night. Individuals using shell were observed both within the interstices of shell aggregates or simply in direct contact with the shell surface. Silver hake, as well as hermit crabs, used both the peaks of sand waves and biogenic depressions more than expected.

Table 3. Standardized abundance (corrected for length of transect; presented as no. ha^{-1}) of taxa from individual transects at the 55 m site. Transects 1 to 3 were made during daylight hours and Transects 4 to 6 at night. Differences between abundance estimates were made using a Mann-Whitney *U*-test (significant at $p < 0.05$); ns: not significant

Taxon	Standardized abundance per transect						Day-night comparison						
	1	2	Day	3	4	Night							
Ocean pout	1732.0	1141.0		1455.4		1109.4		902.5		ns			
Little skate	305.7		142.6		291.1		701.8		543.4		494.9		ns
Red hake	152.8		326.0		271.7		226.4		90.6		349.3		ns
Silver hake	789.6		550.1		2309.3		611.3		67.9		349.3		ns
Longhorn sculpin	713.2		489.0		116.4		588.6		407.5		669.6		ns
Pleuronectiformes	738.7		305.6		349.3		339.6		22.6		203.8		ns
Atlantic rock crab	738.7		366.7		213.5		543.4		339.6		291.1		ns
Hermit crab	3285.8		998.4		4308.2		2037.6		679.2		3318.8		ns

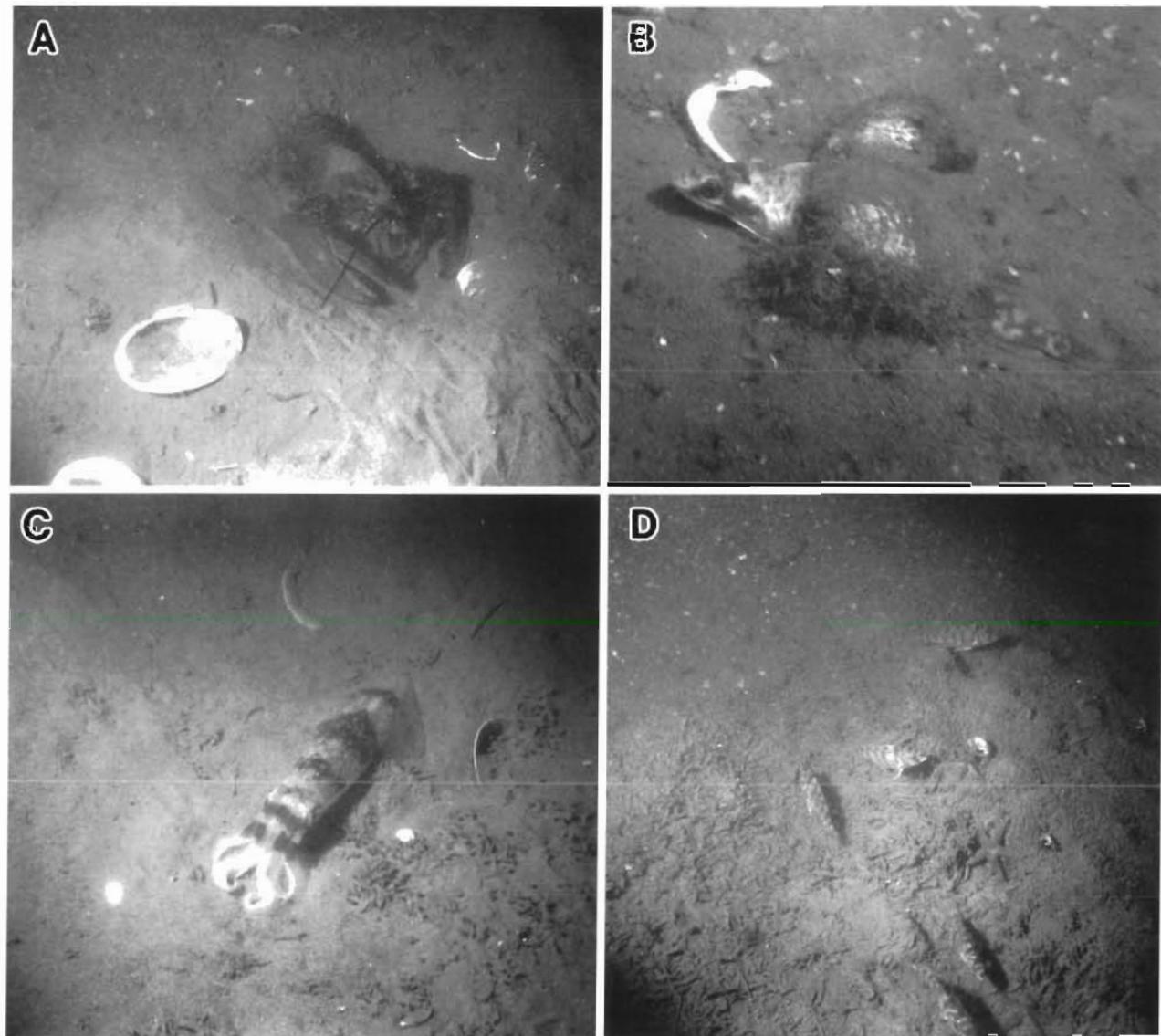


Fig. 2. Inner shelf sites off southern New England, USA. (A) American lobster in a biogenic depression. (B) red hake between ocean quahog valves. (C) longfinned squid in a biogenic depression at night. (D) juvenile scup in a depression probably formed by a skate.

Table 4. Percent difference between observed and expected values (from chi-square test) of abundance of individual taxa associated with each microhabitat type from day and night transects at the 55 m site, southern New England continental shelf. Expected abundances for day and night transects were weighted based on the percent of each microhabitat type observed in Transects 1–3 and 4–6, respectively. Chi-square tests of homogeneity of distribution of abundance were computed for each taxon for diurnal and nocturnal transects (significance levels are ** $p < 0.05$, * $p < 0.10$, ns $p > 0.10$). Microhabitat distributions for diurnal transects ($n = 367$): flat sand 46.32%, shell 35.42%, sand wave crest 16.08%, biogenic depression 2.18%. Microhabitat distributions for nocturnal transects ($n = 322$): flat sand 56.52%, shell 32.30%, sand wave crest 9.94%, biogenic depression 1.24%.

Taxon	Microhabitat type				Chi-square
	Flat sand	Shell	Sand wave crest	Biogenic depression	
Ocean pout (day) (night)	-60	87	-69	302	..
	-82	138	-80	794	..
Little skate	17	-35	-35	471	..
	3	-5	-2	12	ns
Red hake	-67	96	-32	100	..
	2	-52	-61	1775	..
Silver hake	12	-29	15	100	..
	14	-34	20	92	ns
Longhorn sculpin	-81	111	-53	311	..
	-68	94	-85	1346	..
Pleuronectiformes	6	-51	-10	766	..
	-31	-60	-13	3003	..
Atlantic rock crab	-30	61	-71	182	..
	-42	90	-100	392	..
Hermit crab	-7	-13	38	89	..
	1	-52	106	451	..

Behavioral observations during ROV dives, made near dusk and at night, at this and other nearby sites demonstrated that some species produced depression features and others used vacated depressions. For example, juvenile scup and squid were observed in biogenic depressions of variable size (number of observations = 5). The largest, approximately 40 cm across, was apparently produced by a skate (due to the distinctive outline). Smaller depressions generally were occupied by smaller individuals of both scup and squid. These smaller depressions were likely produced by other fishes (e.g. red hake, ocean pout, flounders) and crustaceans (e.g. Atlantic rock crab, American lobster) which excavated the bottom for shelter and prey. Four butterfish were observed singly at the bottom over flat sand, shell, and in a biogenic depression. On one occasion, a butterfish occupied a biogenic depression momentarily before being chased out by a bluefish.

240 m site

Microhabitats included biogenic depressions and burrows. Four of 5 taxa were non-randomly distributed and associated with specific microhabitats (Table 5). White hake, blackbelled rosefish and flounders used biogenic depressions more than expected while conger eels used burrows more than expected. Jonah crabs were randomly distributed throughout the transect.

712 m site

Microhabitats included biogenic depressions, burrows, biogenic depressions with adjacent burrows, and boulders (Fig. 3A, B). Five of 6 taxa were non-randomly distributed and associated with specific microhabitats (Table 6). Witch flounder used depressions more than expected. Northern cutthroat eel and longfinned hake used boulders more than expected. Longfinned hake were associated with biogenic depressions, burrows, and biogenic depressions with adjacent burrows. Galatheid crabs used burrows and biogenic depressions with adjacent burrows more than expected. Red crabs were randomly distributed throughout the transect. Areas of clay outcrops were

observed during the dive but not along the transect path (Fig. 3C). The clay outcrops were heavily burrowed and primarily occupied by red crabs and longfinned hake.

Table 5. Percent difference between observed and expected values (from chi-square test) of abundance of individual taxa associated with each microhabitat type at the 240 m site, southern New England continental shelf. Expected abundances were based on the measured distribution of microhabitat types. A chi-square test of homogeneity of distribution of abundance was computed for each taxon (significant at ** $p < 0.05$, * $p < 0.10$, ns $p > 0.10$). Microhabitat distributions ($n = 1161$): flat sand 83.12%, biogenic depression 12.06%, burrow 4.82%.

Taxon	Microhabitat type			Chi-square
	Flat silty-sand	Biogenic depression	Burrow	
White hake	-2	54	-100	.
Blackbelled rosefish	-83	611	-100	..
Conger eel	-16	-17	312	..
Pleuronectiformes	-33	257	-78	..
Jonah crab	-10	107	-100	ns

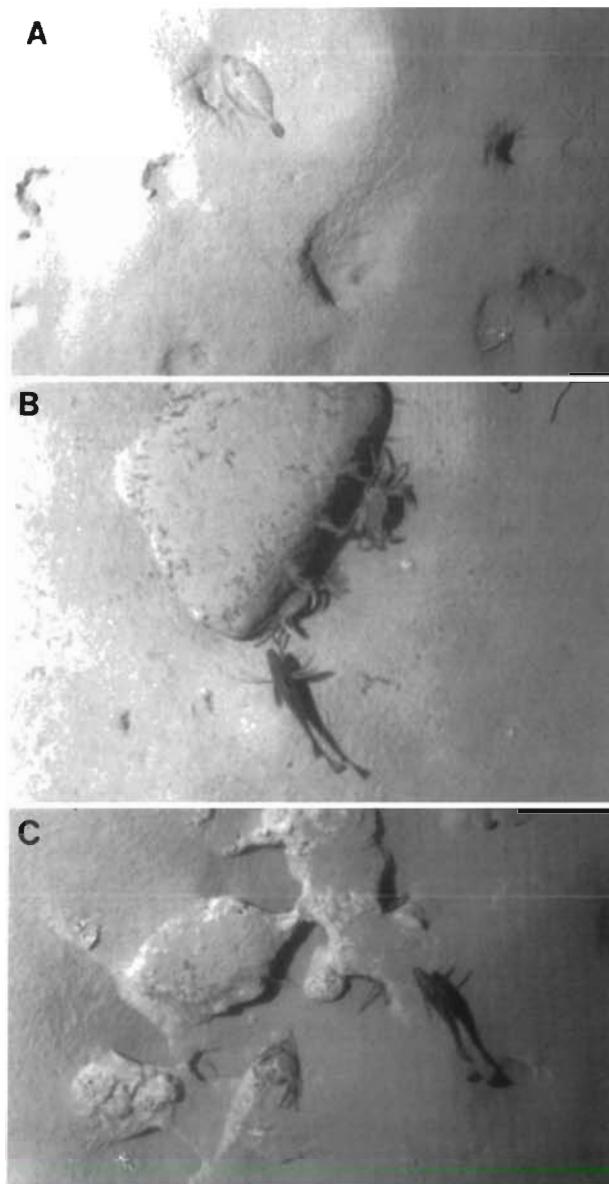


Fig. 3. Slope site off of southern New England, USA. (A) Witch flounder in a biogenic depression and galatheid crab at a burrow entrance adjacent to a depression, (B) longfinned hake and red crabs along the edge of a glacial erratic boulder, (C) red crabs and longfinned hake in exposed clay burrows

DISCUSSION

The use of microhabitat features is a common behavioral attribute of fishes and crustaceans across the continental shelf and upper slope. While patterns of species composition and distribution have been discerned for regional fish assemblages (Colvocoresses & Musick 1984, Overholtz & Tyler 1985, Phoel 1986, Gabriel 1992), small-scale habitat structure contributes to variation in distribution within assemblage types. The use of microhabitats by fishes and crustaceans is apparently facultative, as individuals of most taxa use a variety of microhabitats or were observed to be associated with the background habitat type.

Diel transects at the 55 m inner shelf site indicated silver hake and little skate exhibited diel shifts from use of specific microhabitats during the day to distributions independent of microhabitat type during the night. Silver hake are known to move off the bottom at night to feed (Bowman & Bowman 1980) and, although there was no significant difference in abundance between day and night, feeding behavior may cause shifts in distribution relative to microhabitats. Skates are also known to remain buried in depressions during the day and are more active at night, probably due to diel differences in foraging (Michalopoulos 1990).

The role that use of microhabitats plays in increasing individual fitness may include predator avoidance and prey capture. Individuals occupying various microhabitat features have been observed to retreat into the

Table 6. Percent difference between observed and expected values (from chi-square test) of abundance of individual taxa associated with each microhabitat type at the 712 m site, southern New England continental slope. Expected abundances were based on the measured distribution of microhabitat types. A chi-square test of homogeneity of distribution of abundance was computed for each taxon (significant at $^{**} p < 0.05$, $^{*} p < 0.10$, $^{ns} p > 0.10$). Microhabitat distributions ($n = 2170$): flat silt-clay 80.98%, biogenic depression 16.35%, burrow 1.11%, biogenic depression with adjacent burrow 1.52%, boulder 0.04%.

Taxa	Microhabitat type					Chi-square
	Flat silt	Biogenic depression	Burrow	Biogenic depression/burrow	Boulder	
Witch flounder	-37	202	-100	-100	-100	..
Northern cutthroat eel	16	-85	-87	93	598	..
Longfinned hake	-34	97	61	604	4364	..
Grenadier	2	-32	-100	339	-100	.
Red crab	1	-13	33	62	-100	ns
Galatheid crab	-72	49	3224	996	-100	..

interstices of the shell, among valves on the sediment surface, into depressions in the sediment surface, and into burrows. Laboratory studies have confirmed that the use of microhabitat features can play a functional role in enhancing survivorship. In the presence of a predator, juvenile cod *Gadus morhua* survivorship was enhanced by a shift in substrate preference from sand or gravel-pebble to cobble (Gotceitas & Brown 1993). Individuals used the interstices of the cobble substrate as a refuge. This work illustrated that even relatively subtle changes in habitat complexity can have an effect on predation pattern. Increased habitat complexity has also been shown to increase survivorship of early ontogenetic stages of the American lobster (Wahle 1992a, b, Wahle & Steneck 1992). Use of microhabitats may also play a role in ambush predation tactics by providing a focal site in which the predator may not be recognized by the prey. For example, use of sand wave crest peaks may be a preferred site for ambushing drifting demersal zooplankton and small fishes by silver hake. We have observed other predators using microhabitats as sites for ambush predator tactics as well (i.e. red hake, ocean pout, longhorn sculpin, squid, conger eel, and blackbellied rosefish; unpubl. obs.). Whether for predator avoidance or prey capture, microtopographic features may serve to block visual and acoustic (i.e. proprioceptive) recognition of occupants.

The use of microhabitats, such as biogenic depressions, produced by another species may be a common part of the behavioral repertoire of taxa such as squid, scup, and butterfish. Species which seek refuge from predators during specific periods of the day (e.g. nocturnal, crepuscular), or require particular sites to optimize ambush predation tactics, may not have the behavioral plasticity or morphological attributes to produce their own depression features. This linkage between taxa may influence survivorship rates of cohorts of microhabitat users when population sizes of microhabitat producers are greatly reduced.

The availability of microhabitat resources is dynamic in nature. Sedimentary features such as depressions and burrows can fill in or collapse and shell can become resorted, buried or exposed. At our 55 m station, the coverage of shell has varied from 1987 to 1993 with expansions and contractions in area covered. Eroded sand wave features, observed during the summer at this site, suggest storm events mediate burial and exposure. Ocean quahog shell deployed on the bottom for an experiment south of Block Island (Rhode Island, USA) in 47 m depth was found buried under several cm of sediment after a hurricane passed through the region in 1991. Larval blue mussels *Mytilus edulis* attach to hard rock substrates, small pieces of shell, and to each other to produce extensive

'mats' over sand and mud to depths exceeding 33 m in eastern Long Island Sound (New York, USA). Crustaceans and fishes utilize these mats in a variety of ways, such as for prey, shelter from predators (by burrowing within or under the mat), as well as for sites to reduce energy used for station keeping in strong currents (along edges of the mat). As the mussel population declines through predation and senescence, mussel shell becomes the dominant habitat feature. Large 'windrows' of shell were observed at 4 to 8 m intervals at 20 m depth using an ROV in eastern Long Island Sound during the fall of 1992. The orientation of windrows was north-south, indicating that east-west currents and possibly storm-generated surges interacted to create these features. Juvenile fishes and crustaceans (i.e. scup, American lobster, Atlantic rock crab, Jonah crab, and longfinned squid) were associated with these features. Side-scan sonar surveys and observations with an ROV during spring and summer 1993 showed that windrows were no longer present and the associated organisms were either absent or at lower densities than during the previous survey. It is tempting to speculate that availability of microhabitats from year to year may affect year class strength, or at least that of a specific cohort, since juvenile life stages would utilize these resources for shelter and consequently reduce predator-induced mortality.

While we have shown that use of microhabitats is a common behavioral attribute of fishes and crustaceans in low topography habitats on the continental shelf and upper slope off southern New England, we must ask: How universal are associations with such features by megafaunal species? If use of microhabitat features is mediated by predator and prey densities (i.e. based on predator avoidance and prey capture) then individuals may utilize features based on predation risk and hunger level (Sale 1991, Walters & Juanes 1993). The fish assemblage on the northeast U.S. continental shelf is a predator-dominated system (Sissenwine 1984, Sissenwine et al. 1984). Continental shelf and slope regions support predator and prey densities sufficient to elicit such shelter seeking behavior but the density of deep-sea fishes declines with depth (Sulak 1982). A dive to a 2836 m deep-sea site south of our study area ($39^{\circ} 00.0' N$, $71^{\circ} 00.0' W$) during June 1992 revealed fishes to be widely dispersed and none were associated with any particular microhabitats, although depressions and macroalgal falls were observed (Fig. 4). *Antimora rostrata*, *Coryphaenoides* spp., and *Halosauropsis macrochir* were observed during this dive exhibiting scan and pick foraging behavior. Video of the debris field of the HMS 'Titanic' site ($41^{\circ} 43.8' N$, $49^{\circ} 56.8' W$), taken during July 1991 at 3775 m, provided experimental evidence of the effect of habitat enhancement on deep-sea fishes. The video showed



Fig. 4. A *Coryphaenoides* sp. swimming over the bottom at a 2836 m deep-sea site south of the study area. Note the depression with macroalgal debris

that while munid crabs were occasionally observed burrowed under debris, no fishes were observed using any features for shelter. Only 1 grenadier was observed swimming over the site. These observations indicate that deep-sea fishes do not seek shelter from predators and the density of prey is too low to elicit ambush predator tactics. Sulak (1982) showed that the demersal deep-sea fish fauna in the Middle Atlantic Bight, a eutrophic region of the Atlantic, exhibit 'energetically expensive' life histories (e.g. active foraging). Hence the deep-sea fish fauna of the Middle Atlantic region may not benefit from the use of microhabitat resources.

The role of small-scale habitat features has been central to understanding mechanisms which contribute to variation in populations of coral reef and rock reef fish assemblages (e.g. Sale 1991, Walters & Juanes 1993). The patterns of distributions observed in this study extend these findings to the enhancement of 'fitness' of several species of demersal fish and crustaceans displaying small-scale habitat behavior responses on the continental shelf and slope of southern New England.

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