

# Diversity, Abundance, and Spatial Distribution of Fishes and Crustaceans in the Rocky Subtidal Zone of the Gulf of Maine\*

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Shallow subtidal habitats of the Gulf of Maine harbor important populations of decapod crustaceans and a variety of fish species (Bigelow and Schroeder 1953, Cooper et al. 1975, Hacunda 1981). Because of the economic importance of lobsters, considerable work has been done on the biology and autecology of this species along the northwest Atlantic coast (see, for example, Campbell and Stasko 1986, and papers cited therein). Additional attention has been given to the study of lobster ecology since Mann and co-workers suggested in the 1970s that lobsters were "keystone predators" (sensu Paine 1969) in these systems (Mann and Breen 1972, Breen and Mann 1976, but see Miller 1985). There are relatively few published studies dealing with other common predators, such as fish and crabs, inhabiting shallow subtidal habitats of the coast of Maine. With few exceptions, most studies on fishes have dealt primarily with aspects of feeding and reproductive biology of single species (e.g., cunners: Chao 1973, Olla et al. 1975; sculpins: Moore and Moore 1974; wolffish and cod: Keats

et al. 1986, 1987). Long-term temporal and spatial changes of demersal fish assemblages along this coast have been analyzed by Tyler (1971) and Hacunda (1981), and more recently, MacDonald et al. (1984) have studied temporal variation of inshore fish assemblages in Passamaquoddy Bay, Canada. To date, however, mobile predator assemblages (including fish and crustacean species) have not been comprehensively studied along the coast of the Gulf of Maine.

Our study first describes the composition of large mobile predators, particularly decapod crustaceans and fishes, occurring in rocky subtidal habitats at Pemaquid Point, Maine, and secondly examines their distribution, diversity, and abundance patterns on spatial (bathymetric) and temporal scales. The information gathered in this study is then analyzed in terms of seasonal impacts of those species in shallow rocky shores and the importance of these environments as nursery areas for these species.

## Materials and methods

The study site was a rocky, shallow, sublittoral area off the southwest side of Pemaquid Point, Maine (43°50'N; 69°31'W). This is a wave-

exposed area. The substrate down to ~10–12 m (below Mean Low Water Level, MLWL) consists of a sloping, relatively flat ledge. Large rocks and boulders characterize the bottom between ~12–20 m depth. At depths greater than 20 m the substrate is primarily sand with occasional boulders. A detailed description of this study area, including zonation patterns of benthic organisms, is given in Ojeda and Dearborn (1989).

Two methods were used to sample the mobile fauna of this region: gillnets and underwater observations. To determine diversity and abundance of fish species, two 3 × 40 m experimental gillnets consisting of four panels (graded in mesh size from 10–20 mm to 60–70 mm) were randomly set in parallel on the bottom, perpendicular to the shore at depths between 5 and 23 m, and about 300 m apart.

Fish were sampled monthly for 2 to 3 days from June 1985 to October 1986, except in July, October, and December of 1985, and January 1986. Gillnets were usually set within the first hour after sunrise and retrieved an hour before sunset. All captured fish were fixed in a 5–10% solution of buffered (borax) formalin-seawater mixture, placed in labeled plastic bags, and transported to the laboratory for further analysis. Preserved fish were identified, counted, measured (total length = TL) to the nearest 1.0 mm, and wet weighed to the nearest 1.0 g on a Mettler P1200 balance.

Temporal changes in fish abundance were determined by using a catch-per-unit-effort (CPUE) measurement. This index was calculated as the total number of fish captured

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**Table 1**

List of fish species found in rocky subtidal habitats at Pemaquid Point, Maine. *N* = total number of individuals captured in gillnets; % = percent of captures.

	Common name	<i>N</i>	%	Size range (cm TL)
<b>Class Chondrichthyes</b>				
	<i>Squalus acanthias</i> Linnaeus	42	6.7	87.0–118.0
	<i>Raja erinacea</i> Mitchill	2	0.3	47.0–51.0
<b>Class Osteichthyes</b>				
	<i>Alosa sapidissima</i> (Wilson)	11	1.8	27.5–38.5
	<i>Clupea harengus</i> (Linnaeus)	2	0.3	6.2–6.4
	<i>Osmerus mordax</i> (Mitchill)	2	0.3	21.7–22.7
	<i>Gadus morhua</i> (Linnaeus)	22	3.5	18.7–54.0
	<i>Microgadus tomcod</i> (Walbaum)	2	0.3	23.6–25.1
	<i>Pollachius virens</i> (Linnaeus)	219	35.21	11.5–30.0
	<i>Merluccius bilinearis</i> (Mitchill)	4	0.6	15.2–18.2
	<i>Centropristis striata</i> (Linnaeus)	9	1.4	23.5–26.0
	<i>Pomatomus saltatrix</i> (Linnaeus)	6	1.0	60.0–86.0
	<i>Stenotomus chrysops</i> (Linnaeus)	3	0.5	20.4–23.3
	<i>Tautoglabrus adspersus</i> (Walbaum)	161	25.8	9.5–32.0
	<i>Scomber scombrus</i> Linnaeus	47	7.5	27.3–47.2
	<i>Pholis gunnelus</i> (Linnaeus)	*	—	—
	<i>Ulvaria subbifurcata</i> (Storer)	*	—	—
	<i>Hemitripterus americanus</i> (Gmelin)	22	3.5	23.2–46.0
	<i>Myoxocephalus aeneus</i> (Mitchill)	2	0.3	9.5–13.2
	<i>Myoxocephalus scorpius</i> (Linnaeus)	26	4.2	20.3–33.0
	<i>Myoxocephalus octodecemspinosus</i> (Mitchill)	25	4.0	18.5–43.5
	<i>Cyclopterus lumpus</i> Linnaeus	1	0.2	27.0
	<i>Limanda ferruginea</i> (Storer)	6	1.0	33.0–36.0
	<i>Pseudopleuronectes americanus</i> (Walbaum)	10	1.6	18.5–20.0
<b>Total</b>		<b>624</b>		

\* Not caught in nets.

in both nets divided by the total number of sampling hours in each month.

To determine the spatial distribution as well as temporal changes in abundance of fish, lobsters, and crabs, visual underwater censuses of these species were conducted during the day using SCUBA across bathymetric transects. A total of 34 transects were made during June, August, September, and November 1985, and February, April, June, July, September, and October 1986. Each transect extended from 0 to ~23 m below MLWL, 5 m wide and ~60–70 m long, covering an area of ~300–350 m<sup>2</sup>. The transects were surveyed in segments covering each 3-m depth interval. Two divers independently searched each of these areas exhaustively (in ~20 minutes), recording the number of crabs, lobsters, and fish species (both mobile and benthic ones). Two night-dive transects were conducted during September 1985 to determine nocturnal activity patterns of mobile predators. Four additional transects were carried out in May 1985 to estimate substrate heterogeneity along the depth gradient. Each transect consisted of a polypropylene line extended over the rocky bottom from 0 to 23 m below MLWL.

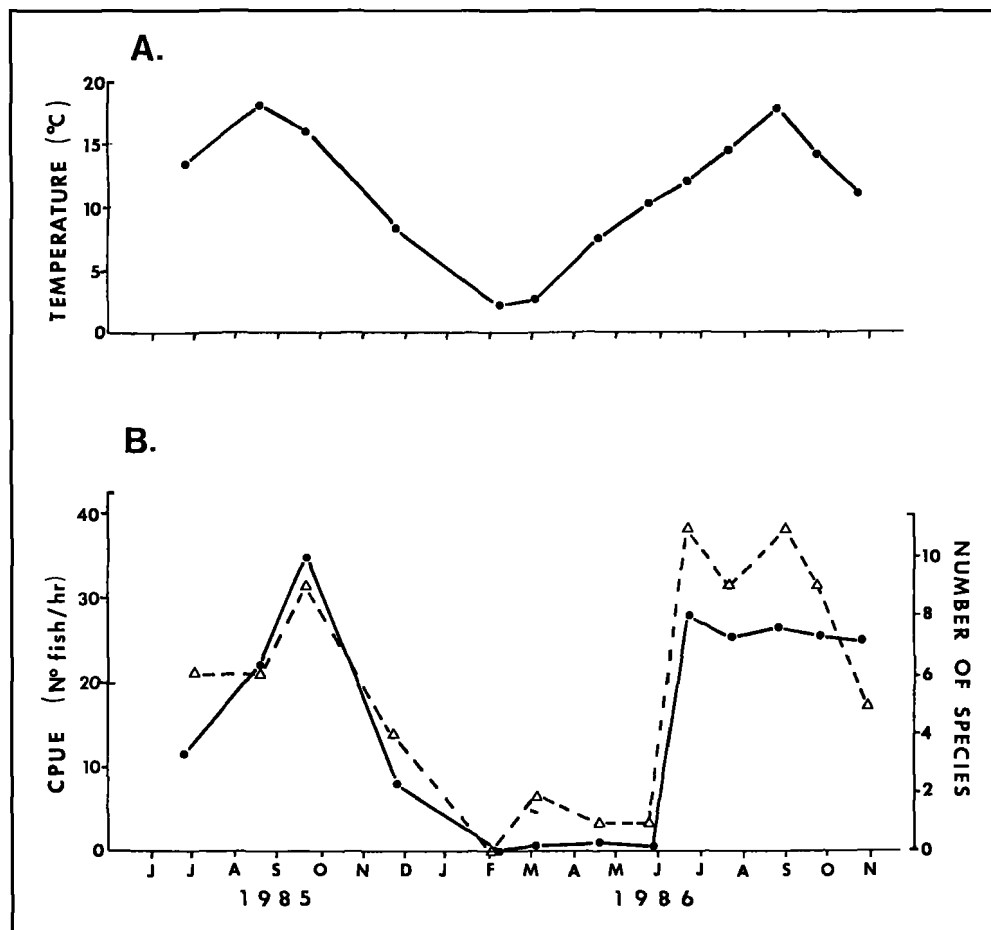
In each of these transects, at depth intervals of 3 m, we recorded the number of crevices, holes, and burrows (shelters) larger than 5 cm in aperture occurring to a distance of half a meter to the right and to the left of the line.

One-way ANOVA followed by a Student-Newman-Keuls (hereafter SNK) multiple comparison test (Sokal and Rohlf 1969) were employed for the detection of changes in abundance of predators and shelters (substrate heterogeneity) over the temporal and bathymetric gradients studied.

## Results

### Species composition

A total of 4 species of decapod crustaceans, including 1 lobster species (*Homarus americanus*) and three species of crabs (*Cancer irroratus*, *C. borealis*, and *Carcinus maenas*), and 23 species of fish (624 specimens) were captured or observed from June 1985 to October 1986 (Table 1).

**Figure 1**

(A) Surface water temperature in Pemaquid Point, Maine, during 1985-86. (B) Temporal variation in the number of species (dashed line) and relative abundance (solid line) of fish captured with experimental gillnets at Pemaquid Point, Maine, during 1985-86. Abundances are expressed as captures per unit effort (CPUE).

The most abundant species were juvenile pollock and cunners (Table 1). Most of these pollock were immature individuals averaging 215 mm TL, which correspond to pollock of about 1 year-old (Bigelow and Schroeder 1953). Six other species were relatively common (represented by more than 2% and less than 10% of the total number of specimens collected: spiny dogfish, cod, mackerel, and sculpins). Most of the cod captured were juveniles averaging 300 mm TL, which correspond to an age of ~2 years (Bigelow and Schroeder 1953). Each of the remaining 13 species (61.9% of the total number of species) were represented by less than 2% of the total number of fish captured (Table 1).

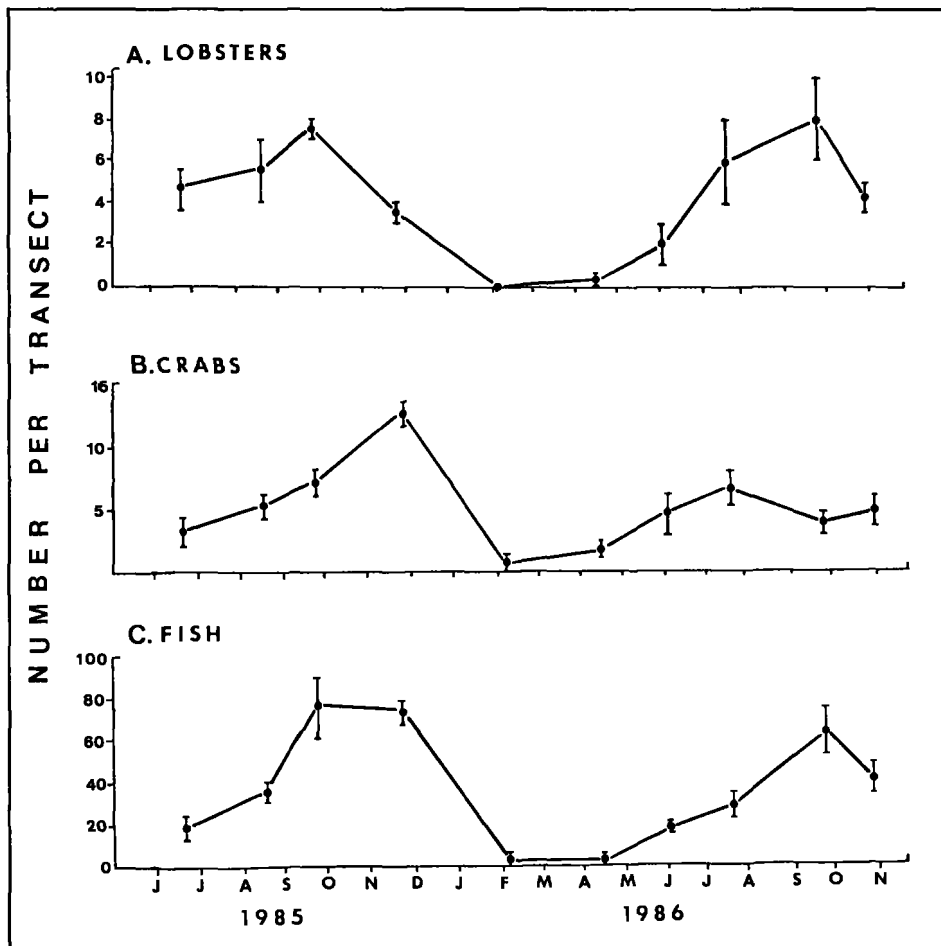
Captures of all three sculpin species, pollock, and cod were significantly greater during the night than during the day ( $\chi^2$  test for goodness of fit,  $P < 0.05$ ) suggesting that these fish are primarily crepuscular and/or nocturnal predators.

On the other hand, cunners, mackerel, and spiny dogfish were captured almost equally during the day and at night ( $P > 0.05$ ). In contrast to mackerel and spiny dogfish, cunners were very rarely observed to be active at night, indicating they are primarily diur-

nal predators in these environments, as previously shown by Chao (1973), Olla et al. (1975), and Dew (1976).

### Temporal patterns

Surface-water temperature of the littoral zone followed a seasonal cycle typical of cold waters of the Gulf of Maine (Fig. 1A), as shown by Tyler (1971) and MacDonald et al. (1984). Maximum values of about 18°C were observed during summer (July-September), and minima of about 1-2°C occurred during winter (February-March). Both the abundance and diversity of fish showed a clear seasonal pattern closely paralleling the seasonal variation of water temperature (Fig. 1B). Fish abundance peaked during summer, reaching values of 30-34 fish/hour, and was lowest (near zero) during winter. Species diversity followed a similar seasonal pattern (Fig. 1B). These results suggest a seasonal migration (inshore-offshore) of most components of this fish assemblage, which appears to be correlated with temperature changes.



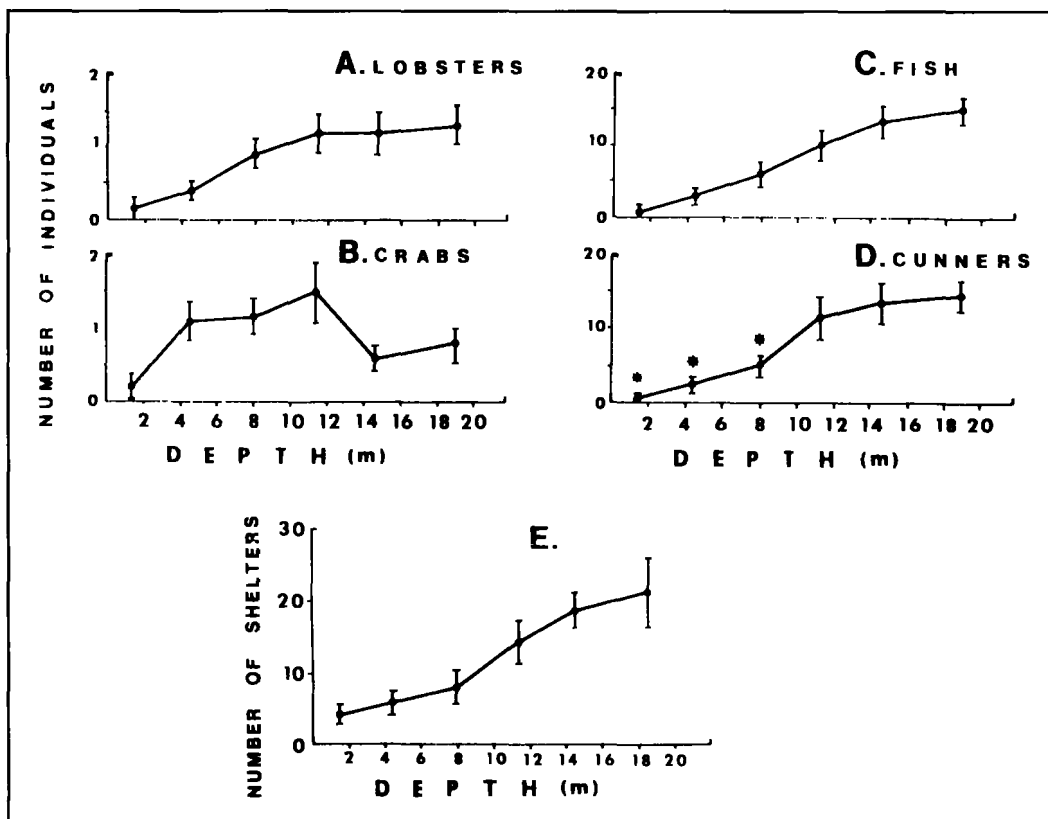
**Figure 2**  
Seasonal variations in the abundance of lobsters (A), crabs (B), and benthic fish (C) along bathymetric underwater transects at Pemaquid Point, Maine. Each vertical bar indicates  $\pm 2$  SE.

The abundance of major components of the catch—lobsters, crabs, and benthic fishes—also varied seasonally (one-way ANOVA,  $P < 0.01$  for all species; Fig. 2). Maximum abundances of lobsters occurred in summer (July–September) at densities of 5–8 individuals per transect ( $\sim 1$  adult lobster per  $26 \text{ m}^2$ ) (Fig. 2A). No lobsters were observed in the winter transects (February 1986). The seasonal distribution of lobsters closely follows the seasonal variation in water temperature (compare Figures 1A and 2A). Highest densities of crabs, however, occurred in late fall (November) 1985, with  $\sim 14$  individuals per transect ( $\sim 1$  adult crab per  $12 \text{ m}^2$ ), and during the summer of 1986, though their densities were markedly lower than those observed in 1985 ( $\sim 5$  crabs per transect or  $\sim 1$  crab per  $33 \text{ m}^2$ ) (Fig. 2B). Few crabs were observed in winter; of those observed, most remained inactive and semiburied in the sand.

Benthic fish such as cunners, rock gunnels, sculpins, shannys, flounders, and rays were markedly most abundant during fall months, reaching densities of  $\sim 75$  individuals per transect in 1985 and  $\sim 60$  in 1986 (Fig.

2C). Their abundance decreased significantly in winter to 2–4 fish per transect, and progressively increased from mid-spring (May–June) until fall as temperature increased. Exhaustive underwater surveys for large predators were carried out in winter (February 1986) with the aid of underwater lights. No cunners or lobsters were observed along these transects despite the special care taken to examine crevices, caves, and spaces underneath boulders and rocks. In addition to a few crabs, three species of fish were commonly observed along these winter transects: rock gunnels, sea ravens, and winter flounders. Rock gunnels were the most abundant fish species, and they were usually observed up to 20 m depth, often associated with clumps of *Modiolus modiolus*. During the rest of the year, this fish species was rarely found at depths greater than 10 m.

This mobile predator assemblage can be divided into distinctive seasonal components. The first is comprised of “summer–fall residents,” species consistently present from late spring until late fall, including pollock, cunners, longhorn and shorthorn sculpins, grubbys,



**Figure 3**  
Bathymetric distribution in the abundances of lobsters (A), crabs (B), benthic fish (C), cunners (D), and number of shelters (E) in the underwater transects conducted at Pemaquid Point, Maine. Each vertical bar indicates  $\pm 2$  SE. Asterisks in D indicate juvenile individuals.

cods, and lobsters and crabs. Lobsters and crabs, however, occurred earlier than these fishes. Crab species are included in this group because their abundance was extremely low during winter, and the few individuals that remained were not active. Summer-fall resident species moved into shallow water or became active (crabs) when the water temperature increased to 8–12°C, generally reaching maximum abundance in midsummer or early fall. The second component was the “regular residents,” species captured or observed active at any season, such as sea ravens, rock gunnells, and winter flounders. These species, however, were generally much less abundant than the summer-fall residents (Table 1). The third temporal component of this fauna was the “summer periodicals” (sensu Tyler 1971), and refers to those species that occurred periodically in the samples during summer. The most abundant and conspicuous species in this group were mackerel, spiny dogfish, bluefish, and, less abundantly, black seabass and yellowtail flounder (Table 1). Finally, there was a group of species that occurred at infrequent intervals and in low numbers during this study. Fish species belonging to this group have been called “occasionals” (Tyler 1971) and include shad, little skate, lumpfish, scup, smelt, Atlantic herring, silver hake, and tomcod.

### Spatial patterns

The abundances of most groups of mobile predators increased with depth, as did the number of shelters (Fig. 3). The number of adult lobsters significantly increased with depth in the first 8 m, then remained relatively constant thereafter to 19 m depth (one-way ANOVA,  $P < 0.01$ ; a *posteriori* SNK test; Fig. 3A). There was no relationship between depth and lobster size, since both large and small individuals were observed at all depths along the transects. Crab species (mostly *Cancer irroratus* and *C. borealis*) showed a somewhat different bathymetric pattern (Fig. 3B). Their abundance markedly increased between 2 and 5 m depth, remained relatively constant at 5–11 m, and decreased at depths greater than 14 m (one-way ANOVA,  $P < 0.01$ , a *posteriori* SNK test). The collective abundance of benthic fishes (e.g., cunners, rock gunnells, radiated shannys, sculpins, and flounders) progressively increased along the bathymetric gradient, reaching highest density at the deeper zone (18–20 m depth; one-way ANOVA,  $P < 0.01$ ; a *posteriori* SNK test) (Fig. 3C). A large proportion of these fish, however, were cunners which comprised about 80% of the total number of individuals observed in the transects. Cunners exhibited a distribution pattern similar to the one described for total fish

(one-way ANOVA,  $P < 0.01$ ; *a posteriori* SNK test; Fig. 3D). In contrast to adult cunners, juvenile cunners (<5 cm) comprised more than 90% of the total cunners sighted in the first three depth stations (i.e., 2–8 m depth) along the transects.

The number of shelters (a measure of substrate heterogeneity) significantly increased with depth (one-way ANOVA,  $P < 0.01$ ; Fig. 3E). This increment is due to the increasing number of large rounded rocks observed at the deeper (10–20 m) transects which create large numbers of interstices (holes) suitable for predators' occurrence.

## Discussion

A diverse assemblage of mobile predators inhabits the shallow rocky subtidal zone at Pemaquid Point, Maine. These subtidal habitats are utilized by these species for multiple purposes such as nursery grounds, feeding grounds, shelter, and reproductive activities (Olla et al. 1975, MacDonald et al. 1984, Keats et al. 1987, Ojeda 1987). The occurrence and abundance patterns of these species are, however, markedly seasonal and closely follow the temperature regime typical of northwest Atlantic waters. This suggests that temperature is one of the major abiotic factors affecting the distribution of these predator species on this coast, a finding in agreement with other studies (Tyler 1971; Hacunda 1981; Ennis 1984b; MacDonald et al. 1984; Keats et al. 1986, 1987).

Four temporally distinct components were recognized in this predator assemblage: summer–fall residents, regular residents, summer periodicals, and occasionals. Similarly, Tyler (1971) distinguished four temporal groups in the demersal fish assemblage occurring in Passamaquoddy Bay, New Brunswick, which have also been recognized in other demersal ichthyofaunas of the Gulf of Maine (Hacunda 1981, MacDonald et al. 1984). Three of the four categories of Tyler (1971) were recognized in this study: “regulars,” “summer periodicals,” and “occasionals.” No representatives of Tyler's (1971) fourth category (“winter periodicals”; i.e., species occurring only during winter) were found in this study. This result, however, should be taken cautiously because no samples were taken in midwinter. The most conspicuous and abundant species of mobile predators in this study were summer–fall residents (e.g., cunners, pollock, lobsters, and sculpins), which occurred for most of the warm period in shallow rocky habitats. Summer–fall residents undergo small-scale migrations, moving into deeper, warmer water ( $>4^{\circ}\text{C}$ ) during winter and returning to shallow subtidal areas in spring. These seasonal movements occur in response to changes in water temperature and prob-

ably to physical disturbances such as strong water surges and storms along some exposed coasts. This seasonal migratory behavior represents a behavioral strategy to avoid freezing that involves no physiological adjustment. An alternative strategy involves the elaboration of macromolecules which possess unique anti-freeze properties (e.g., glycopeptides in sea raven and winterflounder: Duman and De Vries 1974, Slaughter et al. 1981).

There are conflicting results in the literature concerning winter migration and activity of cunners and lobsters. Several authors have shown that cunners and lobsters do not migrate into deeper waters during winter (Green and Farwell 1971, Cooper et al. 1975, Olla et al. 1975, Dew 1976). However, investigations have shown that cunners (Chao 1973) and lobsters (Ennis 1984b) move to deeper waters in winter as suggested in this study. Recently, Ennis (1984b) showed that small-scale movements of lobsters in Newfoundland were related to increased turbulence due to storms. This is a likely explanation for the absence of lobsters and cunners during winter at Pemaquid Point in this study. As mentioned above, Pemaquid Point is an exposed site (Ojeda 1987). During winter, this area is severely affected by periodic storms and heavy water motion that usually generate strong turbulence over a wide depth range. For organisms that remain in dormant states in shallow waters during winter (such as cunners), water movements may severely restrict their distribution. Most studies documenting the presence of cunners in inshore habitats during winter have been conducted in bays or in other protected areas away from heavy water motion (e.g., Green and Farwell 1971, Olla et al. 1975, Dew 1976). In contrast, documentation of offshore movements of cunners during winter comes from studies conducted on exposed coasts, such as that of Chao (1973). A similar situation seems to occur in lobsters (Ennis 1984b) and probably with crab species which strongly suggests that water movement from turbulence and heavy surge is an important factor, in addition to water temperature, affecting the temporal and spatial distribution of large organisms in shallow subtidal environments of the Gulf of Maine.

Shallow rocky subtidal habitats along the northern New England coast harbor a diverse community of marine organisms providing abundant food resources to seasonal fish residents, occasional migratory fish species, and large crustacean predators (Ojeda 1987). This is so despite the general paucity of kelp beds in this coast, which are an important determinant of the abundance and diversity of nearshore fish and large decapod crustaceans on other temperate coasts (Quast 1968, Moreno and Jara 1984). In addition to acting as feeding grounds, shallow rocky environments also

provide large mobile predators with microhabitats for shelter against predation, and bases for reproductive activities and nursery grounds. Of particular relevance in these environments is the spatial heterogeneity of the bottom. Large rocks and boulders which typically occur at depths greater than 10 m at the study site are important microhabitats for territorial predatory species such as cunners and lobsters (Pottle and Green 1979, Ennis 1984a). The increased number of lobsters and fish (mostly cunners) observed along the bathymetric gradient is probably related to the availability of such microhabitats (see Figure 3). As shown elsewhere (Ojeda and Dearborn 1989), the substrate heterogeneity at Pemaquid Point progressively increases with depth as bottom irregularities such as cracks, crevices, holes, and rocks become more common. In addition to microhabitat availability, the observed bathymetric distribution of large predators may represent an avoidance response by these species to strong water turbulence and wave surge that commonly affect the shallower end of this subtidal zone (especially at low tides).

The occurrence in this study of numerous juvenile pollock and cod provides a good example of the importance of shallow, rocky, subtidal zones as nursery grounds as shown by MacDonald et al. (1984) and Keats et al. (1987). Juvenile pollock were the most abundant species of the nearshore fish assemblage (Table 1). These findings, in addition to feeding data presented elsewhere (Ojeda 1987), suggest that pelagic fish species may play important roles in rocky nearshore benthic communities by affecting the distribution and abundance of their benthic prey. Moreover, the one-way offshore migration exhibited by these species indicates that they may be important linkages in the transfer of energy from nearshore to offshore ecosystems.

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