

Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: seasonal and bathymetric distribution*

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ABSTRACT: Community structure of the macroinvertebrate fauna inhabiting a rocky subtidal habitat at Pemaquid Point, Maine, USA, was studied, using qualitative and quantitative descriptions of the distribution, diversity and abundance of benthic species, as well as their spatial (bathymetric) and temporal (seasonal) changes. A total of 60 species of macroinvertebrates representing 9 phyla were found in the 133 (0.25 m²) disruptive benthic samplings obtained by SCUBA between August 1984 and October 1986. Crustaceans, mollusks and polychaetes were best represented accounting for ca 77 % of the total number of species identified. Green sea urchin *Strongylocentrotus droebachiensis* and horse mussel *Modiolus modiolus* were consistently the most important (in biomass and density) assemblage components. Bathymetrically, there were clear patterns in the composition and abundance of macroinvertebrates. Sea urchins decreased in abundance with depth (from 5 to 18 m), while the opposite was observed in horse mussels. Distribution and abundance patterns of remaining benthic macroinvertebrates were strongly influenced by the spatial distributions of sea urchins (at 5 and 10 m depth) and horse mussels (at 18 m). Species richness was higher in the deepest zone (18 m; 41 species) than in the shallower zones (5 and 10 m; 34 and 31 species respectively), due to the presence of clumps of *M. modiolus*. Comparative analysis at 18 m depth showed that the invertebrate fauna within *Modiolus* beds is significantly more abundant, dense, and diverse than that outside pointing out the functional importance of *Modiolus* beds in providing spatial refuges from predators, and suitable and stable microhabitats for numerous invertebrates. No significant temporal changes were observed in the biomass and density of the invertebrate community. Number of species, however, showed marked seasonal variations. Maximum values occurred during summer, intermediate values in fall and spring, and minimum values in winter, probably related to migration or changes in activity of some species. Results of this and other studies indicate that coralline communities, despite their low primary productivity, are ecological systems with relatively high species diversity and secondary productivity, sometimes comparable to systems dominated by kelps.

INTRODUCTION

Kelp forests and systems dominated by encrusting organisms and sea urchins are probably the most conspicuous and prevalent communities of rocky subtidal habitats of most temperate coasts (Mann 1972, Miller & Mann 1973, Steneck 1978, 1986, Duggins 1980, Ayling 1981, Choat & Schield 1982, Moreno & Sutherland

1982, Hagen 1983, Logan et al. 1984, Santelices & Ojeda 1984, Dayton 1985a, b, Sebens 1985, 1986a, b, Johnson & Mann 1986a). Characteristically, kelp forest communities are highly productive and structurally complex. Because of the ecological and economic importance of kelp species, communities dominated by these large brown algae have been studied extensively throughout the world (e.g. reviews by North 1971, Dayton 1985).

In contrast, communities dominated by encrusting organisms such as crustose coralline algae and large herbivores such as sea urchins have low productivity and species diversity, and in general have received relatively little attention.

Crustose coralline communities (or 'barren grounds'

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sensu Lawrence 1975) have recently stimulated considerable research particularly on ecological mechanisms responsible for their origin and maintenance. Basically, kelp forest and crustose coralline communities have been shown to represent alternative states (Mann 1977, Harrold & Reed 1985, Scheibling 1986). The transition from one state to the other is usually attributed to changes in the abundance of sea urchins. At high densities, urchins are known to deplete the marine flora (mostly kelp), producing large 'barren' patches dominated by crustose red algae. The nearshore ecosystem along coastal Atlantic Canada (Nova Scotia) has recently experienced this kind of dramatic change of state. Destructive overgrazing by sea urchins transformed kelp forests into crustose coralline communities in the mid 1960's, and the more recent (in the 1980's) mass mortalities of sea urchins have caused the recovery of kelp (Mann 1977, Pringle et al. 1980, Wharton & Mann 1981, Miller 1985, Scheibling 1986; see Pringle 1986 for review).

Rocky subtidal habitats of the New England (USA) coast are dominated largely by crustose coralline communities (Steneck 1986), dense populations of green sea urchins *Strongylocentrotus droebachiensis* and a diverse fauna both of sessile and mobile forms (Steneck 1978, 1986, Larson et al. 1980, Logan et al. 1983, 1984, Sebens 1985, 1986a, Witman 1985). In these environments, kelp species (mainly *Laminaria* and *Alaria*) and other macroalgal associations are in general less common, usually occupying a narrow zone in shallow waters, or a more extensive band in some protected habitats where urchins are absent or rare (Sebens 1985, 1986a; pers. obs.). Vertical rocky surfaces of these subtidal habitats support diverse assemblages of organisms, usually dominated by a suite of encrusting invertebrate species (Sebens 1986a, b).

The distributional patterns and other relevant aspects of the ecology of crustose coralline algal species inhabiting subtidal rocks of the Gulf of Maine have recently been documented by Steneck (1978, 1982) and Garwood et al. (1985). Similarly, the structure and organization of several encrusting invertebrate communities occurring in the sublittoral zone of the New England coast have been examined by Osman (1977) and Sebens (1982, 1986a, b). Other important aspects related to the community organization of these subtidal systems have recently been reported by Witman (1985) and Harris (1986).

Studies describing invertebrate macrofauna inhabiting crustose coralline communities in the Gulf of Maine are also limited. Although Logan et al. (1983) have recently described spatial patterns of distribution of the species comprising coralline-dominated communities of the Bay of Fundy (New Brunswick, Canada), other important autecological aspects of some of the most

conspicuous macroinvertebrates as well as temporal changes in the structure of such communities remain unknown.

This study describes the community structure of macroinvertebrates inhabiting a crustose coralline community in a rocky subtidal habitat off the coast of Maine. This characterization involves qualitative and quantitative descriptions of the distribution, diversity and abundance of benthic macrofauna as well as their spatial (bathymetric) and temporal (seasonal) changes. Large mobile predators (such as decapod crustaceans and fish of large size) are excluded in this study as well as the epibenthic invertebrate fauna typical of vertical walls. The large mobile fauna associated with this community is discussed separately elsewhere (Ojeda & Dearborn unpubl.). As noted previously, the invertebrate assemblages inhabiting vertical and undercut rocky surfaces have been analyzed extensively by Sebens (1982, 1986a, b; and papers cited therein).

The ecological patterns described in this study have important implications since they provide a base line for future research and the required ecological background toward our understanding of the organization and the dynamic processes operating in this kind of community.

DESCRIPTION OF STUDY SITE

This study was conducted in the shallow subtidal zone off the southwest end of Pemaquid Point, Maine, USA (43° 50' N; 69° 31' W) (Fig. 1). The site is exposed to the prevailing southeast ocean swells and consists of a sloping bedrock surface extending down to ca 18 to 20 m depth (Fig. 2). The shallower portion of this bedrock (between 12 and 15 m depth) consists of a broad ledge. The substrate here is relatively flat, almost free of silt and cobble, and occasionally cut by crevices and small cracks. Large rocks and boulders are commonly found on shelves of bedrock at depths of 15 to 20 m. The substrate at depths greater than 20 m consists primarily of sand with occasional round boulders (Fig. 2).

The zonation pattern of species found in the study area is quite uniform and representative of wave-exposed habitats of the New England coasts. The shallowest subtidal zone (0 to 5 m below Mean Low Water Level; MLWL) at this site is clearly dominated by macroalgal species. Extending from the low intertidal zone to the uppermost sublittoral zone there is a conspicuous belt of *Chondrus crispus*. A narrow band of kelp species (primarily *Laminaria saccharina*, *L. digitata*, and *Alaria esculenta*) occurs immediately below the *Chondrus* zone. Most of these kelps, however, are juveniles (less than 1 m long) with few adult individuals

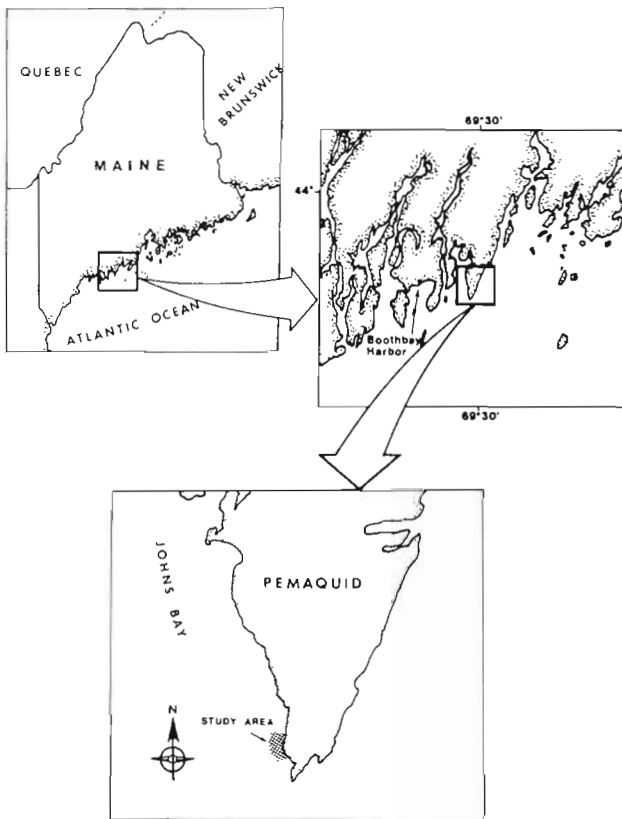


Fig. 1. Maine, USA, showing location of study site

reaching sizes larger than 2 m. The understory of the kelp zone is mostly composed of dense tufts of *Coralina officinalis*, and small patches of *Phycodrys rubens*, *Phyllophora* sp., and *Ceramium rubrum*. The deeper border of the macroalgal zone is occupied by a diverse algal turf primarily consisting of elongated individuals

of *Enteromorpha* spp. *Ulva* spp. *Chordaria flagelliformis*, *Polysiphonia* spp., *Chaetomorpha melagonium* and *C. linum* (Fig. 2).

Most of the primary substratum (ca 70 to 80 %) across the rock ledge (between 4 and 15 m depth) is covered by crustose coralline algae which form a nearly continuous pink carpet. A similar situation is observed on the top surfaces of the rocks and boulders found in the deeper zone (between 15 and 20 m depth). The shallow portion of the coralline zone (between 4 and 15 m) is dominated by the corallines *Lithothamnium glaciale*, *L. lemoineae*, *Clathromorphum circumscriptum*, and *Phymatoliton rugulosum*. The top surfaces of the large boulders and rocks of this zone (between 16 to 20 m) are mostly dominated by *Lepthophytum laeve* and *Phymatolithon laevigatum*. A detailed description of the crustose coralline assemblages inhabiting this locality was given by Steneck (1978).

The most conspicuous organism inhabiting horizontal and sloping rock surfaces of the coralline zone is the green sea urchin *Strongylocentrotus droebachiensis*, which forms dense aggregations extending from 3 to 12 m deep. At this location green urchins occur to depths of 20 to 25 m, however, their abundance declines sharply below 15 m (Fig. 2). Patchily distributed clumps of the horse mussel *Modiolus modiolus* occur at depths of 10 to 20 m. Their large shells are usually covered with encrusting coralline algae, barnacles, and small tunicates. The interstices between the mussels and the web of byssus threads create a suitable habitat and shelter for numerous invertebrate organisms. At the deeper edge of the rocky boulder field (ca 17 to 20 m) isolated individuals of *Agarum cribosum* are usually found attached to top surfaces of large rocks and boulders (Fig. 2).

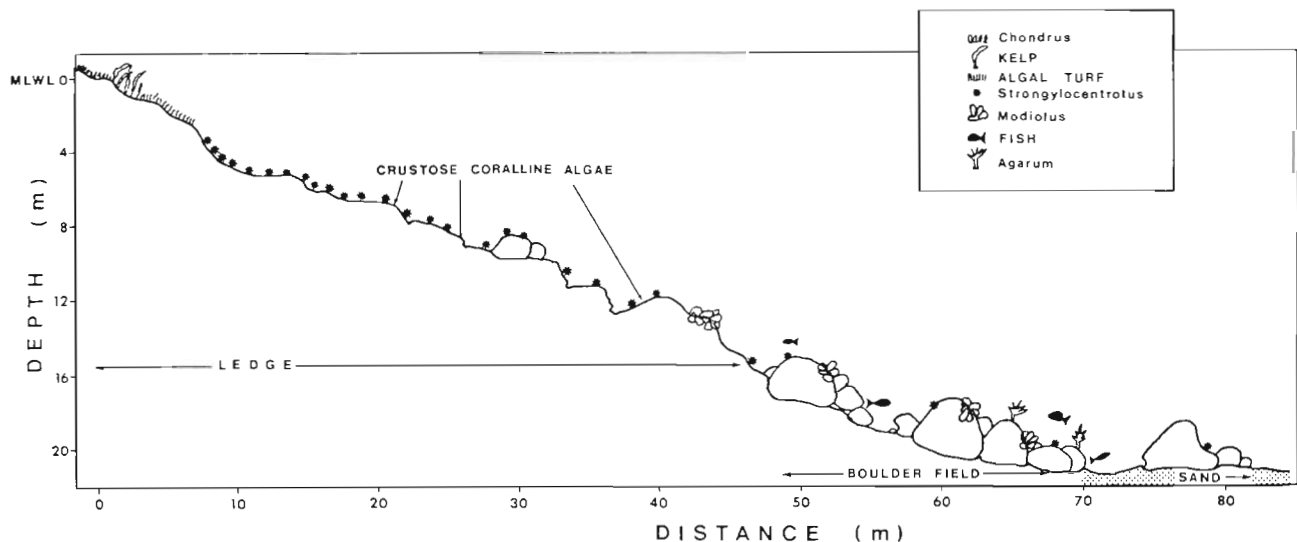


Fig. 2. Transectional view of a typical subtidal coralline community at Pemaquid Point, Maine

MATERIALS AND METHODS

Nine disruptive samplings were conducted seasonally using SCUBA from August 1984 to October 1986. In each of the seasonal samplings several transects were carried out perpendicular to the shore. Four to 8 quadrat samples (0.25 m^2) (Pringle 1984) were randomly taken from 3 different depth ranges (4 to 6 m, 9 to 11 m, and 16 to 20 m; hereafter designated 5, 10 and 18 m respectively) according to a stratified random sampling design (Elliott 1977). All macroinvertebrates found within the quadrat were removed from the substrate with the aid of scraping knives and forceps. The organisms then were either manually collected and deposited in diver sampling bags of 1 to 2 mm mesh size or vacuumed with an airlift device (Chess 1978, Witman 1985). All sampled organisms of each quadrat were placed in labelled plastic bags, fixed in a 5 to 10 % solution of buffered (borax) formalin-seawater mixture, and transported to the laboratory for analysis.

In the laboratory, the organisms were sorted, identified to the lowest taxon possible, usually to species, counted, measured with a caliper to the nearest 0.1 mm and weighed on a Mettler P1200 balance to the nearest 0.1 mg.

In order to establish spatial patterns of species associations, a cluster analysis based on Ward's method which uses Euclidean distance as a metric (CLUSTER Procedure; SAS 1986) was performed using mean density values at 3 depths (5, 10 and 18 m) of the 24 most abundant macroinvertebrate taxa found in the samples. The data on macroinvertebrate densities and biomasses were tested for homogeneity of variances using the F_{\max} test (Sokal & Rohlf 1981). The results of this test on densities and biomasses showed that the variances were nonhomogeneous over the bathymetric and temporal gradients studied. Therefore a logarithmic transformation ($\log [n+1]$; Sokal & Rohlf 1981, p. 419) was used on all these data before further analysis. One-way ANOVA followed by a Student-Newman-Keuls (SNK) multiple comparison test (Sokal & Rohlf 1981) were employed for the detection of changes in density and biomass of macroinvertebrates over bathymetric and temporal gradients.

RESULTS

Community structure

A total of 60 species of macroinvertebrates representing 9 phyla were found in the 133 (0.25 m^2) benthic samples collected from August 1984 to October 1986 (Table 1). Crustaceans, mollusks and polychaetes are the best-represented taxonomic groups with 18, 14,

and 14 species respectively. They account for about 77 % of the total number of species recognized in these samples (Table 1).

The green sea urchin *Strongylocentrotus droebachiensis* is numerically the most important macroinvertebrate in this community with average density of 100 ind. m^{-2} , and accounting for about 56 % of the total number of individuals collected in the benthic samples (Table 2). *Modiolus modiolus*, *Tonicella ruber*, and *Ophiopholis aculeata* are the next species in the ranking of abundances, with density values of ca 9 to 13 ind. m^{-2} (Table 2). The remaining 56 species (93 % of the total number of species) contribute together only 23.8 % of the total number of individuals collected. Few of these 56 species however, are represented with more than 1 ind. m^{-2} (Table 2).

Strongylocentrotus droebachiensis is the dominant species in biomass in the samples with an average biomass of 2699 g m^{-2} , representing 65.5 % of the total biomass (Table 2). It is followed by *Modiolus modiolus*, with average biomass of 1303 g m^{-2} (30.9 % of the total biomass). These 2 species together account for about 95 % of the total biomass of macroinvertebrates (Table 2). Most of the remaining 58 species are represented with less than 10 g m^{-2} , contributing relatively little to the overall biomass in this community (usually less than 1 %; Table 2).

Spatial patterns

The bathymetric range of distribution of all macroinvertebrate species found in the samples is also presented in Table 1. Fifteen species (25.4 % of the total) restrict their bathymetric distribution exclusively to the shallowest subtidal zone sampled (5 m). Most of these species were gastropod mollusks (e.g. *Lacuna vincta* and *Littorina littorea*), and small crustaceans such as amphipods and isopods (Table 1). Most of the species of this group were found associated with the macroalgal turf typical of this sublittoral zone (Fig. 2). Two other species (3.4 % of the total) were exclusively found at depths of 5 and 10 m, while a group of 17 species (28.8 % of the total) was widely distributed along the bathymetric gradients analyzed (Table 1). The most abundant species of this community (e.g. sea urchins, mussels, chitons, brittle stars; see Table 2) belong to this group (Table 1). Two other groups of species were found to be restricted to the deepest zone: one composed of 9 species (15.2 % of the total) which occur at depths of 10 and 18 m; and, another group of 13 species (22.4 %) found only in the 18 m samples (Table 1). Most of the species of this latter group were closely associated with the *Modiolus* clumps.

The total number of species (species richness) was markedly higher in the samples taken at 18 m depth

(41 species, 69.5 % of the total) and lower at the intermediate depth of 10 m (31 species, 52.5 % of the total). The samples taken at 5 m depth contained a few more species than those found at 10 m depth (34 species, 57.6 %).

An analysis of the bathymetric variation of total macroinvertebrate biomass values (Fig. 3) shows no significant changes with depth (1-way ANOVA; $p > 0.08$). In contrast, the density of invertebrates significantly declines with depth (1-way ANOVA; $p < 0.01$), from

about 60 ind. 0.25 m^{-2} at 5 m depth to about 36 ind. 0.25 m^{-2} at 10 and 18 m (Fig. 3). Analysis of the variations in density and biomass of the 7 most important species of this community (Fig. 3) shows 2 clear bathymetric patterns among these species: (1) a general decrease of both biomass and density with depth, exhibited by *Strongylocentrotus droebachiensis* and *Asterias vulgaris* (1-way ANOVA; $p < 0.01$ in both species), and (2) a general increase of both density and biomass with depth, exhibited by *Modiolus modiolus*,

Table 1 Taxonomic list and bathymetric distribution (depth range) of the macroinvertebrate species found in subtidal benthic samples taken at Pemaquid Point, Maine

Species	Depth range (m)	Species	Depth range (m)
PORIFERA		<i>Pherusa plumosa</i> (Muller)	18
<i>Scypha ciliata</i> Fabricius	10–18	<i>Capitella capitata</i> (Fabricius)	18
<i>Halicondria panicea</i> (Pallas)	5	<i>Pectinaria granulata</i> (Linnaeus)	18
<i>Cliona celata</i> Grant	18	ARTHROPODA (Crustacea)	
PLATYHELMINTHES		Cirripedia	
<i>Notoplana atomata</i> (Muller)	5–10	<i>Balanus balanoides</i> (Linnaeus)	10
NEMERTEA		Isopoda	
<i>Amphiphorus</i> sp.	18	<i>Idothea balthica</i> (Pallas)	5
CNIDARIA		<i>Idothea phosphorea</i> Harger	5
Anthozoa		Amphipoda	
<i>Metridium senile</i> (Linnaeus)	5–18	<i>Gammarus oceanicus</i> Segerstrale	18
MOLLUSCA		<i>Gammarellus angulosus</i> (Rathke)	5–18
Gastropoda		<i>Calliopius laeviusculus</i> (Kroyer)	5–10
<i>Crepidula fornicata</i> Linnaeus	10–18	<i>Jassa falcata</i> (Montagu)	5
<i>Crepidula plana</i> Say	10–18	<i>Unciola inermis</i> (Say)	5
<i>Tectura</i> (= <i>Acmaea</i>) <i>testudinalis</i> (Muller)	5–18	<i>Caprella linearis</i> (Linnaeus)	5
<i>Lacuna vincta</i> (Montagu)	5	<i>Caprella septentrionalis</i> Kroyer	5
<i>Littorina littorea</i> (Linnaeus)	5	<i>Aeginella longicornis</i> (Kroyer)	5
<i>Buccinum undatum</i> (Linnaeus)	10–18	Decapoda	
<i>Nucella</i> (= <i>Thais</i>) <i>lapillus</i> (Linnaeus)	5–18	<i>Cancer irroratus</i> Say	5–18
Polyplocophora		<i>Cancer borealis</i> Stimpson	5–18
<i>Tonicella ruber</i> (Linnaeus)	5–18	<i>Hyas araneus</i> (Linnaeus)	5
Bivalvia		<i>Lebbeus polaris</i> (Sabine)	18
<i>Mytilus edulis</i> Linnaeus	5	<i>Evalus pusiolus</i> (Kroyer)	5–18
<i>Modiolus modiolus</i> (Linnaeus)	5–18	<i>Crangon septemspinosa</i> Say	18
<i>Hiatella arctica</i> (Linnaeus)	10–18	<i>Pagurus pubescens</i> Kroyer	5–18
<i>Mya arenaria</i> Linnaeus	5	ECHINODERMATA	
<i>Astarte subequilata</i> Sowerby	18	Asteroidea	
<i>Spisula solidissima</i> (Dillwyn)	18	<i>Asterias vulgaris</i> (Verrill)	5–18
ANNELIDA		<i>Henricia sanguinolenta</i> (Muller)	5–18
Polychaeta		Ophiuroidea	
<i>Lepidonotus squamatus</i> (Linnaeus)	5–18	<i>Ophiopholis aculeata</i> (Linnaeus)	5–18
<i>Harmothoe imbricata</i> (Linnaeus)	5–18	Echinoidea	
<i>Harmothoe oerstedii</i> (Linnaeus)	18	<i>Strongylocentrotus droebachiensis</i> (Muller)	5–18
<i>Amphitrite johnstoni</i> Malmgren	10–18	Holothuroidea	
<i>Pista maculata</i> (Dalyell)	10–18	<i>Psolus fabricii</i> (Duben and Koren)	10
<i>Thelepus cincinnatus</i> (Fabricius)	10–18	<i>Cucumaria frondosa</i> (Gunnerus)	5–18
<i>Eulalia viridis</i> (Linnaeus)	5	CHORDATA	
<i>Eteone longa</i> (Fabricius)	18	Ascidacea	
<i>Nereis pelagica</i> Linnaeus	5–18	<i>Dendrodoa carnea</i> (Agassiz)	10–18
<i>Potamilla reniformis</i> (Leuckart)	5	<i>Molgula</i> sp.	10–18
<i>Nainereis quadricuspida</i> (Fabricius)	18		

Table 2. Average density (ind. m⁻²) and average biomass (g m⁻²) of the 22 most abundant macroinvertebrate taxa found in the 133 subtidal benthic samples collected at Pemaquid Point, Maine. In parentheses: standard error

Taxon	Density	Biomass
<i>Strongylocentrotus droebachiensis</i>	100.4 (74.0)	2699.0 (1416.4)
<i>Modiolus modiolus</i>	14.4 (11.2)	1303.2 (960.0)
<i>Tonicella ruber</i>	13.3 (6.8)	1.5 (0.8)
<i>Ophiopholis aculeata</i>	8.8 (7.2)	7.2 (5.6)
Polychaetes	8.8 (2.0)	1.6 (0.4)
<i>Asterias vulgaris</i>	6.0 (2.0)	4.4 (2.8)
<i>Tectura testudinalis</i>	4.0 (0.8)	2.4 (0.8)
<i>Lacuna vineta</i>	0.2 (0.1)	0.2 (0.1)
Amphipods	3.7 (2.1)	•
<i>Idothea</i> spp.	2.4 (1.1)	•
<i>Caprella</i> spp.	1.7 (0.9)	•
<i>Cancer</i> spp.	1.0 (0.3)	0.3 (0.1)
<i>Crepidula</i> spp.	0.9 (0.4)	0.9 (0.3)
<i>Dendrodoa carnea</i>	0.7 (0.3)	•
<i>Balanus balanoides</i>	0.6 (0.1)	4.0 (2.7)
<i>Mya arenaria</i>	0.5 (0.1)	0.7 (0.2)
<i>Nucella lapillus</i>	0.6 (0.3)	0.2 (0.1)
<i>Hiatella arctica</i>	0.5 (0.1)	0.9 (0.2)
<i>Buccinum undatum</i>	0.5 (0.2)	0.2 (0.1)
<i>Crangon septemspinosa</i>	0.5 (0.2)	•
<i>Pagurus pubescens</i>	0.3 (0.1)	0.1 (0.1)
<i>Eualus pusiulus</i>	0.3 (0.1)	•

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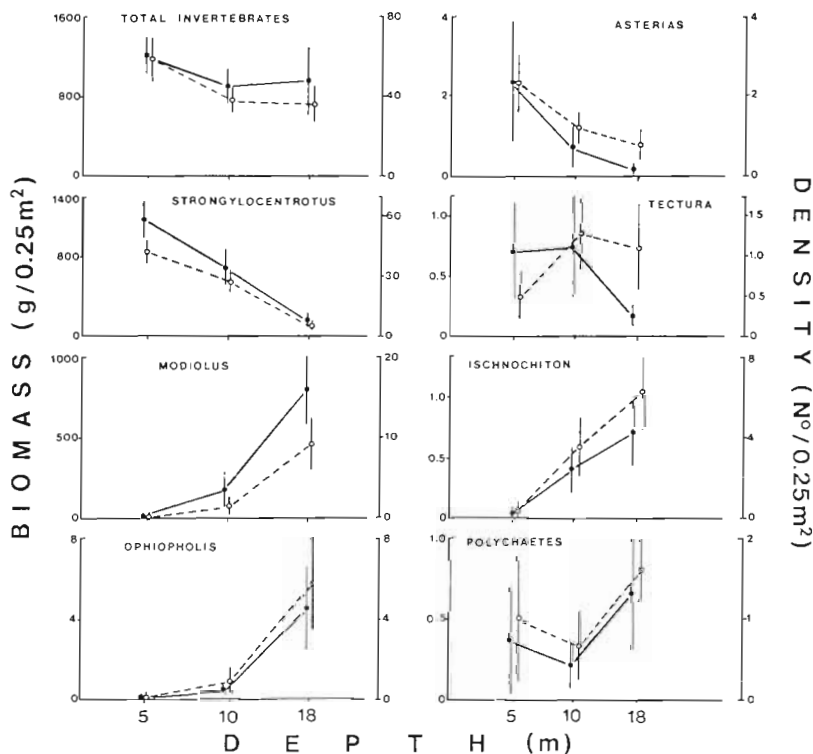


Fig. 3. Bathymetric variation in biomass ($\bar{X} \pm 2$ SE; ●) and density ($\bar{X} \pm 2$ SE; ○) of total invertebrates, and of the 7 most common invertebrate taxa occurring in the subtidal benthic community studied

Ophiopholis aculeata and *Tonicella ruber* (1-way ANOVA; $p < 0.01$ in all these species). Limpet *Tectura testudinalis* shows a significant decline in biomass from

10 to 18 m depth (1-way ANOVA; $p < 0.01$; and a posteriori SNK test) with no significant differences between 5 and 10 m. The bathymetric variation of the

densities of *T. testudinalis* (Fig. 3) shows, however, a significant increase from 5 to 10 m (1-way ANOVA; $p < 0.01$, and a posteriori SNK test). The opposite trends in biomass and density exhibited by *Tectura* suggest that the mean size of their individuals decrease with depth.

Polychaetes (all species grouped) show no significant bathymetric change in their abundances (both in biomass and density; 1-way ANOVA; $p > 0.20$ and $p > 0.17$, respectively) (Fig. 3). The bathymetric patterns of variation observed in this group of polychaetes is probably due to their association with other benthic species such as macroalgae which were occasionally found within the quadrats sampled at 5 m. The hold-fasts of these macroalgae and the sediment accumulated among them probably provide suitable microhabitats for some polychaete species such as *Nereis pelagica* and *Lepidonotus squamatus*. A similar situation occurs at 18 m depth, but in this case it is the presence of *Modiolus modiolus* which significantly increases the opportunities of microhabitat utilization for the polychaete fauna. At this depth (18 m) there is also a greater number of polychaete species (12; see Table 1) with 6 of them living exclusively within the *Modiolus* beds.

The cluster analysis separated the 24 commonest species of benthic invertebrates into 2 major groups (Fig. 4). The first cluster (A) is formed by 14 taxa that were most abundant at 5 and/or 10 m depth. The most abundant species of Group A is the sea star *Asterias vulgaris* which appears closely associated with some species that are typical of the intertidal-subtidal border such as *Lacuna vineta*, *Idothea* spp., and juvenile *Cancer* spp. Another important component of Group A in the cluster is the limpet *Tectura testudinalis*, which shows its maximum abundance on shallow rocks usually covered by the crustose coralline alga *Clathromorphum circumscriptum* (Steneck 1982; pers. obs.). This alga has recently been shown to be the dominant crustose species in shallow rocks at Pemaquid Point (Garwood et al. 1985).

The second group recognized in the cluster (Group B; Fig. 4) consists of 11 species. Their association in this group reflects that they all attain maximum abundances around the 18 m depth. The most conspicuous organism of this group is the horse mussel *Modiolus modiolus*, which commonly forms patchy clumps at around 18 m and is the dominant species in terms of biomass in the deepest zone (Fig. 3). Other important species of Group B are the ophiuroid *Ophiopholis aculeata* and the red chiton *Tonicella ruber*. The spatial distributions of these 2 species as well as of the remaining species forming Group B, however, are not random at the 18 m depth. Indeed, the distribution and abundance patterns of most of these species, as well as of a

significant number of other species not included in the cluster analysis, are strongly correlated with the presence of the *Modiolus* clumps typical of this zone (Figs. 2 and 3). A comparative analysis of the differential distribution of macroinvertebrates found at 18 m depth within *Modiolus* beds (16 quadrats), and outside *Modiolus* beds (18 quadrats) shows that the invertebrate fauna inhabiting *Modiolus* clumps is significantly more abundant, dense, and diverse than the fauna occurring outside the beds (Table 3). Sea urchins are significantly most numerous (but not largest) within the *Modiolus* beds as are *O. aculeata*, *T. ruber*, and the polychaete fauna (Table 3). In the latter categories, however, both biomass and densities are significantly higher within the mussel beds than outside them (Table 3). Note, however, that at 18 m depth (*Modiolus* zone), *Strongylocentrotus droebachiensis*, in contrast to *O. aculeata* and *T. ruber*, occurs at much lower densities than in the shallow zones (Fig. 3). Similar results have been reported by Witman (1985) for the benthic community occurring inside and outside beds of *M. modiolus* at the Isles of Shoals, Maine.

Strongylocentrotus droebachiensis does not show any significant association with any of the species analyzed in the cluster in Fig. 4. This means that the

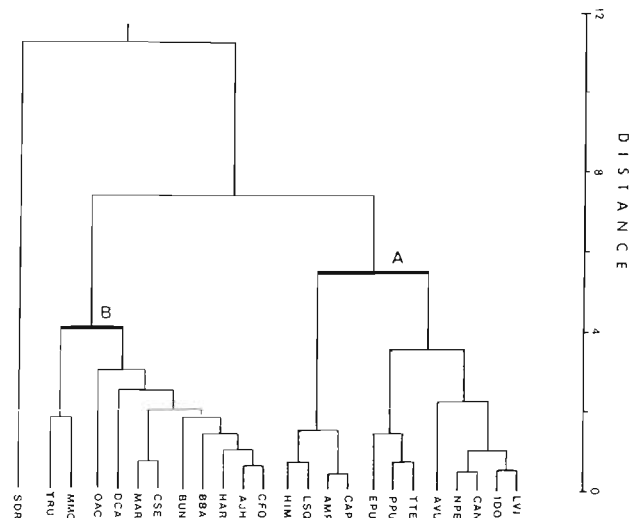


Fig. 4. Dendrogram of similarity (expressed as the Euclidean distance) based upon the mean density values of the 24 most common taxa found at 3 depths (5, 10 and 18 m) in a subtidal coralline community at Pemaquid Point, Maine. LVI = *Lacuna vineta*; IDO = *Idothea* spp.; CAN = *Cancer* spp.; NPE = *Nereis pelagica*; AVU = *Asterias vulgaris*; TTE = *Tectura testudinalis*; PPU = *Pagurus pubescens*; EPU = *Eualus pusillus*; CAP = *Caprella* spp.; AMP = amphipods; LSO = *Lepidonotus squamatus*; HIM = *Harmothoe imbricata*; CFO = *Crepidula fornicata*; AJH = *Amphitrite johnstoni*; HAR = *Hiatella arctica*; BBA = *Balanus balanoides*; BUN = *Buccinum undatum*; CSE = *Crangon septemspinosa*; MAR = *Mya arenaria*; DCA = *Dendrodoa carnea*; OAC = *Ophiopholis aculeata*; MMO = *Modiolus modiolus*; TRU = *Tonicella ruber*; SDR = *Strongylocentrotus droebachiensis*

Table 3. Comparisons of the biomass and density of invertebrates, number of species, and abundance patterns of 4 invertebrate species found in 16 and 18 quadrats of 0.25 m² taken at 18 m depth inside and outside *Modiolus* beds, respectively. Biomass is expressed in g, density in no. of individuals

Taxon	Inside Mean \pm SE	Outside Mean \pm SE	t-statistic
Invertebrates			
Biomass	1590.8 \pm 250.5	295.2 \pm 56.6	5.325**
Density	53.5 \pm 6.0	14.4 \pm 2.4	5.685**
No. of species	9.9 \pm 0.9	3.5 \pm 0.6	5.466**
<i>Strongylocentrotus droebachiensis</i>			
Biomass	164.6 \pm 46.8	145.2 \pm 32.8	0.354
Density	8.0 \pm 1.6	3.4 \pm 0.7	2.744**
<i>Ophiopholis aculeata</i>			
Biomass	7.5 \pm 2.3	1.3 \pm 2.9	3.689**
Density	9.7 \pm 2.5	1.2 \pm 0.4	3.689**
<i>Tonicella ruber</i>			
Biomass	0.9 \pm 0.2	0.3 \pm 0.1	2.524*
Density	8.6 \pm 1.6	2.6 \pm 0.5	3.734**
Polychaetes			
Biomass	0.9 \pm 0.4	0.1 \pm 0.05	1.989*
Density	4.1 \pm 1.1	1.2 \pm 0.4	2.651**

* p < 0.05; ** p < 0.01

abundance patterns of sea urchins do not seem to be correlated with any other invertebrate species pattern.

Seasonal patterns

Temporal variations in the occurrence of all macroinvertebrate species found in the 9 subtidal seasonal samples taken at Pemaquid Point are summarized in Table 4. Of the total of 59 species collected in all these samples, 13 (22%) of them were consistently found in all seasonal samples and seemingly constitute permanent populations in this community (*Crepidula fornicata*, *Tectura testudinalis*, *Tonicella ruber*, *Modiolus modiolus*, *Hiatella arctica*, *Lepidonotus squamatus*, *Harmothoe imbricata*, *Nereis pelagica*, *Balanus balanoides*, *Calliopius laeviusculus*, *Asterias vulgaris*, *Ophiopholis aculeata* and *Strongylocentrotus droebachiensis*). As noted above, these are also the most abundant species in this community (Table 2). The presence of the 46 remaining species was restricted to some months or seasons of the year (Table 4). Most were of a rare occurrence in the samples and generally were represented by few individuals. Some show, however, a consistent temporal pattern of occurrence in the samples (e.g. *Nucella lapillus*, *Idothea* spp., *Pagurus pubescens* and *Jassa falcata* which occur in the summer samples; Table 4), while others do not exhibit any clear seasonal pattern.

An analysis of the temporal variation of the total

number of species found in each of the 9 seasonal samples (Table 4) shows a clear pattern, with maximum values of species richness occurring in summer samples intermediate values during the spring samples, and minimum values in the fall and winter samplings. Since sample size (effort) was quite similar among seasons (see Table 4) the diversity pattern found does not represent a sampling artifact.

Temporal variations in biomass and density of the macroinvertebrate fauna is shown in Fig. 5. In general, no significant change was observed for the invertebrate biomass values at any of the 3 depths (1-way ANOVA; p = 0.52, p = 0.23, and p = 0.62 at 5, 10, and 18 m, respectively).

Analysis of the temporal density values, however, showed (Fig. 5) a significant pattern of variation at 5 m depth, with one statistically significant peak in October 1984 (1-way ANOVA; p < 0.03, a posteriori SNK test). No peak, however, was observed in October 1986. The density values observed for 10 and 18 m depth did not disclose any clear significant temporal pattern of variation (1-way ANOVA; p = 0.57 and p = 0.90, respectively; Fig. 5).

Analysis of the temporal changes in the abundance of *Strongylocentrotus droebachiensis* shows that at 5 m depth there was a significant increase in density in October 1984 (1-way ANOVA; p < 0.03 and a posteriori SNK test; Fig. 6). With respect to biomass changes at 5 m (Fig. 6), no significant differences were detected among these values (1-way ANOVA; p = 0.08). No

Table 4. Presence of macroinvertebrate species found in 9 seasonal subtidal transects carried out at Pemaquid Point, Maine. Presence (X) indicates occurrence of a given species in at least one of the 16 to 30 quadrats of 0.25 m² sampled in each transect

Taxon	1984			1985				1986	
	Aug	Oct	May	Sep	Nov	Feb	Jun	Aug	Oct
PORIFERA									
<i>Scypha ciliata</i>				X				X	
<i>Halicondria panicea</i>		X	X	X	X		X		X
<i>Cliona celata</i>	X								X
PLATYHELMINTHES									
<i>Notoplana atomata</i>	X			X					
NEMERTEA									
<i>Amphiphorus</i> sp.				X				X	
CNIDARIA									
Anthozoa									
<i>Metridium senile</i>	X		X				X	X	
MOLLUSCA									
Gastropoda									
<i>Crepidula fornicata</i>	X	X	X	X	X	X	X	X	X
<i>Crepidula plana</i>	X	X		X		X		X	X
<i>Tectura testudinalis</i>	X	X	X	X	X	X	X	X	X
<i>Lacuna vincta</i>				X					
<i>Littorina littorea</i>	X			X	X			X	
<i>Buccinum undatum</i>	X	X		X					X
<i>Nucella lapillus</i>	X	X		X	X		X	X	
Polyplocophora									
<i>Tonicella ruber</i>	X	X	X	X	X	X	X	X	X
Bivalvia									
<i>Mytilus edulis</i>				X		X			
<i>Modiolus modiolus</i>	X	X	X	X	X	X	X	X	X
<i>Hiatella arctica</i>	X	X	X	X	X	X	X	X	X
<i>Mya arenaria</i>				X					
<i>Astarte subequilatera</i>				X					
<i>Spisula solidissima</i>								X	
ANNELIDA									
Polychaeta									
<i>Lepidonotus squamatus</i>	X	X	X	X	X	X	X	X	X
<i>Harmothoe imbricata</i>	X	X	X	X	X	X	X	X	X
<i>Harmothoe oerstedii</i>								X	
<i>Amphitrite johnstoni</i>	X	X	X	X	X		X	X	X
<i>Pista maculata</i>						X			
<i>Thelepus cinnatus</i>						X			
<i>Eulalia viridis</i>					X				
<i>Eteone longa</i>					X			X	
<i>Nereis pelagica</i>	X	X	X	X	X	X	X	X	X
<i>Potamilla reniformes</i>					X		X		
<i>Naineris quadricuspida</i>					X				
<i>Pherusa plumosa</i>			X			X			
<i>Capitella capitata</i>						X			
<i>Pectinaria granulata</i>			X					X	
ARTHROPODA (Crustacea)									
Cirripedia									
<i>Balanus balanoides</i>	X	X	X	X	X	X	X	X	X
Isopoda									
<i>Idothea balthica</i>		X		X				X	X
<i>Idothea phosphorea</i>	X			X			X	X	

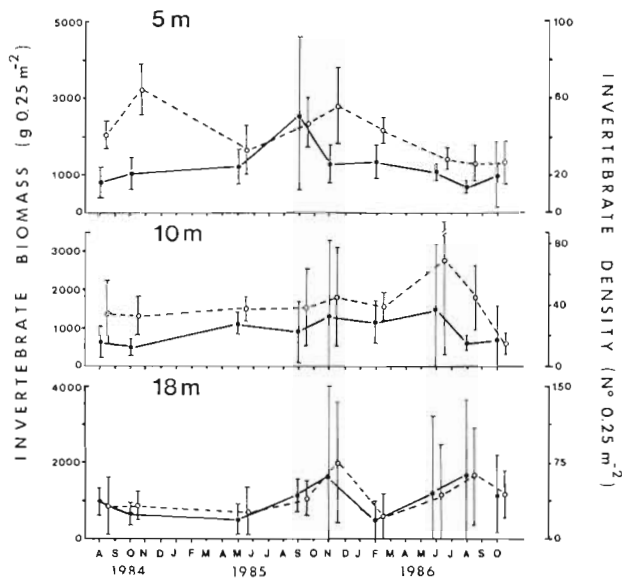


Fig 5. Temporal changes in biomass ($\bar{X} \pm 2$ SE; ●) and density ($\bar{X} \pm 2$ SE; ○) of macroinvertebrates at 3 depths (5, 10 and 18 m)

undercut rocky surfaces were not investigated in this study. They generally harbor different kind of benthic communities, usually dominated by sponges and tunicates. Recently, such communities have been studied by Noble et al. (1976), Sebens (1982, 1986a, b), Logan et al. (1984) and Witman (1985).

Relatively little is known about rocky sublittoral benthic communities of the Gulf of Maine, particularly regarding their composition and community structure. Comparable sublittoral studies conducted by Noble et al. (1976) and Logan et al. (1983, 1984) in the Bay of Fundy, Canada, have recognized the existence of 2 distinctive types of benthic communities occupying different microhabitats: the crustose coralline algae community, which is dominant on upper surfaces from 0 to 20 m depth, and the community dominated by the brachiopod *Terebratulina septentrionalis*. Communities dominated by this brachiopod occur cryptically on the undersides of rocks and crevices of the upper sublittoral zone dominated by crustose algae (0 to 20 m depth), and on upper surfaces of rocks and ledges at greater depths (> 20 m) (Noble et al. 1976, Logan et al. 1983, 1984). Logan et al. (1983) reported a total of 84 species of invertebrates inhabiting crustose coralline communities in the Bay of Fundy; most of these species were the same as those reported in this study. The differences in the specific composition and total number of species between this study and of Logan et al. (1983) is probably due to the fact that those authors included invertebrate species found both on horizontal rocky surfaces and vertical walls. A

similar situation occurs when our results are compared with those reported by Witman (1985) for the rocky sublittoral zone off the Isles of Shoals, Maine. He reported a total of 171 invertebrate species of which 80 were frequently found in the benthic samples. Witman's (1985) study showed strong similarities in community composition with this study. Most of the invertebrate species found at Pemaquid Point were also recorded in similar subtidal habitats off the Isles of Shoals (see Table 1 in this study and Table A1 in Witman 1985). Furthermore, horizontal habitats studied by Witman (1985) and in this study were both dominated by sea urchins, horse mussels, chitons and limpets. The observed differences in number of species with Witman's (1985) study are probably attributable to the greater depth of the Isles of Shoals communities (30 m), and to the inclusion of the invertebrate fauna typical of vertical walls in that study.

Although crustose coralline communities have often been considered systems of very low diversity and productivity (for which they have been named 'barren grounds' or 'barren communities', see Lawrence 1975 for review), the results of this study and those cited above demonstrate that, despite their low primary productivity, coralline communities are ecological systems with relatively high species diversity and secondary

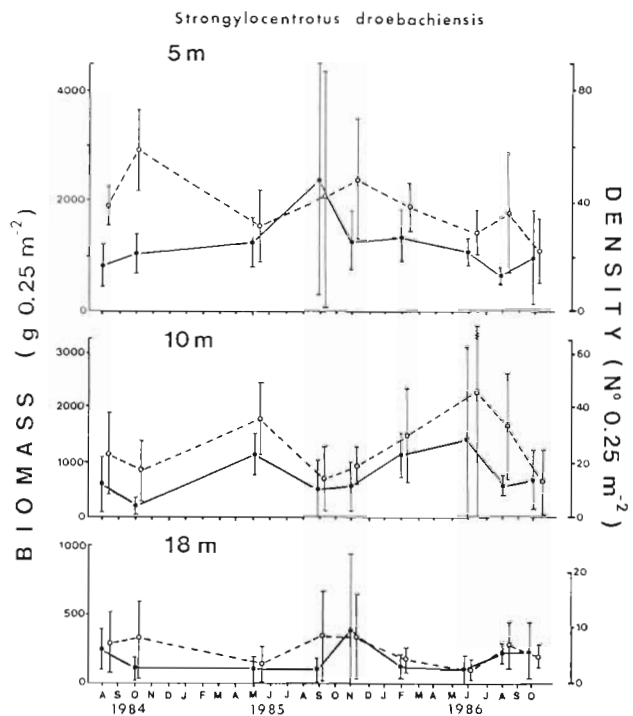


Fig 6. *Strongylocentrotus droebachiensis*. Temporal changes in biomass ($\bar{X} \pm 2$ SE; ●) and density ($\bar{X} \pm 2$ SE; ○) at 3 depths (5, 10 and 18 m)

productivity, sometimes comparable to systems dominated by kelps (e.g. Shannon's H diversity index for macroinvertebrates = 1.83 in this study and $H = 2.23$ in Ojeda & Santelices 1984). Accordingly, the term 'barren ground' should be used more cautiously, only in reference to the general absence of macroalgae due to heavy overgrazing by sea urchins. In this study we use the term 'crustose coralline communities' because we believe it clearly denotes the most evident algal feature of these systems.

This study shows clear bathymetric trends in the composition and abundance of macroinvertebrates. The observed patterns of species distribution, however, are strongly influenced by the particular spatial distribution of the 2 most abundant invertebrate species in this community: *Strongylocentrotus droebachiensis* and *Modiolus modiolus* (Table 2). The shallow zone (3 to 12 m depth) is mostly dominated by sea urchins which from dense aggregations of up to 240 ind. m^{-2} , and comprise more than 90 % of the total biomass at these depths (Table 2). This zone is strongly affected by the grazing activities of sea urchins, which at these high densities are able to limit the distribution and abundance of almost any fleshy macroalgae. Experimental removals of green urchins conducted by Breen & Mann (1976) in Nova Scotia, and by Himmelman et al. (1983) in the St. Lawrence estuary, have demonstrated their ecological importance in determining diversity, abundance and distributional patterns of macroalgal species. The recent mass mortalities of urchins and the dramatic growth of fleshy algae along the Nova Scotia eastern coasts (Miller & Colodey 1983, Scheibling & Stephenson 1984, Scheibling 1986) have confirmed, on a large scale, the importance of sea urchins in rocky sublittoral environments. Crustose coralline algae, however, remain relatively unaffected by sea urchins because of their effective structural defense mechanisms against grazing (Paine & Vadas 1969, Steneck 1982, 1986, Johnson & Mann 1986a), thus monopolizing most of the primary substrate of rocky surfaces of sublittoral habitats, as observed in this study.

Most of the invertebrate species found exclusively at 5 m depth were typical intertidal forms that extended their distribution to the shallowest sublittoral zone (e.g. gastropod mollusks and amphipods), or were species closely related to the macroalgal turf of this shallow zone (e.g. polychaetes and small clams). The existence of this macroalgal turf as well as of a narrow band of kelp in the uppermost portion of the sublittoral zone (0 to 2 m below MLWL) is due to the general absence of sea urchins in this zone. Strong water movements, and wave turbulence, in addition to sea bird predation (Himmelman & Steele 1971) are probably major factors limiting the distribution of sea urchins into this shallow-

est subtidal zone, and the low intertidal zone as well (Himmelman 1986). The large aggregations of urchins in the shallow zone (5 m depth) were commonly observed feeding on drift algae as reported elsewhere (Lawrence 1975, Johnson & Mann 1982, Himmelman 1986, Sebens 1986a).

The reduction in number of species, and in abundance of invertebrates observed in the mid-sublittoral zone (9 to 11 m depth), is probably a result of intense grazing by *Strongylocentrotus droebachiensis*. The general absence of particular microhabitats that usually provide spatial refuges from predators may also contribute to this phenomenon. Indeed, the bedrock in the mid-sublittoral zone is markedly flat with few topographic irregularities such as large crevices and small cracks. Such spatial refuges are particularly relevant because sea urchins also feed upon a number of invertebrate species (Himmelman et al. 1983, Witman 1985, Sebens 1986a). Sea urchins, therefore, in addition to the mobile predator fauna of these environments, may be also exerting important influences in the abundance and distributional patterns of invertebrates in this community (Himmelman & Steele 1971, Keats et al. 1984, Witman 1985, Johnson & Mann 1986b, Ojeda & Dearborn unpubl.).

In the Gulf of Maine, settlement of *Strongylocentrotus droebachiensis* larvae has been shown to be random (Harris et al. 1984). The relative scarcity of sea urchins found in the deeper zone (16 to 20 m depth; Fig. 3) is probably related to differential survival. Low survivorship of urchins in this zone could be a result of low availability of food, or of heavy mortality exerted by the abundant mobile predators found at these depths (Ojeda & Dearborn unpubl.).

The change in species composition of macroinvertebrates observed at the deeper zone (18 m depth) as well as the marked increase in species richness (Table 1) were associated with increases in the abundance of *Modiolus modiolus* occurring in this zone (i.e. to the large numbers of individual *Modiolus* clumps; Fig. 3). Indeed, most of these macroinvertebrate species occur exclusively inside *Modiolus* beds (Table 3). A similar phenomenon has been documented in other populations of *M. modiolus*. Brown & Seed (1977), for example, found 90 invertebrate taxa associated with subtidal clumps of *M. modiolus* in Northern Ireland. Similarly, subtidal *Modiolus* beds off the Isles of Shoals studied by Witman (1985) contained significantly higher densities of invertebrates (infauna) than other subtidal habitats.

Experimental studies conducted by Witman (1985) on the ecological causes of such differential distribution and abundance of invertebrates have shown a functionally important role of *Modiolus* beds as spatial refuges from predators. This role, which is a by-product

of the structural complexity of mussel beds (Witman 1985, Suchanek 1986), is particularly significant because it has been suggested that predation and grazing by urchins are major determinants of community structure in New England rocky subtidal habitats (Witman 1985).

Modiolus clumps, however, also provide suitable and stable microhabitats for numerous invertebrates that are probably more important for specific life history processes of these species than for protection from predators (Brown & Seed 1977). This is probably the case with some infaunal organisms such as polychaetes and clams inhabiting the sediment and detritus that usually accumulate at the base of the mussels (Witman 1985, Suchanek 1986, pers. obs.). These kinds of microhabitats are relatively rare on rocky substrates, which explains why some of these species were exclusively found inside the mussel beds. Alternatively, the shells and the intertices between the mussels, as well as the web of byssus threads, may represent optimal feeding grounds for some epifaunal species. This is likely the situation occurring with some suspension and filter feeders such as barnacles, tunicates and ophiuroids which exploit the turbulences and slow water flows created by mainstream currents colliding with individual mussels (Connell 1972, Wainwright & Koehl 1976). Furthermore, because of the 3 dimensional asymmetric configuration of individual mussel clumps (i.e. mussels oriented in different directions) those turbulences (eddies) may also enhance retention of food particles inside the clumps, favoring prey capture in suspension-feeding organisms such as some octocorals and ophiuroids (Patterson 1984, Mary W. Wright pers. comm.).

Although the experimental results presented by Witman (1985) support the predation-refuge hypothesis, additional experiments to test the hypothesis of microhabitat selection are necessary before any conclusion is made on the causes explaining this phenomenon.

The invertebrate community, in general, did not show drastic temporal changes in abundance of organisms (biomass and density; Fig. 5) during the time span of this study (27 mo). However, it could be possible that on a longer temporal scale, these communities might be drastically affected by exceptional climatic events such as violent storms or hurricanes. Along the bathymetric gradient, the general temporal patterns in biomass and density observed in this subtidal community were mostly determined by the abundance pattern exhibited by *Strongylocentrotus droebachiensis* (at 5 and 10 m depth), and by *Modiolus modiolus* in the deeper zone (18 m depth) (Fig. 3). The only significant increase in the abundance (density) of macroinvertebrates was observed in October 1984 at 5 m depth (Fig.

5). It was due to a significant increase in density of *S. droebachiensis* (Fig. 6).

Population dynamic of sea urchins along this coast most likely represents population changes resulting from the combined and compensatory interactions of several processes involving recruitment, migration, and differential predation. Bathymetric migrations, for example, probably occur in response to the more severe climatic conditions observed in the shallowest subtidal zone during winter. Himmelman (1986) found that populations of green sea urchins of exposed locations in Newfoundland migrate in winter to greater depths where they encounter more favourable conditions than shallow habitats. On the other hand, seasonal changes in the abundance of sea urchins in the shallowest zone may well be the result of differential mortalities primarily affecting the juveniles. Drastic temperature changes and severe storms occurring in late fall and winter along New England coasts could account for seasonal mortalities of small sea urchins. Similarly, predation exerted by benthic mobile predators (lobsters, crabs and fishes) has also been shown to drastically affect the abundance and distribution patterns of sea urchins populations in these environments (Himmelman & Steele 1971, Johnson & Mann 1982, Keats et al. 1984, 1986, Witman 1985, Himmelman 1986, Ojeda 1987). Despite all these antecedents, at present, the relative importance of these processes is unclear.

The number of macroinvertebrate species (species richness) showed marked seasonal variations during this study. Maximum values were observed during summer, intermediate values in fall and spring, and a minimum value in winter of 1986 (Table 4). Most of these seasonal changes, however, were due to temporal variations in the occurrence of rare species (Table 4). In contrast, the most conspicuous and abundant species, such as sea urchins, mussels, limpets, chitons and sea stars, were permanent members of this community (Table 4).

The observed seasonal pattern of species richness, therefore, could be ascribed to seasonal inshore movements of some migratory invertebrate species (e.g. shrimps, amphipods), and to seasonal increase in the activity of other species such as gastropods mollusks associated with increasing temperature.

In summary, the results of this study agree with other studies in documenting well-defined patterns of zonation of benthic macroinvertebrates species inhabiting crustose coralline communities of shores of the Gulf of Maine (Noble et al. 1976, Logan et al. 1983, 1984, Sebens 1985, 1986a, Witman 1985). These patterns are the result of the combined effect of several ecological factors such as predation, competition, and physical disturbances (Sebens 1985, 1986b, Witman 1985, Ojeda 1987).

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