THE UNIVERSITY OF MAINE

10.0 Appendices

10.1 APPENDIX A – GULF OF MAINE RESOURCE SUPPLEMENTAL INFORMATION

10.1.1 Appendix A.1 – Journal Articles

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'

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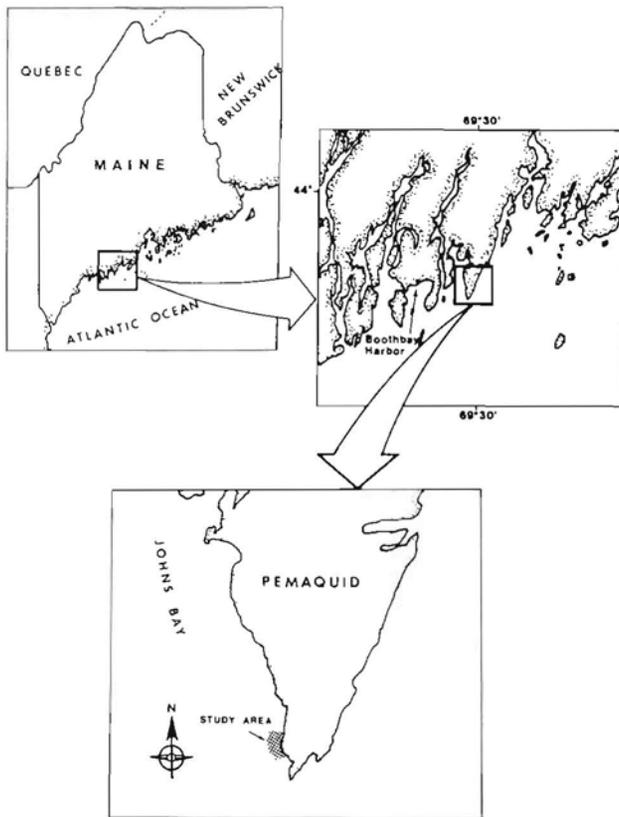
Fig 1. Maine, USA, showing location of study site

of *Enteromorpha* spp. *Ulva* spp. *Chordaria flagelliformis*, *Polysiphonia* spp., *Chaetomorpha melagonium* and *C. linium* (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 weft 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).

reaching sizes larger than 2 m. The understory of the kelp zone is mostly composed of dense tufts of *Corallina 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
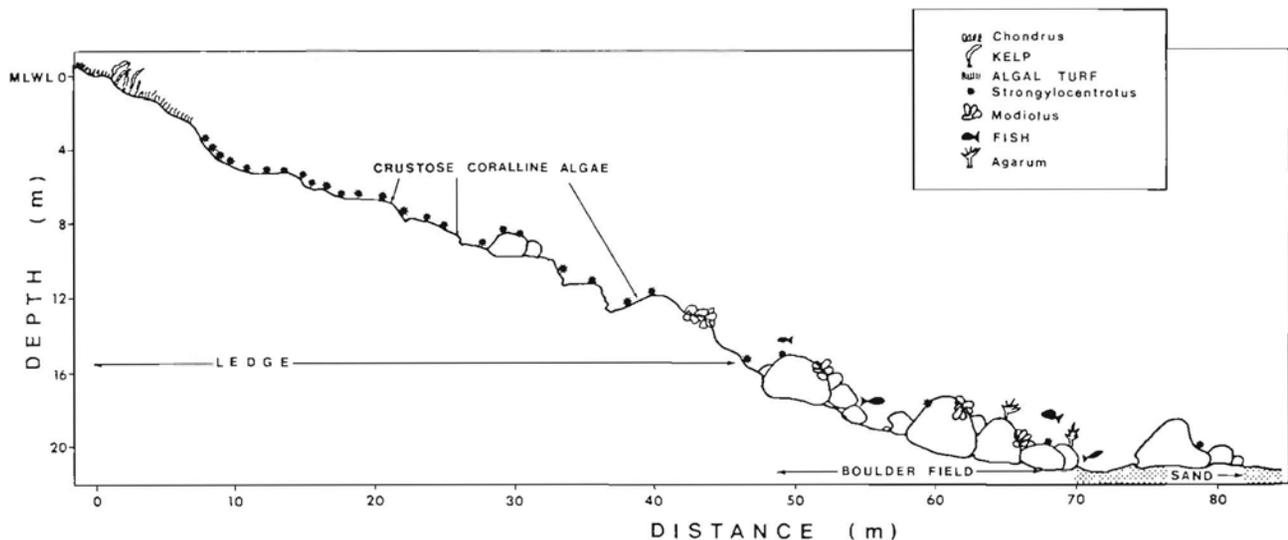

Fig 2. Transectional view of a typical subtidal coralline community at Pemaquid Point, Maine

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		*Pherusa plumosa* (Muller)	18
Scypha ciliata Fabricius	10–18	*Capitella capitata* (Fabricius)	18
Halicondria panicea (Pallas)	5	*Pectinaria granulata* (Linnaeus)	18
Cliona celata Grant	18	ARTHROPODA (Crustacea)	
PLATYHELMINTHES		Cirripedia	
Notoplana atomata (Muller)	5–10	*Balanus balanoides* (Linnaeus)	10
NEMERTEA		Isopoda	
Amphiphorus sp.	18	*Idothea balthica* (Pallas)	5
		Idothea phosphorea Harger	5
CNIDARIA		Amphipoda	
Anthozoa		*Gammarus oceanicus* Segerstrale	18
Metridium senile (Linnaeus)	5–18	*Gammarellus angulosus* (Rathke)	5–18
MOLLUSCA		*Calliopius laeviusculus* (Kroyer)	5–10
Gastropoda		*Jassa falcata* (Montagu)	5
Crepidula fornicata Linnaeus	10–18	*Unciola inermis* (Say)	5
Crepidula plana Say	10–18	*Caprella linearis* (Linnaeus)	5
Tectura (=Acmaea) testudinalis (Muller)	5–18	*Caprella septentrionalis* Kroyer	5
Lacuna vincta (Montagu)	5	*Aeginella longicornis* (Kroyer)	5
Littorina littorea (Linnaeus)	5	Decapoda	
Buccinum undatum (Linnaeus)	10–18	*Cancer irroratus* Say	5–18
Nucella (=Thais) lapillus (Linnaeus)	5–18	*Cancer borealis* Stimpson	5–18
Polyplacophora		*Hyas araneus* (Linnaeus)	5
Tonicella ruber (Linnaeus)	5–18	*Lebbeus polaris* (Sabine)	18
Bivalvia		*Eualus pusiolus* (Kroyer)	5–18
Mytilus edulis Linnaeus	5	*Crangon septemspinosa* Say	18
Modiolus modiolus (Linnaeus)	5–18	*Pagurus pubescens* Kroyer	5–18
Hiatella arctica (Linnaeus)	10–18	ECHINODERMATA	
Mya arenaria Linnaeus	5	Asteroidea	
Astarte subequilatera Sowerby	18	*Asterias vulgaris* (Verrill)	5–18
Spisula solidissima (Dillwyn)	18	*Henricia sanguinolenta* (Muller)	5–18
ANNELIDA		Ophiuroidea	
Polychaeta		*Ophiopholis aculeata* (Linnaeus)	5–18
Lepidonotus squamatus (Linnaeus)	5–18	Echinoidea	
Harmothoe imbricata (Linnaeus)	5–18	*Strongylocentrotus droebachiensis* (Muller)	5–18
Harmothoe oerstedi (Linnaeus)	18	Holothuroidea	
Amphitrite johnstoni Malmgren	10–18	*Psolus fabricii* (Duben and Koren)	10
Pista maculata (Dalyell)	10–18	*Cucumaria frondosa* (Gunnerus)	5–18
Thelepus cincinnatus (Fabricius)	10–18	CHORDATA	
Eulalia viridis (Linnaeus)	5	Ascidiacea	
Eteone longa (Fabricius)	18	*Dendrodoa carnea* (Agassiz)	10–18
Nereis pelagica Linnaeus	5–18	*Molgula* sp.	10–18
Potamilla reniformes (Leuckart)	5		
Nainereis quadricuspida (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	
Strongylocentrotus droebachiensis	100.4	(74.0)	2699.0	(1416.4)
Modiolus modiolus	14.4	(11.2)	1303.2	(960.0)
Tonicella ruber	13.3	(6.8)	1.5	(0.8)
Ophiopholis aculeata	8.8	(7.2)	7.2	(5.6)
Polychaetes	8.8	(2.0)	1.6	(0.4)
Asterias vulgaris	6.0	(2.0)	4.4	(2.8)
Tectura testudinalis	4.0	(0.8)	2.4	(0.8)
Lacuna vincta	0.2	(0.1)	0.2	(0.1)
Amphipods	3.7	(2.1)	•	
Idothea spp.	2.4	(1.1)	•	
Caprella spp.	1.7	(0.9)	•	
Cancer spp.	1.0	(0.3)	0.3	(0.1)
Crepidula spp.	0.9	(0.4)	0.9	(0.3)
Dendrodoa carnea	0.7	(0.3)	•	
Balanus balanoides	0.6	(0.1)	4.0	(2.7)
Mya arenaria	0.5	(0.1)	0.7	(0.2)
Nucella lapillus	0.6	(0.3)	0.2	(0.1)
Hiatella arctica	0.5	(0.1)	0.9	(0.2)
Buccinum undatum	0.5	(0.2)	0.2	(0.1)
Crangon septemspinosa	0.5	(0.2)	•	
Pagurus pubescens	0.3	(0.1)	0.1	(0.1)
Eualus pusiolus	0.3	(0.1)	•	

• Less than 0.1 g
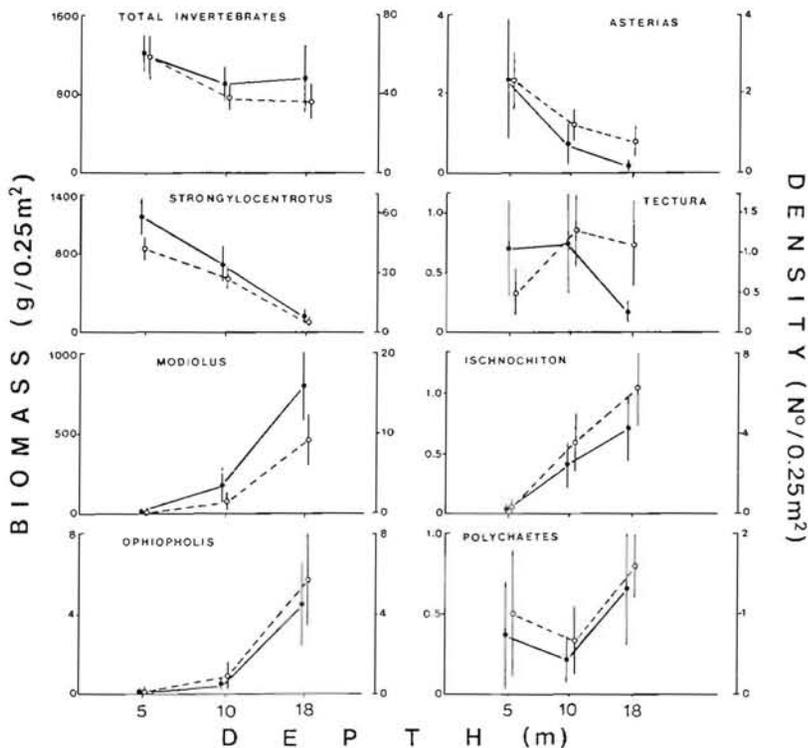
Fig 3. Bathymetric variation in biomass ($\overline{X} \pm 2$ SE; •) and density ($\overline{X} \pm 2$ SE; ○) of total invertebrates, and of the 7 most common invertebrate taxa occurring in the subtidal benthic community studied

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 holdfasts 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 vincta*, *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
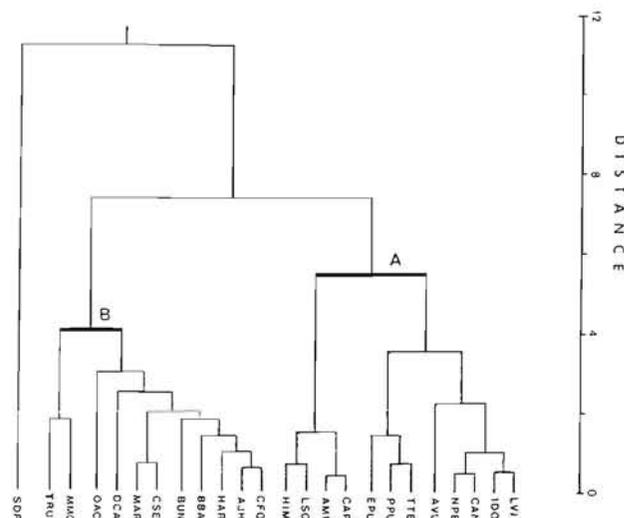

Fig 4. Dendogram of similarity (expressed as the Euclidean distance) based upon the mean density values of the 24 most common taxa found at 3 depths (5, 10 and 18 m) in a subtidal coralline community at Pemaquid Point, Maine. LVI = *Lacuna vincta*; IDO = *Idothea* spp.; CAN = *Cancer* spp.; NPE = *Nereis pelagica*; AVU = *Asterias vulgaris*; TTE = *Tectura testudinalis*; PPU = *Pagurus pubescens*; EPU = *Eualus pusiolus*; CAP = *Caprella* spp.; AMP = amphipods; LSQ = *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 ± SE	Outside Mean ± SE	t-statistic
Invertebrates			
Biomass	1590.8 ± 250.5	295.2 ± 56.6	5.325**
Density	53.5 ± 6.0	14.4 ± 2.4	5.685**
No. of species	9.9 ± 0.9	3.5 ± 0.6	5.466**
Strongylocentrotus droebachiensis			
Biomass	164.6 ± 46.8	145.2 ± 32.8	0.354
Density	8.0 ± 1.6	3.4 ± 0.7	2.744**
Ophiopholis aculeata			
Biomass	7.5 ± 2.3	1.3 ± 2.9	3.689**
Density	9.7 ± 2.5	1.2 ± 0.4	3.689**
Tonicella ruber			
Biomass	0.9 ± 0.2	0.3 ± 0.1	2.524*
Density	8.6 ± 1.6	2.6 ± 0.5	3.734**
Polychaetes			
Biomass	0.9 ± 0.4	0.1 ± 0.05	1.989*
Density	4.1 ± 1.1	1.2 ± 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 statiscally 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 ocurrence 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									
Scypha ciliata				X				X	
Halicondria panicea		X	X	X	X		X		X
Cliona celata	X								X
PLATYHELMINTHES									
Notoplana atomata	X			X					
NEMERTEA									
Amphiphorus sp.				X				X	
CNIDARIA									
Anthozoa									
Metridium senile	X		X				X	X	
MOLLUSCA									
Gastropoda									
Crepidula fornicata	X	X	X	X	X	X	X	X	X
Crepidula plana	X	X		X		X		X	X
Tectura testudinalis	X	X	X	X	X	X	X	X	X
Lacuna vincta				X					
Littorina littorea	X			X	X			X	
Buccinum undatum	X	X		X					X
Nucella lapillus	X	X		X	X		X	X	
Polyplacophora									
Tonicella ruber	X	X	X	X	X	X	X	X	X
Bivalvia									
Mytilus edulis				X		X			
Modiolus modiolus	X	X	X	X	X	X	X	X	X
Hiatella arctica	X	X	X	X	X	X	X	X	X
Mya arenaria				X					
Astarte subequilatera				X					
Spisula solidissima								X	
ANNELIDA									
Polychaeta									
Lepidonotus squamatus	X	X	X	X	X	X	X	X	X
Harmothoe imbricata	X	X	X	X	X	X	X	X	X
Harmothoe oerstedi								X	
Amphitrite johnstoni	X	X	X	X	X		X	X	X
Pista maculata						X			
Thelepus cincinnatus						X			
Eulalia viridis					X				
Eteone longa					X			X	
Nereis pelagica	X	X	X	X	X	X	X	X	X
Potamilla reniformes					X		X		
Nainereis quadricuspida					X				
Pherusa plumosa			X			X			
Capitella capitata						X			
Pectinaria granulata			X					X	
ARTHROPODA (Crustacea)									
Cirripedia									
Balanus balanoides	X	X	X	X	X	X	X	X	X
Isopoda									
Idothea balthica		X		X				X	X
Idothea phosphorea	X			X			X	X	

Table 4 (continued)

| Taxon | 1984 | | 1985 | | | 1986 | | | |
	Aug	Oct	May	Sep	Nov	Feb	Jun	Aug	Oct
Amphipoda									
Gammarus oceanicus	X		X	X	X			X	
Gammarellus angulosus		X		X			X		
Calliopius laeviusculus	X	X	X	X	X	X	X	X	X
Jassa falcata	X			X			X	X	
Unciola inermis				X					X
Caprella linearis	X	X	X		X	X	X	X	
Caprella septentrionalis	X	X		X			X		
Aeginella longicornis	X							X	
Decapoda									
Cancer spp.	X	X		X	X		X	X	X
Hyas araneus	X	X						X	
Lebbeus polaris		X							
Eualus pusiolus						X	X		X
Crangon septemspinosa							X	X	
Pagurus pubescens	X			X			X		
ECHINODERMATA									
Asteroidea									
Asterias vulgaris	X	X	X	X	X	X	X	X	X
Henricia sanguinolenta		X			X			X	
Ophiuroidea									
Ophiopholis aculeata	X	X	X	X	X	X	X	X	X
Echinoidea									
Strongylocentrotus									
droebachiensis	X	X	X	X	X	X	X	X	X
Holothuroidea									
Psolus fabricii	X		X					X	
Cucumaria frondosa	X		X		X			X	X
CHORDATA									
Ascidiacea									
Dendrodoa carnea	X	X			X	X		X	
Molgula sp.	X		X						
No. of species	34	27	23	35	27	22	27	37	23
No. of quadrats (0.25 m^2) sampled	14	27	20	12	12	12	12	12	12

significant density change was observed at 10 m depth (1-way ANOVA; p = 0.11; Fig. 6). A similar pattern was found with respect to the biomass values. In this case, however, a significant decrease was observed in October 1984 and in August 1986 (1-way ANOVA; p < 0.06 and a posteriori SNK test). The temporal variation in the abundance of sea urchins at 18 m (Fig. 6), both in density and biomass, did not disclose any clear pattern, and no statistically significant differences were detected among these values (1-way ANOVA; p = 0.67 and p = 0.81 for density and biomass, respectively).

No clear temporal patterns in density and biomass were observed for Modiolus modiolus at 10 and 18 m depths. Moreover, no significant differences were observed among the density and biomass values at both depths during the seasonal samplings (1-way ANOVA; p = 0.23 and p = 0.22 for density and biomass values respectively at 10 m; and p = 0.60 and p = 0.85

for density and biomass values respectively at 18 m depth). These results, however, should be taken cautiously, because they could represent an artifact of the random sampling associated with the extremely patchy spatial distribution of Modiolus.

DISCUSSION

A total of 60 invertebrate species were recorded in the benthic samples obtained from the subtidal crustose coralline community studied at Pemaquid Point, Maine. Numerous diving observations by one of the authors (F.P.O.) along the coast of Maine indicate that these species seem to constitute the typical invertebrate fauna of horizontal and sloping rock substrates of subtidal environments of this coast. Other conspicuous habitats of these environments such as vertical and
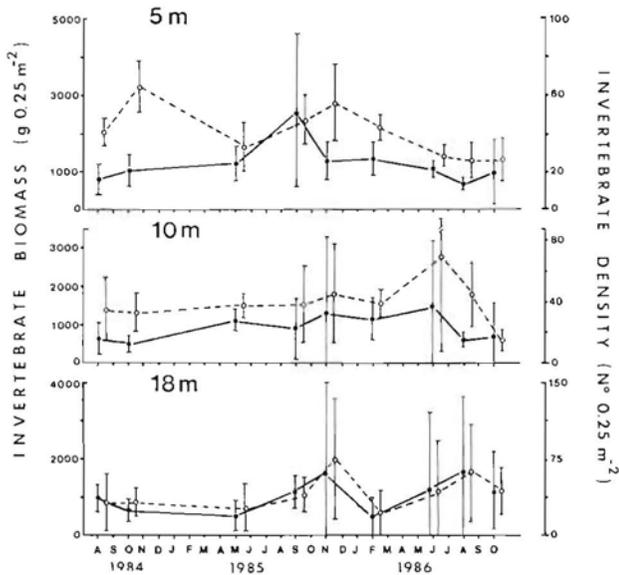
Fig 5. Temporal changes in biomass ($\overline{X} \pm 2$ SE; ●) and density ($\overline{X} \pm 2$ SE; ○) of macroinvertebrates at 3 depths (5, 10 and 18 m)

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
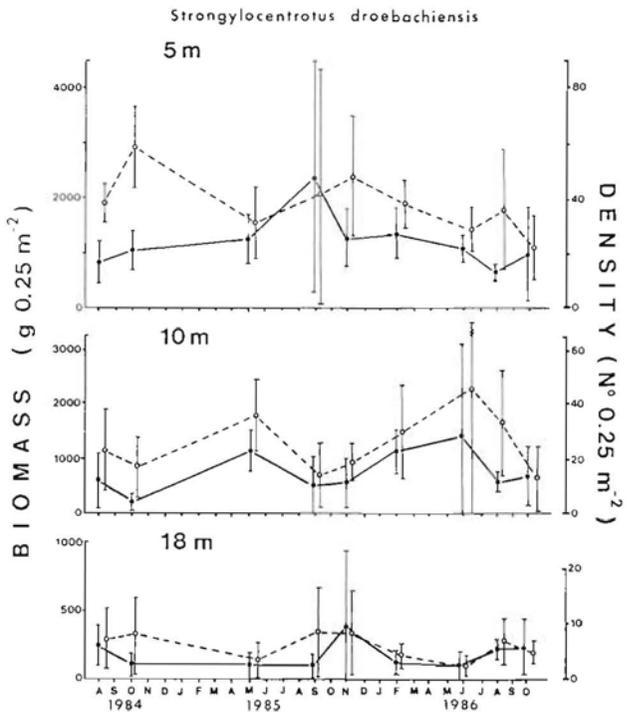

Fig 6. *Strongylocentrotus droebachiensis*. Temporal changes in biomass ($\overline{X} \pm 2$ SE; ●) and density ($\overline{X} \pm 2$ SE; ○) at 3 depths (5, 10 and 18 m)

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, Suchaneck 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, Suchaneck 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 weft 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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SEASON OF ATTACHMENT AND GROWTH OF SEDENTARY MARINE ORGANISMS AT LAMOINE, MAINE [1]

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INTRODUCTION

In recent years a number of studies have been made of the ecology of sedentary marine organisms in various regions. Interest in this subject has been stimulated by the problem of fouling of ships, buoys and other immersed objects. Aside from practical applications these animal and plant communities are of general ecological interest. Examples of papers dealing with this subject are those of Visscher ('27), Coe ('32), Pomerat and Reiner ('42), and Engle & Loosanoff ('44). None have dealt with the faunal region represented by Frenchman's Bay on the Coast of Maine, although a general biological survey of the Mt. Desert region has been made (Procter, '33), and its results have been useful in the present study. The objectives of the study at Lamoine were: (1) To identify the species of "foulers"; (2) To determine the seasonal range of attachment and the time of maximal attachment; (3) To study the growth of individual species after attachment; and (4) To correlate the amount and type of fouling with ecological conditions. Preliminary observations were made during the summer of 1942, and more extensive surveys carried out in 1943 and 1944. Dr. Benjamin Speicher has assisted in identification, and has given valuable suggestions based on several summers' observations at Lamoine.

GENERAL METHODS

Panels for use as collectors were made by cutting in two a 1 ft. by 2 ft. asbestos shingle commonly used for house siding. These are light grey in color, furnish a good surface for attachment and show no sign of deterioration in sea water. These panels were nailed to the side arms of a wooden cross with the flat surfaces in a horizontal position. The panel holders were sometimes anchored and marked by a buoy. In other instances they were suspended from a pier. The 1943 series of panels was mostly anchored. The 1944 series included both types, but accidents and storms caused the loss of most of the anchored group. The panels were exposed according to a schedule which left some immersed for relatively short periods (to determine season of attachment), and others for longer periods (to observe growth.)

During 1943 a number of small celluloid panels, 9×8 cm., were exposed. These proved useful for studying time of attachment, but growth was poor on them and they were not used for growth studies. Film-formers can be observed easily on these transparent sheets.

At each visit during 1943 the surface water temperature was recorded and salinity determinations were made for a period of two months. Results are tabulated in table I.

TABLE I. *Surface water temperatures and salinities at Lamoine, Maine in 1943*

Date	Temperature °C.	Salinity
May 2	4.4	32.66
May 16	7.7	31.96
May 27	8.3	——
June 12	12.2	32.26
June 26	13.3	32.56
July 10	16.1	32.40
July 28	15.6	32.44
Aug. 11	15.6	——
Aug. 22	15.0	——
Sept. 9	13.9	——
Oct. 23	11.0	——

At the end of the exposure period the panels were wrapped individually in cheesecloth and preserved in formalin

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solution. Later the organisms were identified, counted and measured. Organisms attached to buoys, panel holders and ropes were scraped into jars, preserved and studied in a similar manner. Counts of the larger and rarer species were made on the entire panel. Smaller and more abundant organisms were counted in random sq. inch areas and the density of each species calculated in numbers per sq. ft. The rate of attachment has been expressed as numbers per sq. ft. per week (No./sq. ft./wk.).

General Description of the Area

Observations were limited to the vicinity of the University of Maine Marine Biological Laboratory which is located on the northern shore of Eastern Bay, an arm of Frenchman's Bay. In 1943 the first collectors were set out on May 2 and the last ones taken up on October 23. In 1944 the corresponding dates were June 2 and September 25. All but one of the collectors were suspended from the old coaling pier at the station, or were anchored near it. The one exception was exposed at Googin's ledge about one-half mile out from shore. The tidal range in the bay is 10 to 11 feet. A beach of coarse gravel slopes gently to a depth of about 12 feet at mean low water, then drops off rapidly to a depth of 40 feet. The slope is so steep that two collectors slid down and were lost in the deep water. Along the shore are dense beds of *Mytilus edulis*. *Mya arenaria* is fairly common. In the shallow area occur large numbers of the echinoderms, *Asterias vulgaris, Echinarachnius parma* and *Strongylocentrotus drobachiensis*. Rocks on the beach and the pilings on the pier are densely encrusted with the common barnacle, *Balanus balanoides,* between the tide levels. Below the low water mark the pilings are inhabited by *Metridium dianthus, Cucumaria frondosum, Tubularia crocea* and other species of similar habitat. Rockweeds such as *Fucus* are common but do not reach maximum abundance. During the summer this area is subjected to only moderate wave action. Tidal currents are of moderate strength near shore where observations were made.

General Nature of Collections

The collections made are poor in number of species as compared with more southerly regions. As a general thing it may be stated that growth is also slow. At certain seasons of the year, however, the density of attaching forms is very high and approaches the maximum possible concentration. It is possible to classify the species into four groups:

(1) Film formers. These include the diatoms, the minute filamentous or encrusting green and brown algae, together with certain protozoa of the class Suctoria. They can be studied best on glass or celluloid panels. No detailed study of these organisms has been made for this report, although material has been preserved for such a project.

(2) Primary attached forms. These are the barnacles, mussels and hydroids, bryozoans and tubeworms whose planktonic larvae attach to the collectors and develop into the adult form. The larger green and brown algae are also classified in this group.

(3) Casually attached or adherent forms. This is a rather heterogeneous group. On some of the panels large mussels were found which could not possibly have developed directly from their larval form during the period of exposure of the panel. Presumably they had been torn loose from a mussel bed and transported by water currents to the panels. During August both starfish and sea urchins climbed up the anchor ropes to the panels and practically denuded some of them. The sea slug, *Dendronotus arborescens,* and the polychaete *Lepidonotus squamatus* were other casual visitors. Possibly the polychaete, *Polydora ciliata,* should be included here. It occurred in great numbers on panels in sheltered locations during the month of August.

(4) Detritus. This may be either organic or inorganic. Pieces of kelp and

rockweed were frequently entangled with the collectors. These were discarded and not weighed. Silt sometimes accumulated on the upper surfaces of the collectors to a weight of over 1,000 grams/sq. ft. A very striking phenomenon during August, 1943, was the retention of silt by the tubes formed by the spionid worm, *Polydora ciliata*. The mass of tubes and silt covered some panels solidly to a depth of 25 mm. and eliminated other species with the exception of the common mussel. This phenomenon was repeated to a less degree in 1944. To a lesser extent *Obelia articulata* entrapped inorganic silt.

SEASONAL CHARACTERISTICS

The seasonal picture is pieced together from a study of the collected panels and field observation. It would undoubtedly be possible to date events more accurately by carrying out similar observations while in actual residence at the station. Panels were collected or observed at two-week intervals during both summers. The seasonal characteristics of both years are similar, but show some differences.

May (1943): A slight growth of film-forming organisms was the only finding. A filamentous diatom, *Fragillaria* sp., and *Acineta tuberosa* (Suctoria) were abundant. Water temperatures were below 10° C. during this month.

June (1943): A dense growth of algae was evident with *Cladophora rupestris* most abundant. On June 12 actinulae of *Tubularia* were collected. Attachment of *Balanus balanoides* began before June 12, but reached its peak during the latter part of June. It is possible that a few mussel larvae set in the last week of June, but the great peak of the mussel attachment came in July. Among the film-formers were Suctoria, Chlorophyceae and many diatoms.

June (1944): Algae were scant. The Bryozoans, *Electra pilosa*, *Tegella unicornis* and *Hippothoa hyalina*, attached throughout the month. Only a few *Balanus balanoides* and no mussels were found on the panels taken up June 25.

July (1943): The first two weeks in July were characterized by a very heavy set of *Mytilus*. This continued throughout the month, but less intensely. *Tubularia* continued to grow and establish new colonies. A few *B. balanoides* were found to have attached after July 10. Towards the end of the month this species was replaced by *B. crenatus*. New growth of *Cladophora* was very scant. In its stead the panels and ropes showed a development of the hydroid, *Obelia articulata*. During the last two weeks of the month swarms of the spionid worm, *Polydora ciliata*, became evident for the first time. Their activity is described above.

July (1944): *Balanus balanoides* set in large numbers during the first two weeks of this month. The maximum was about 2 weeks later than 1943. *Mytilus* set very heavily between July 9 and July 25. A very few were collected on July 9. *Polydora ciliata* was scarce. Five species of Bryozoa were collected during this month.

August (1943): In August the water temperature began to fall slowly and there was a diminution in the number of new attached forms. *Mytilus* larvae still set, but in tremendously reduced numbers. There was even a regression in total fouling brought about by several factors. Practically all the panels were visited by one or more of the common echinoderm species. In some cases these removed all mussels, algae, barnacles and similar forms. In other instances the cleanup action was less complete. Another cause of reduction was the loosening of the *Polydora* tubes so that wave action or other disturbance caused the entire mass of adherent material to slip off. An interesting sessile protozoan was a blue species tentatively identified as a species of *Platycola*. During August, *B. crenatus* occurs in considerable numbers. Its occurrence, however, was somewhat sporadic and was restricted to the deeper panels.

August (1944): The set of *Mytilus* continued heavy into early August and in

reduced numbers throughout the month. Loss of two panels prevented counting of the late set. *Balanus crenatus* again appeared throughout the month. Large numbers of *Spirorbis spirorbis* were collected. Bryozoan species were similar to those of July.

September and October (1943): It was not possible to visit the station regularly during these months. However, the overall picture was that of a declining population with very little new growth. An exception was *Obelia articulata* which made good growth on panels exposed between September 9 and October 23. Some *Mytilus* were found on the same panels but they were limited to the line of contact between frame and panel. It is probable that they simply shifted their point of attachment a few millimeters. New colonies of *Lichenopora* developed during these months. However on the greater part of the surface of many panels, the only new growth was limited to diatoms. In particular no barnacles attached to test panels set out September 9 or later. *B. balanoides* and *Tubularia* underwent degeneration and were dead or in very poor condition by October 23.

September (1944): Newly attached species during the first half of the month included *Tegella unicornis, Lichenopora verrucaria, Spirorbis spirorbis,* and *Mytilus edulis.* Three panels exposed from September 17 to September 25 showed only *Spirorbis* and a single individual each of *Mytilus edulis* and *Balanus crenatus.* Throughout the month large numbers of young *Anomia simplex* became attached to the panels. The effect of predation was noted in both August and September of this year.

GROWTH RATE OF SEDENTARY ORGANISMS

By a study of the size range of members of a species in the collection from panels exposed for known periods of time, it is possible to construct a curve of growth. Providing the dates of larval attachment are known, one can calculate the extremes in age represented by the individuals on any panel. For example take a species with an attachment period during the month of July. If a panel is set out the first of July and taken up on August 30, the ages of this species will range between approximately four and eight weeks. We may assume that the smallest size group is four weeks old, the largest group is eight weeks old, and others will be intermediate. Results on those species for which adequate data were obtained during the survey are recorded below. When three numbers are given they signify minimum, average and maximum size within the age group. Growth figures for 1943 and 1944 were averaged and no significant difference was found unless specifically indicated. All depths are given relative to mean low water level.

Tubularia crocea:

Attachment period: Macroscopic colonies develop from early July to mid-August. Actinulae of this species were collected June 12, 1943. Maximum attachment during late July and early August.

Density and rate of growth: At 15 ft. from July 23 to Aug. 20, 0.5 per cent of surface/week; from Aug. 4 to Sept. 3, 0.75 per cent of surface/week.

4 weeks: 20 mm. high. Colonies 10–20 mm. in diameter containing 10 to 20 polyps.

8 weeks: 40–60 mm. high. Colonies may contain hundreds of polyps. Great variation between individual colonies.

During September and October there is a great reduction in polyps and only broken stalks were found on October 23, 1943.

Obelia articulata and *O. dichotoma:*

In the early season collections of 1943 and 1944 a species of *Obelia* was found which could not be positively identified because of immaturity. In September and October of 1943 an abundant growth of *O. articulata* was found on many panels. If these were mature individuals

of the earlier type the attachment period may begin as early as late June. It certainly extends into mid-September. Growth is scanty during July, but is rapid during August and September. On Sep. 9, 1943, colonies averaged 40–70 mm. high. On Oct. 23 they ranged from 50–150 mm. (average 100 mm.). Although bulky the weight of this species is low. In 1944 *O. articulata* was not found. A hydroid was found to attach commonly during June and July in 1944, but it grew poorly. Although not well preserved for taxonomic purposes it is believed to be *Obelia dichotoma.*

Bougainvillea carolinensis:

In 1944 this species was found closely associated with *Obelia dichotoma* on two panels exposed at 3 feet. Attachment period in July. Growth scanty. Maximum height, 15 mm.

Balanus balanoides:

Attachment period (1943) : Middle of May to middle of July. Maximum during June. (1944) About two weeks later than in 1943. Maximum during first two weeks of July.

Attachment density on lower surface (1944)

Depth	Dates	No./sq. ft./week
3 ft.	June 25–Aug. 4	340
15 ft.	June 25–July 23	500
30 ft.	July 9–Aug. 4	1340

The growth of the 1943 specimens is tabulated below. The 1944 individuals grew much more slowly and their average growth is approximately the minimum given here. The reason appears to be the unfavorable location of the 1944 group on the lower surface of deep panels. The 1943 series was collected near the surface.

Diameter of base: mm.

Age	Min.	Ave.	Max.
4 weeks	1.0	4.0	8.0
8 weeks	1.5	6.0	9.0
12 weeks	2.0	8.0 (?)	14.0

This species has a very high mortality rate in September and October.

Balanus crenatus:

Late July to mid-September. Maximum probably during the middle of August. Not found at surface or at 3 feet Average growth is similar to that of *B. balanoides,* but the maximum size reached during the season was less. Attachment density, July 23–Sept. 17, 1944, 15 ft., 18/sq.ft./week.

Mytilus edulis:

Attachment period (1943) : Last week in June to the third week of August. Maximum during the first ten days of July.

(1944) Very few during early July. Sudden rise shortly after July 9, and continuous high rate through the first week of August. Continues at a slower rate as late as Sept. 3, but none after Sept. 17.

Attachment density on lower surface (1944)

Depth	Dates	No./sq. ft./week
3 ft.	June 18–July 9	80
3 ft.	July 9–Aug. 4	20,000
3 ft.	Aug. 20–Sept. 3	2,000
3 ft.	Sept. 3–Sept. 17	130

The general picture is similar to that described by Engle and Loosanoff ('44) at Milford, Conn. with the beginning of the attachment period from 3 to 4 weeks later. The decline following the maximum is less abrupt at Lamoine than at Milford.

Approximately equal density was found on the 15 ft. panels, but much lower numbers on the 30 ft. group. This is due in part to the attacks of bottom-dwelling animals on the deep panels, so that the difference is not a measure of rate of attachment. Engle and Loosanoff (*op. cit.*) found attachment all the way to the bottom, but the greatest depth studied was 6 ft.

The measurements given below were made on mussels of the 1943 collections and represent the length of the valve in millimeters.

Growth: Length of valve in mm.

Age	Min.	Ave.	Max.
1 week	—	0.25	—
4 weeks	1.0	2.0	4.0
8 weeks	1.0	3.0	5.0
12 weeks	2.0	6.0	8.0
16 weeks	3.0	8.0	18.0

The variation in size increases with advancing age. This is probably due to competition for space. Unfavorably situated animals obtain less food, and are eventually crowded out. Data on growth at different depths was obtained in 1944 and is summarized below:

Average length in mm. of Mytilus *at different depth levels*

Depth	Age	
	4 weeks	11 weeks
Surface float	2.5	8.0
Panel 3 ft.	0.98	6.7
Panel 15 ft.	0.74	2.3
Panel 30 ft.	0.85 (?)	2.0 (?)

All of these mussels were continuously submerged, a favorable factor for rapid growth as has been shown by Coulthard ('29).

Molluscs (other than *Mytilus*):

From July onward a few *Mya arenaria* approximately 2 mm. in length were collected on the panels. A single *Cardium pinnulatum* was found in October, 1943. Large numbers of *Anomia simplex* were collected during late August and September, 1944. Their maximum density of attachment was 3000/sq.ft./week, at 3 ft. between Sept. 3 and Sept. 25.

Spirorbis spirorbis:

This small worm attached from June to September, and seemed to become pro-

Attachment density on lower surface (1944)

Depth	Dates	No./sq. ft./week
15 ft.	June 2–June 18	0.5
15 ft.	June 18–July 9	12.0
15 ft.	July 9–Aug. 4	0—Crowded out by *Mytilus*
15 ft.	Aug. 4–Sept. 3	575.0

gressively more abundant during the season. It is less abundant at 3 ft. than at the two deeper levels.

Bryozoa:

Five species of Bryozoa were identified on the panels in 1944. All are recorded as common in Procter's ('33) survey of the Mt. Desert Region. They were found at all depths and on certain panels were the dominant foulers. In order of abundance they are: *Tegella unicornis, Lichenopora verrucaria, Hippothoa hyalina, Callopora craticula,* and *Electra pilosa.* A few *Tegella* attached in June, but the maximum density (60 to 100/sq.ft./week) was during July and August. The 15 ft. level was preferred. On one panel exposed from June 2 to Sept. 25 *Tegella* covered 40 per cent of the surface with colonies ranging up to 26 mm. in diameter. Average colonies grew from 10 to 15 mm. in diameter. The season and density of attachment of *Lichenopora* were similar, but the growth was much slower. The maximum size of colonies was 7 mm. with an average for 8-week colonies of 5 mm. It was less abundant at 3 ft. than at the two deeper levels. *Electra pilosa* var. *dentata* was found throughout the season in moderate numbers. Although it is commonly stated to be a rapidly growing species, it was overgrown by both *Callopora* and *Tegella.* *Hippothoa* attaches from June to September, but grows more rapidly during August. Four-week colonies are from 3.6–4.0 mm. diameter; six-week colonies have a maximum diameter of 8.5 mm. *Callopora* is predominantly a late summer form. It makes rapid growth and colonies attain a size of 10 mm. in about six weeks.

Cladophora rupestris:

It is uncertain that all the specimens of *Cladophora* were of this species, since some were observed in a very immature condition. It is predominantly an early season form becoming established in May, but making little growth until June and July. At the end of June filaments ex-

tended up to 4 cm. At the end of July the maximum length was about 15 cm. This was the only alga to grow well on the submerged panels or wooden frames. An idea of its growth may be obtained from the following figures for wet weight of material scraped from panels on which this was the dominant form.

Weight of Cladophora from panels (1943)

Depth	Dates	Grams/sq. ft.
Surface	May 2–June 26	7.2
Surface	May 2–July 10	22.0
Surface	May 2–Aug. 28	84.0

Algae:

Ulva lactua, Punctaria latifolia and *Capsosiphon fulvescens* grew well on the wooden floats and occupied most of the available space. Many young mussels were attached to them. The average length of the thallus of each species during the last of August, 1943, was: *Ulva,* 10 cm.; *Punctaria,* 20 cm.; and *Capsosiphon,* 18 cm. The wet weight of these algae ranged from 114 to 176 grams per sq. ft.

WEIGHT OF ORGANISMS AND SEDIMENTS

The wet weights of most samples were taken after preservation in formalin solution. The material was allowed to drain and pressed gently to remove adherent drops, but still contained much capillary water. Most of the 1943 samples were dried at room temperature and reweighed. The average dry weight of 21 samples was 27 per cent of the wet weight.

Conditions at Lamoine favor sedimentation, and heavy accumulations of silt were found on many of the panels. This is a serious hazard for sedentary organisms on the upper surface of the panels. The highest sample weights (ranging from 300 to 1000 grams/sq.ft.) occurred on the upper surface of panels densely covered by *Mytilus* and *Polydora.* The worm tubes helped to hold the sediments in place. It is estimated that 90 to 95 per cent of these samples was inorganic material.

Well developed *Cladophora* in midsummer of 1943 weighed up to 85 grams/ sq.ft. Algae on surface floats attained a weight of 94 to 176 grams/sq.ft. during the summer period of 3 to 4 months. *Mytilus* in practically pure population attained weights of from 60 to over 200 grams/sq.ft. from July to October. *Obelia articulata* was the only other species quantitatively to dominate a panel. Wet weights ranged up to 40 grams per sq. ft. On the lower surfaces of the 1944 panels weights of less than 5 grams/sq.ft. were found after a month's exposure, and seasonal growth reached a maximum wet weight of approximately 50 grams/sq.ft. The weights of organisms on the upper surfaces were less than this, because of smaller numbers and the effects of heavy silt deposits mentioned above.

Except in cases where one form preempts all available space and then increases in mass through growth, there is little correlation between the duration of exposure, and weight of accumulated organisms. Instead the weights seem to depend upon the dominant species, and this in turn is dependent upon the season of exposure and the amount of predation. In Maine waters panels exposed in May are covered with algae, so that later season species do not find a suitable foothold. *Mytilus* is an exception as it attaches readily to algae and to the stalks of hydroids. Panels set out in July and August showed the most rapid fouling due to the great numbers of *Mytilus edulis, Balanus balanoides,* and Bryozoa. Only scattered new growth appeared after August.

EFFECT OF DEPTH, MODE OF SUSPENSION, AND SELECTION OF UPPER AND LOWER SURFACES

As explained above panels were exposed in two different ways. One group was anchored so that it remained at a fixed distance above the bottom. Another series was suspended from the Marine Station pier. Previous discussions with Dr. L. W. Hutchins of the Woods Hole

Oceanographic Institution, had suggested the possibility that there was a difference between buoy fouling, and the fouling of suspended panels. Unfortunately a heavy storm carried off most of the anchored panels in 1944, so that direct comparison is not possible. The chief difference noted over the two-year period is the more abundant algal growth on the anchored series. This may be due to better illumination in open water, and to smaller accumulation of silt on these panels. Bryozoa grew more luxuriantly on the suspended series. Mussels and barnacles were found equally on each.

The best data on depth distribution come from the panels suspended from the pier in 1944. Relative to mean low water these were placed at depths of 3 ft., 15 ft., and 30 ft. Within this depth range there are no absolute qualitative differences and quantitative differences must be accepted with caution, since the number of panels studied to date is not large enough for statistical analysis. This is particularly true at 30 ft. since these panels were heavily grazed by starfish and sea urchins. Characteristics of depth distribution are summarized for the more important species and groups.

Cladophora grew fairly well on the early season panels at 3 ft. and 15 ft. but was scanty at 30 ft. Hydroids were found at all depths with *Tubularia* most abundant at 3 ft. and *Obelia* at 15 ft. Bryozoa were most abundant and grew best at 15 ft. *Balanus balanoides* set about uniformly at all three depths, but *Balanus crenatus* was restricted to 15 and 30 ft. *Mytilus* set most densely at the two upper levels and grew better near the surface as described above.

There is a striking difference between the fouling of the upper and lower surfaces. The upper surface is more suitable for *Cladophora* and *Polydora* though neither species is restricted to this habitat. The lower surface was much more favorable for barnacles, *Tubularia* and Bryozoa. The count of mussels was higher on the upper surface in 7 instances and on

the lower surface in 18 instances. Because sediments on the upper surface interfere with counting and measurement as well as with the growth of sedentary organisms, the quantitative data of this report have come from the lower surfaces. This result agrees with that of Pomerat and Reiner (*loc. cit.*). These authors discuss the mechanism of attachment in terms of geotropic and phototropic factors. In long periods of exposure such as were used in the Lamoine experiments, silting and predation appear to be the most important factors affecting the success of individuals once they have succeeded in becoming attached. Both of these hazards are greater on the upper surface.

Summary

(1) An investigation of the growth of sedentary organisms at Lamoine, Maine, was carried out during the summers of 1943 and 1944. The more common species are: *Tubularia crocea, Obelia articulata, Obelia dichotoma, Balanus balanoides, Balanus crenatus, Mytilus edulis, Spirorbis spirorbis, Polydora ciliata, Callopora craticula, Electra pilosa, Hippothoa hyalina, Lichenopora verrucaria, Tegella unicornis, Cladophora rupestris, Capsosiphon fulvescens, Punctaria latifolia* and *Ulva lactua.*

(2) Data are presented concerning the seasonal occurrence of these species, their relative abundance and rate of growth. Fouling occurs throughout the period from June to September, but is most rapid during July and August.

(3) Preliminary observations on the influence of depth, method of panel suspension, location and other ecological factors are reported.

Literature Cited

Coe, Wesley R. 1932. Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La-Jolla, California. Bull. Scripps Inst. Oceanog., Tech. Ser. 3: 37–86.

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