



Community Development and Persistence in a Low Rocky Intertidal Zone

Jane Lubchenco; Bruce A. Menge

Ecological Monographs, Vol. 48, No. 1. (Winter, 1978), pp. 67-94.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28197824%2948%3A1%3C67%3ACDAPIA%3E2.0.CO%3B2-L>

Ecological Monographs is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

COMMUNITY DEVELOPMENT AND PERSISTENCE IN A LOW ROCKY INTERTIDAL ZONE¹

JANE LUBCHENCO²

Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138 USA

AND

BRUCE A. MENGE

Zoology Department, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. This paper analyzes the factors controlling the development and persistence of patterns of distribution, abundance, and diversity of space users in the low rocky intertidal zone of New England. The spatial structure of this community changes along a wave exposure gradient. Mussels (*Mytilus edulis*) dominate at headlands exposed to wave shock, the alga *Chondrus crispus* (Irish moss) dominates at sites protected from wave shock, and both are abundant at areas intermediate in exposure to waves. Using a combination of experiments (exclosures, enclosures, removals) and observations, we evaluated the effects of several factors on this system, including (1) predation, (2) herbivory, (3) plant-plant competition, (4) plant-animal competition, and (5) physical disturbance from high-energy waves.

The interaction having the greatest effect on the structure of this low zone association was predation. At protected sites, the starfish *Asterias forbesi*, *Asterias vulgaris*, and the snail *Thais lapillus* prey heavily on *Mytilus*, which is the functionally dominant competitor in the low (and mid) zone(s). When secondary succession is initiated by removal of all erect animals and plants, community development in the absence of these predators (predator exclusion) results in competitive elimination of both the barnacle *Balanus balanoides* and *Chondrus* by *Mytilus*. A similar result occurs if predators are excluded from unaltered stands of *Chondrus*. Controls in these experiments (i.e., with predators present) usually either developed to, or remained as stands of *Chondrus*. At intermediate sites, patches of *Mytilus* occasionally escaped from predation, suggesting predation intensity is patchy in space and time. Persistence of *Chondrus* is thus a by-product of the activities of predators at protected sites. At exposed sites, predators do not control the mussels. As a consequence, *Mytilus* outcompetes *Chondrus* and *Balanus* for space and achieves structural dominance.

Periwinkle abundance decreases, and abundance and seasonality of ephemeral algae increase with increasing wave shock. Results of manipulations during both primary and secondary succession indicate that *Littorina littorea*, the only large, abundant herbivore in the low zone, has no direct effect on perennating (regrowing vegetatively) or established *Chondrus*, or on its extensive, encrusting holdfast. However, this periwinkle exerts an important indirect effect by consuming seasonally abundant ephemeral algae, which slow the rate of succession by suppressing growth of *Chondrus*. Once *Chondrus* is established, *L. littorea* damps variations in its abundance by cropping epiphytic ephemeral algae.

The role of other herbivores seems negligible. Experiments show that limpets and sea urchins potentially could control *Chondrus* (and its holdfast), but they are normally too scarce to have a detectable effect on the algae.

Chondrus thus monopolizes space at protected areas because (1) its competitors (mussels and epiphytic ephemeral algae) are removed by their consumers (predators and herbivores), (2) it has escaped control by herbivores, and (3) it can outcompete other perennial algae by virtue of its ability to perennate, and thus maintain its occupancy of space.

The organization of this portion of the New England rocky intertidal region is thus similar in important ways to that of the mid zone (Menge 1975, 1976). Predation intensity, at least partly a function of wave shock, is great at relatively protected sites and determines the observed structural pattern (domination of space by algae). Since consumers are ineffective in controlling prey at exposed sites, mussels outcompete other space users and monopolize space on the shore. Thus, predators apparently determine the "trajectory" followed during succession. The persistence of algae is strongly dependent on the removal of mussels by predators. Herbivores, though ineffective in controlling the structurally dominant perennial algae, control the abundance of ephemeral algae and hence both determine the rate at which a *Chondrus* bed develops and stabilize established beds of Irish moss by reducing variability in its abundance. Thus, herbivores evidently control the rate of community development (succession) and enhance the persistence of this alga.

Disturbance from wave shock seems to operate in a fashion similar to both types of consumers by removing mussels and ephemeral algae. However, this sort of removal tends to be more catastrophic, frequently clearing large areas of space and initiating secondary succession, especially at exposed sites. The role of disturbance is thus largely that of inducing, rather than suppressing, variability in this system.

¹ Manuscript received 31 August 1976; accepted 27 July 1977.

² Formerly Jane Lubchenco Menge. Present address: Zoology Department, Oregon State University, Corvallis, Oregon 97331, USA.

Key words: *Asterias spp.*; *Chondrus crispus*; community, organization, structure; competition; disturbance; herbivores; *Littorina littorea*; *Mytilus edulis*; New England; predators; stability; succession; *Thais lapillus*.

INTRODUCTION

Two ecological problems of considerable theoretical and practical importance are (1) understanding the causes of patterns of species diversity and (2) documentation and evaluation of the causes of patterns of community stability. Insights gained into these key problems should contribute greatly toward the further development of a broad theory of community organization (e.g., Connell 1975, Dayton 1971, Paine 1974, Menge and Sutherland 1976, Rex 1976). An understanding of broad scale geographic patterns of community organization seems ultimately dependent on syntheses of results from experimental and comparative studies of the structure of local natural communities in a wide range of habitats. Such studies (e.g., Dayton 1971, 1975a, Hall et al. 1970, Paine 1974, Root 1973, Woodin 1974, Hurd and Wolf 1975, Menge 1976, Osman 1977) provide a level of resolution of, and insight into, origins of community patterns that the correlations of strict comparative studies do not usually allow.

The structure of communities has several important characteristics (Menge 1976) which are usually treated as separate phenomena, but are in fact intimately related and can best be understood if investigated together. In particular, patterns of species diversity, succession, and stability and life histories need to be better integrated. Further, the regulating mechanisms must be separated from the patterns. For example, patterns of species diversity and their causes have attracted great attention in recent years. Several studies suggest that though comparable diversities may occur in different states of a system, the regulating processes are different. Thus, low algal diversity can result from competitive exclusion in the absence of herbivores or from overgrazing by dense populations of herbivores (Paine and Vadas 1969, Dayton 1975a, 1975b, Lubchenco 1978). Relatively high local diversities in some marine systems may be regulated by predation and disturbance in some cases (Paine 1966, 1971, 1974, Menge 1976, Dayton 1971, Osman 1977) and by competition for space in others (Jackson and Buss 1975, *personal communication*). Similar cases of systems or portions of systems with comparable diversities but with different regulatory agents apparently also occur in freshwater (Brooks and Dodson 1965, Maguire 1971, Sprules 1972) and terrestrial communities (Harper 1969, Platt 1975). Other aspects of community structure (e.g., size, distribution, abundance) may also result from different processes (e.g., Connell 1961a, 1961b, Menge 1972b, 1973, 1976, Dodson 1974, Paine 1976). Such examples serve to emphasize the importance of focusing on both pattern and process in studies of community organization.

A closely related concern is that of community stability and the general process underlying dynamic patterns of stability or succession (Goodman 1975). The term stability has numerous definitions (e.g., Oriens 1975) but here we follow two general operational meanings suggested by Margalef (1969). "Persistence stability" is defined as variation in species abundance around some equilibrium or average state. Small variations imply high persistence and vice versa. Extreme variation may in time lead to extinction. "Adjustment stability" is defined as the ability of a system to return to its previous state following a perturbation. Communities which return quickly have high adjustment stability, those returning slowly have low adjustment stability. We view succession to be the process(es) involved in community development or the return of a community to a predisturbance state after perturbation.

Renewed interest in succession has been directed toward reevaluation of both the traditionally accepted concept of succession and mechanisms of succession, perhaps primarily because both seem overburdened with exceptions (Horn 1971, 1975a, 1975b, Connell 1972, Drury and Nisbet 1973, Pickett 1976, Connell and Slatyer 1977). As pointed out by Connell and Slatyer, most interpretations of succession commonly assume interspecific competition is the driving biological agent during community development and ignore the role of consumers as agents regulating the process of succession. However, results from studies of community organization (see above references) strongly imply that successional sequences may also depend on other processes, such as predation, herbivory, or physical and biotic disturbance. Finally, successional patterns seem very dependent on the life histories of component species (Keever 1950, Connell 1972, Drury and Nisbet 1973, Goodman 1975). Successional rates and sequences may depend on dispersal abilities, growth rates, reproductive output, etc., and a thorough understanding of community development and persistence must depend on knowledge of the important component species.

The rocky shores of temperate regions have proven to be excellent systems to use in pursuing problems of community organization (e.g., Connell 1961a, 1961b, 1970, 1971, Paine 1966, 1969, 1971, 1974, 1976, Paine and Vadas 1969, Dayton 1971, 1975a, 1975b, Menge 1976, Lubchenco 1978). Recent studies in the comparatively simple high (>+1.83 m above MLW) and mid (+0.46 to +1.83 m above MLW) rocky intertidal areas of New England indicate that there is an inverse relationship between the influence of competition and predation in structuring this community (Menge 1976, Menge and Sutherland 1976). The rela-

tive importance of these biological effects is seemingly dependent on the susceptibility of the activity of the main mid zone predator, the gastropod *Thais lapillus*, to exposure to wave action (Menge 1976, 1978a, 1978b). At areas exposed to high energy waves, mussels (*Mytilus edulis*) monopolize mid intertidal space because predators are ineffective in preventing them from outcompeting other sessile invertebrates and algae. At more protected areas, predators prevent mussels from monopolizing primary substratum, and 20–90% of the primary space is unoccupied (Menge 1976). This free primary space is available for colonization by various mobile invertebrates and algae. Canopy-forming fucoid algae escape control by herbivores and establish a dense stand in the mid zone (Menge 1975). These stands increase the spatial heterogeneity of the community and provide habitats for many invertebrates. The combined effects of availability of free primary space and increased spatial heterogeneity result in protected habitats having about twice the species richness of exposed areas.

In contrast to the mid zone, the low rocky intertidal zone (–0.61 to +0.46 m below and above MLW) of New England is somewhat richer in predators and herbivores. Space in the low zone tends to be monopolized by mussels at exposed areas or by the shrubby red alga, *Chondrus crispus* (Irish moss) at protected areas. This paper presents an experimental investigation of community organization in the low zone. We shall focus on factors affecting (1) the utilization of space in this zone and (2) the persistence of the two major space users, *Mytilus* and *Chondrus*. Because we are interested in the processes which control and regulate community structure, we examine the effects of competitors, consumers and the physical environment on the distribution, abundance, and life history of these species. Hopefully, by understanding how agents of natural selection (competition, predation, the physical environment) influence the species which comprise this local community, we can better appreciate how community structure develops through evolutionary time.

STUDY AREAS

Field observations and experiments were carried out at 5 main sites along the shore of New England. Sites were chosen on the basis of (1) how well they represented the range of physical and biological conditions existing along these rocky areas and (2) inaccessibility to the public. All areas consist of a sloping bedrock surface with a minimum of cobbles and silt. The precise location and a description of each area and an objective measure of exposure of each site to wave action based on rates of loss of experimental cages at each area are noted in Menge (1976). Since all areas are relatively free from human disturbance, cage loss can be attributed to storms and wave action. The exposure measure agrees well with our 6-yr. year-

around subjective impressions of exposures of the sites. Thus, the study sites can be arranged along a gradient of exposure to wave action from most to least exposed as follows: Pemaquid Point, Maine; Chamberlain, Maine; Little Brewster Cove (Little Brewster Island), Massachusetts; Grindstone Neck, Maine; and Canoe Beach Cove (Nahant), Massachusetts.

METHODS

General methods described here are used throughout this paper. Other specific techniques are indicated where appropriate. Temporal patterns in the utilization of space by plants and sessile animals and in the densities of mobile animals are quantified by periodic transects. The transect method (Menge 1972a, 1976) uses ten 0.25-m² quadrats placed at randomly determined sites along a 30-m line laid parallel to the water's edge. The line is placed at approximately the same tidal level and on the same stretch of shore at each area on every sample date. The abundance of sessile species is estimated as percent cover of primary, understory, or canopy space. This estimate is obtained by placing a 0.25-m² Plexiglas panel bearing 100 randomly plotted dots over the substratum and counting the number of dots whose projection hits a particular species. Species present under this panel which are not hit by a dot are arbitrarily assigned an abundance of 0.5% cover. The abundance of mobile species is estimated as numbers per 0.25 m², .04 m² or .01 m², depending on size and abundance of the species. In this paper, density data are expressed as numbers per square metre.

Primary space occupants include barnacles, mussels, other bivalves, sponges, ectoprocts, hydroids, holdfasts of erect algae, encrusting algae, and lichens. Understory or secondary space is occupied by the thalli of *Chondrus* and other erect, shrubby plants. "Free space" is defined as primary space available for colonization by barnacles or mussels, and thus includes both "bare" space (free from macroscopic organisms) and space occupied by encrusting organisms like the algal crusts, lichens, etc. Thus, free space is 100% minus total cover of barnacles, mussels, and holdfasts of erect algae. Ephemeral algae settle on free space, barnacles, mussels, or erect algae.

Percent cover data are bimodally distributed and violate the assumption of a normally distributed "population." For statistical tests, such data were transformed with the angular transformation (Sokal and Rohlf 1969). In all figures, mean percent cover \pm 95% confidence intervals are plotted in degrees, although the ordinate labels are backtransformed to percent cover for easier interpretation (e.g., Fig. 1). Percent cover data not treated statistically are not transformed.

Experimental manipulations of predator and herbivore densities were done using stainless steel mesh cages (see, e.g., Connell 1961a, 1961b, 1970, Dayton

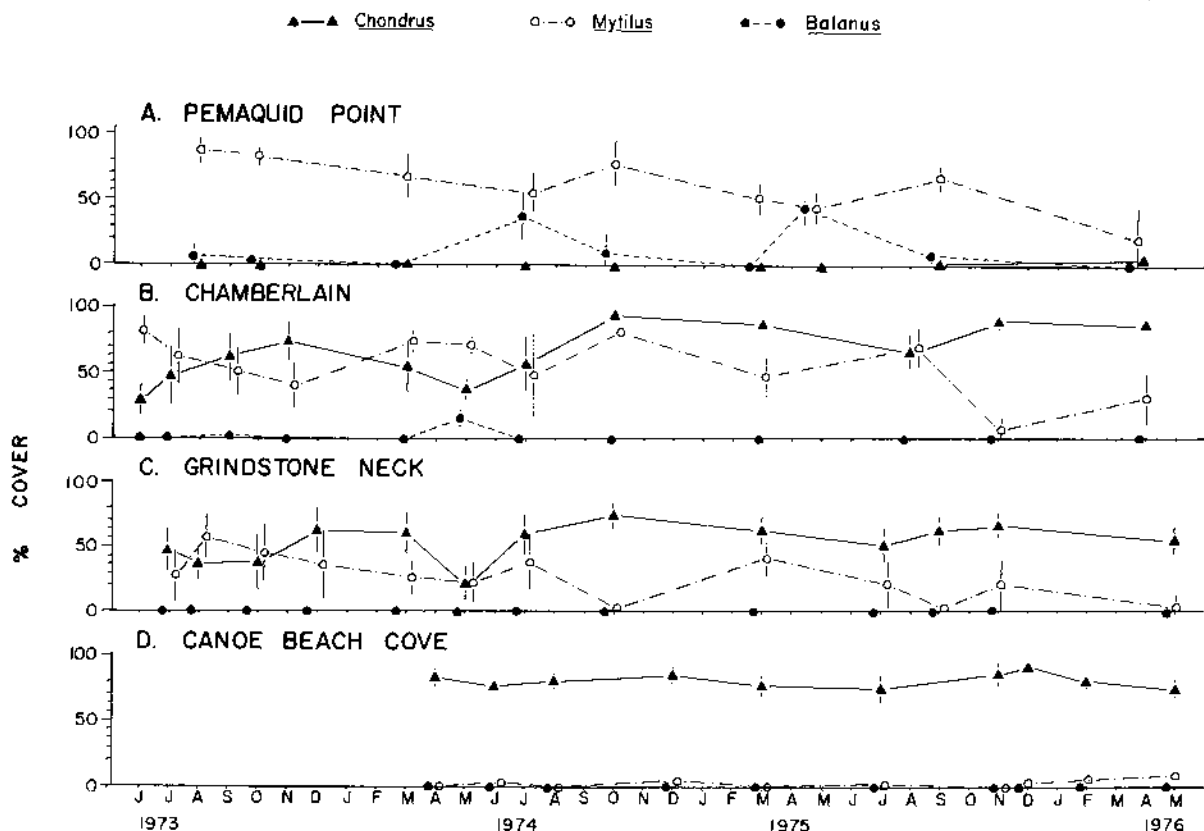


FIG. 1. Utilization of space in the low zone at areas ranging from exposed (A. Pemaquid) to protected (D. Canoe Beach Cove). *Mytilus* and *Balanus* occupy primary space; *Chondrus* occupies secondary or understory space. *Chondrus* holdfasts without erect thalli are not included here. Only data for the most abundant species on sloping shores are included; other perennial species are sometimes common in other circumstances (e.g., *Gigartina* on vertical substrata) but are relatively scarce at our sites. All data are transformed (see Methods section). Points are means; bars indicate 95% confidence intervals of ten 0.25-m² quadrats at each area.

1971, Menge 1976). Variations on the basic consumer exclusion cage manipulations with associated controls will be described below with the appropriate experiments.

COMMUNITY STRUCTURE PATTERNS

We first describe patterns of community structure in the low zone (space utilization by sessile animals and plants, abundance and diversity of sessile and mobile consumers, and consumer diets). Results of experiments analyzing effects of predators, herbivores, competitors, and physical factors on the establishment and persistence of the low zone community follow.

There are striking differences in community structure between sites exposed to and protected from wave action in the low zone. First, exposed low areas exhibit structural dominance by *Mytilus*, while relatively protected low zones exhibit structural dominance by *Chondrus*. Second, ephemeral algae (see species list in Appendix 1) tend to be more dense at exposed than at protected areas and more abundant

in late winter to spring (March to June) than the remainder of the year. Third, grazers and predators generally tend to be scarce at exposed areas and common at relatively protected areas (with exceptions noted below).

Space utilization

Patterns of space utilization by the 3 most abundant space users (abundance of other species was usually <5% cover) for the 5 study areas are shown in Figs. 1, 2, Table 1. Space in the low zone of the most exposed area, Pemaquid Point, is occupied primarily by *Mytilus* (Fig. 1a). Severe wave action during storms usually removes the mussels each winter, thus freeing space and allowing barnacles (*Balanus balanoides*) to become abundant for brief periods of time (e.g., July 1974, May 1975; Fig. 1a). Mussels then usually increase in abundance and again form a monopoly. *Chondrus* is essentially absent from this area (Fig. 1a).

In contrast, *Chondrus* is a persistent occupier of a major fraction (50–90%) of primary and secondary space at the other 4 study areas. At Chamberlain,

Chondrus and *Mytilus* together dominate the low zone. Their abundances are inversely proportional for much of the observed period (Fig. 1b). At Little Brewster Cove and Grindstone Neck, the abundances of *Chondrus* and *Mytilus* fluctuate seasonally, and each is sometimes abundant (Table 1, Fig. 1c). At the most protected area, Canoe Beach Cove, patterns of space occupancy seem less variable seasonally than at the other areas. Here, *Chondrus* is always the most abundant sessile species, occupying between 87% and 92% of low intertidal space. Mussels and barnacles are essentially absent from Canoe Beach Cove (Fig. 1d). A pattern not obvious in Fig. 1 or Table 1 is that *Chondrus* stands at Grindstone Neck and Little Brewster Cove are not as continuous as those at Chamberlain or Canoe Beach Cove. The former tend to be patchier than the latter; this is reflected in the relatively greater variation in mean percent cover and the confidence limits observed for mussels and *Chondrus* at these areas (Fig. 1, Table 1).

Abundance of ephemeral algae (species which usually persist for only a few months) is indicated in Fig. 2. These data are pooled over all ephemeral species (see species list in Appendix 1). Two basic patterns emerge from Fig. 2. First, ephemerals are always scarce in the low intertidal of Canoe Beach Cove. Second, ephemeral algae are strongly seasonal at all areas but Canoe Beach Cove. These algae are usually dense in late winter and spring (March to May) and scarce in other seasons (Fig. 2). Further, at Pemaquid Point, ephemerals tend to be more dense than at the other areas (Fig. 2) and abundant in winter as well as spring. We have never been able to quantify this last pattern because the low intertidal at Pemaquid Point is usually inaccessible in winter due to near constant, severe wave action.

There are a number of other plant and animal species which occur in the low zone, but because they consistently occupy a total of <5% cover, they are not considered in this paper. The more common of these species are listed in Appendix 1.

In summary, the most striking feature of space uti-

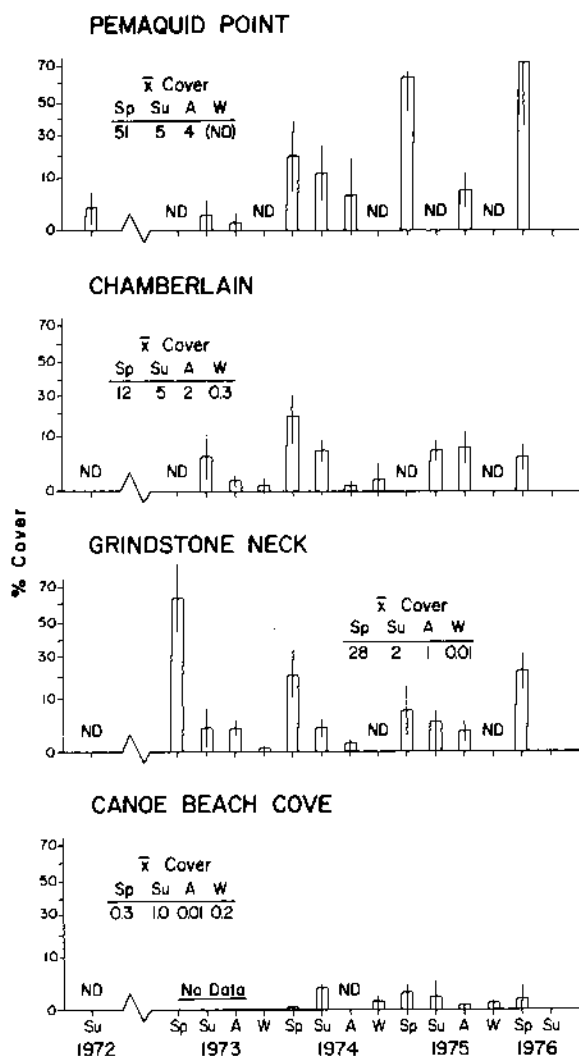


FIG. 2. Seasonal abundance of ephemeral algae in the low zone at areas along a wave exposure gradient. Histograms indicate means, lines show 95% confidence intervals. All data are transformed. ND indicates no data were taken during that season. Inserts indicate mean percent cover of ephemeral algae averaged over each season. See Appendix 1 for a list of ephemeral algae.

TABLE 1. Utilization of space in the low intertidal zone at Little Brewster Cove. Because Little Brewster Island is not reliably accessible during the winter, there are no data for that time of year.

Species ^a	Data format ^b	Mean percent cover				
		18 Jul 1973	27 Jun 1974	16 Aug 1974	18 May 1975	21 Aug 1975
<i>Mytilus edulis</i>	Percent	44.2	0	0	1.2	27.3
	Degrees	41.7 ± 14.2	0 ± 0	0 ± 0	3.88 ± 3.7	27.8 ± 14.0
<i>Balanus balanoides</i>	Percent	0.1	0.2	0	3.6	0.4
	Degrees	2.1 ± 3.6	2.4 ± 3.7	0 ± 0	7.1 ± 6.3	2.0 ± 2.1
<i>Chondrus crispus</i>	Percent	62.8	68.7	95.2	86.9	81.6
	Degrees	52.4 ± 11.6	56 ± 16	77.3 ± 8.5	70.5 ± 6.8	68.7 ± 11.7

^a As in other figures and tables, *Mytilus* and *Balanus* are given as percent cover of primary space; *Chondrus* abundance is given as percent cover of secondary, i.e., understory space. Thus, just *Chondrus* thalli are included, and not prostrate holdfasts without erect thalli.

^b Means are given as actual mean percent cover (not transformed) and degrees = cover ± 95% confidence interval (transformed).

TABLE 2. Mean density of common animal species in low zone during summer and autumn at 5 study areas. Density is standardized to numbers per square metre from densities in quadrats ranging in size from 10 cm² to 0.25 m². Range of average densities is shown in parentheses

Species	Pemaquid Point	Chamberlain	Little Brewster Cove	Grindstone Neck	Canoe Beach Cove
<i>Asterias forbesi</i> (seastar)	0	3.4 (0-15.2)	12.7 (2-26.4)	0	14.0 (6.4-19.6)
<i>A. vulgaris</i> (seastar)	0.05 (0-0.4)	49.1 (0-182)	3.1 (0-4.8)	6.3 (0-24)	2.0 (0-4)
<i>Leptasterias tenera</i> (seastar)	0.05 (0-0.4)	5.1 (0-20.4)	0	0.1 (0-0.4)	0
Total asteroid abundance	0.1	57.6	15.8	6.4	16.0
<i>Thais lapillus</i> (gastropod)	41.9 (5-98)	42.6 (3-119)	37.3 (13-78)	712 (1-9,171)	6.2 (1-14)
Total predator abundance	42	100	53	718	22
<i>Littorina littorea</i> (gastropod)	0.1 (0-0.8)	0	381 (326-442)	130 (2-1,031)	810 (612-1,786)
<i>L. obtusata</i> (gastropod)	1.3 (0-10)	1.0 (0-14)	0.3 (0-0.8)	3.6 (0-24)	1.4 (0-3.2)
<i>L. saxatilis</i> (gastropod)	0.5 (0-1.2)	0.4 (0-1.2)	1.3 (0-4)	4.8 (0-22)	0.2 (0-2.5)
<i>Acmaea testudinalis</i> (limpet)	2.5 (0-7)	0.4 (0-2.2)	2.5 (0.4-3.6)	15.7 (1.6-58)	0.5 (0.2-4)
Total herbivore abundance	4.4	1.8	385	154	812
<i>Balanus balanoides</i> (barnacle)	1,970 (0-3,200)	59 (0-360)	21 (0-570)	8.4 (0-30)	0
<i>Mytilus edulis</i> (mussel)	18,775 (13,050-46,100)	10,493 (40-82,500)	150 (0-40,400)	6,376 (0-62,000)	16 (0-20)
Total species (N)	14	20	14	19	22
Sample dates (N)	8	10	3	16	5

lization patterns at these areas are (1) *Chondrus* is the most common space occupier at all areas but Pemaquid Point, where (2) *Mytilus* is generally the most common space user, (3) *Chondrus* seems patchier at Grindstone Neck and Little Brewster Cove than at other areas, and (4) ephemeral algae are most abundant in spring at all areas except the most protected one, Canoe Beach Cove, where they are rare throughout the year.

Abundance and diversity

Overall means and range of mean densities (averaged over summer and autumn sample dates, when mobile consumers are most active) of the most conspicuous invertebrates and total species richness in the low zone are given in Table 2. In contrast to the mid zone where starfish are virtually absent (Menge 1976), the asteroids *Asterias vulgaris* (northern New England) and *Asterias forbesi* (southern New England) are relatively abundant in the low zone of all areas except the most exposed site, Pemaquid Point (Table 2). Another low zone seastar, *Leptasterias tenera*, is relatively rare and always small (usually <1 cm) at all areas. *Thais* is common in the low zone at all areas except the most protected one (Canoe Beach Cove). At the only protected area where *Asterias* spp. are relatively scarce (Grindstone Neck), *Thais* is especially abundant in the

low intertidal (712/m²). Other predators of barnacles, bivalves, and snails occasionally found in the low intertidal zone are the nudibranch *Onchidoris fusca* (max abundance = 4.2/m² at Chamberlain) and the crabs *Cancer borealis* (max abundance = 0.3/m² at Little Brewster Cove), and *Carcinus maenas* (max abundance = 0.7/m² at Little Brewster Cove). The scavenger-predator gastropod *Buccinum undatum* is occasionally relatively common (max abundance = 4.2/m²) at Grindstone Neck. Although some data are available indicating that crabs can be voracious predators of mussels (Ebling et al. 1964, Seed 1969), the importance of crab predation at our areas is as yet unclear. Because most crabs in the low zone are small (<2 cm carapace diam) they may be relatively unimportant. The abundance of terrestrial and pelagic predators has not been estimated nor have their diets been quantified. Observations on the most likely predators (Herring and Great Black-backed Gulls, *Larus argentatus* and *Larus marinus*; rats, *Rattus norvegicus*; and cunners, *Tautoglabrus adspersus*) indicate that at our study sites they rarely consume low zone space occupiers. The most important low zone predators appear to be *Asterias* spp., *Thais*, and perhaps crabs. Note that total predator density is least at the most protected site, Canoe Beach Cove (Table 2).

Littorina littorea is the most abundant herbivore in

the low zone at calm areas (Table 2). Other herbivores present include the snails *Littorina saxatilis*, *Littorina obtusata*, *Acmaea testudinalis*, *Lacuna vincta*, *Margarites helicina*, the amphipod *Amphithoe rubricata*, the isopod *Idotea phosphorea* and rarely the sea urchin *Strongylocentrotus droebachiensis*. *Lacuna* and *Margarites* each have a brief peak density in early summer, then almost disappear for the remainder of the year (personal observations). Neither of these gastropods nor the crustacea has been investigated in this study. All readily pass through cage mesh, and thus when present, are usually in comparable densities in and out of all cage treatments. Total herbivore density is low at the exposed site, Pemaquid Point (4.4/m²) and high at 3 of 4 relatively protected areas (Little Brewster Cove, 385/m²; Grindstone Neck, 154/m²; Canoe Beach Cove, 812/m²). Herbivore density at Chamberlain (1.8/m²), the most exposed of the protected sites, is comparable to that at Pemaquid Point. Herbivore biomass data show the same patterns (Menge 1975).

The most common low zone sessile invertebrates are *Balanus balanoides* and *M. edulis* (Table 2). Other sessile species occasionally found in the low region are *Balanus crenatus*, *Balanus balanoides*, *Modiolus modiolus*, *Saxicava* sp., and *Metridium senile*. None of these is abundant and combined they usually occupy <1% of the space at any area.

The number of species observed in the low zone was lowest at the most exposed area and a relatively protected area (14 spp., Pemaquid Point and Little Brewster Cove, respectively) and greatest at the remaining relatively protected areas (19–22 spp., Table 2). Thus, with 1 exception the more protected areas harbor a greater number of species than does the exposed area. Causes of the relatively low diversity at Little Brewster Cove have not been investigated but may be partly a consequence of (1) the relatively small number of sampling dates there, (2) the relatively small area of the site because of the steep slope (≈30–40° inclination), or (3) pollution from Boston Harbor.

Consumer diets

The 4 most abundant low intertidal consumers are *L. littorea*, *Thais*, *A. vulgaris*, and *A. forbesi* (Table 2). Diet composition of the carnivorous species can be determined by turning the predator over and, if feeding is detected, by identifying the prey (e.g., Connell 1961a, Paine 1966, 1969, 1971, Mauzey 1966, Mauzey et al. 1968, Menge 1972a, 1972b, 1973, 1974, 1976). Summaries of the diets of *Thais* at 2 areas and of *Asterias vulgaris* at Grindstone Neck are given in Table 3. The intertidal diet of *A. forbesi* has been sampled less intensively but both intertidal and subtidal data indicate the diet of this species is nearly identical to that of *A. vulgaris*. In the low zone at these areas, *Thais* preys almost exclusively on *Mytilus* (89–97% of

TABLE 3. Percent of prey species in the diets of predators in the low intertidal at 2 study sites

Prey species	Percent in diet		
	Grindstone Neck		Chamberlain
	<i>Asterias^a vulgaris</i>	<i>Thais^b lapillus</i>	<i>Thais^c lapillus</i>
<i>Mytilus edulis</i> (mussel)	47.3	96.6	89.1
<i>Balanus balanoides</i> (barnacle)	38.2	2.9	8.7
<i>Lacuna vincta</i> (gastropod)	7.0	0	0
<i>Acmaea testudinalis</i> (limpet)	1.6	0	0
Unidentified amphipod (crustacean)	1.0	0	0
<i>Littorina obtusata</i> (gastropod)	0.9	0	0
<i>Margarites</i> sp. (gastropod)	0.7	0	0
<i>Thais lapillus</i> (gastropod)	0.7	0.3	1.1
<i>Littorina littorea</i> (gastropod)	0.6	0	0
<i>Saxicava</i> sp. (bivalve)	0.6	0.3	1.1
<i>Balanus crenatus</i> (barnacle)	0.6	0	0
<i>Asterias vulgaris</i> (seastar)	0.4	0	0
Unidentifiable	0.4	0	0
Prey items eaten (N)	696	350	92
Species eaten (N)	12+	4	4

^a Data from summer and autumn, 1971–1974.

^b Data from summers 1972–1974.

^c Data from summer 1973.

the prey eaten, Table 3) but occasionally consumes one other species (*Saxicava*) and cannibalizes (Table 3). At Grindstone Neck *A. vulgaris* is more generalized and feeds primarily on *Mytilus* (47%) and *Balanus* (38%, Table 3) but includes at least 9 other species in its diet. *Asterias* occasionally cannibalizes as well (Table 3). Thus, 2 of the most abundant animal space occupiers in the low zone, *Mytilus* and *Balanus* (Fig. 1), are the primary prey of the 2 most common low intertidal predators.

Diets of grazers like *L. littorea* are more difficult to determine, because these consumers usually do not eat their prey in discrete, measurable units. However, qualitative diets were obtained from extensive field and laboratory observations and experiments. *Littorina littorea* is a generalist both in size and type of food consumed and in habitats occupied (Menge 1975). Food choice experiments in the laboratory indicate *L. littorea* strongly prefers ephemeral algae (e.g., greens such as *Enteromorpha*, *Spongomorpha*, *Ulva*, and *Monostroma*; browns such as *Petalonia* and *Scytosiphon*; and reds such as *Ceramium* and *Porphyra*; Menge 1975, Lubchenco 1978). *Chondrus* is one of the least preferred prey of *L. littorea* and is rarely consumed by it. Healthy *L. littorea* often died after 5–9 mo in the laboratory when the only food available was *Chondrus* whereas *L. littorea* feeding on various other algae survived well, and grew and reproduced normally (Menge 1975). These results contradict speculation by earlier workers that *L. littorea* actively grazes *Chondrus* (e.g., MacFarlane 1952). Field observations at high tide verify laboratory results; lit-

torines graze micro- and macroscopic ephemeral epiphytes from *Chondrus* but do not usually graze *Chondrus* itself. Field experiments discussed below confirm that under field conditions this grazer does not normally eat this alga.

In contrast, *Strongylocentrotus* readily consumes *Chondrus* and can eat the whole plant including the encrusting holdfast (Lubchenco 1978). However, this herbivore is not usually abundant in intertidal areas of New England (mean densities range from 0 to 0.9/m² at all areas) and thus probably has little effect on abundance of Irish moss in the low zone. However, sea urchins are sometimes abundant subtidally and in intertidal regions elsewhere (e.g., in the Bay of Fundy and the west coast of North America). In the Bay of Fundy, *Chondrus* is not dominant where urchins are abundant (Lubchenco 1978). This, and the fact that urchins are sometimes important determinants of community structure (e.g., Jones and Kain 1967, Vadas 1968, Paine and Vadas 1969, Dayton 1975a, 1975b), prompted us to examine the effects of sea urchins, as well as those of the abundant low zone herbivores, on abundance and distribution of *Chondrus*.

Acmaea occurs almost exclusively on relatively smooth surfaces. Experiments indicate it does not affect the upright portion of Irish moss, but can remove the encrusting holdfast of this alga when no thallus is present. Similar species of West Coast limpets (*Collisella* and *Notoacmaea*) are known to graze primarily diatoms and algal sporelings (Nicotri 1977).

Thus, the most abundant herbivore in intertidal *Chondrus* beds (*L. littorea*) does not consume either the erect or encrusting portions of this plant. The herbivores that can eat all or part of Irish moss (sea urchins and limpets, respectively) are either not present or are not abundant.

In summary, community structure in the low zone is dominated by three abundant space-occupying species, *Mytilus*, *Chondrus*, and *Balanus*. At the exposed area, *Mytilus* dominates space; at all other areas, *Chondrus* occupies most of the space (Fig. 1). Abundance patterns of consumers are correlated inversely with wave action. At the exposed area (Pemaquid Point), herbivores and the predaceous seastars are essentially absent, although another predator (*Thais*) is fairly common. At a somewhat less exposed area (Chamberlain), all predators are abundant but herbivores are nearly absent. At protected areas all consumers are abundant (Table 2).

COMMUNITY DYNAMICS: ROLE OF BIOLOGICAL INTERACTIONS AND WAVE SHOCK

The spatial patterns described above prompt at least 2 questions about the low zone community: how do these structural patterns arise, and why do they persist? In the following section we describe the results of manipulations of the agents which seemed most likely to play a role in development and persistence of

the low zone community. Specifically, we determine the factors responsible for the domination of space at Pemaquid Point by mussels and at the remaining areas by *Chondrus*. The mechanisms studied include (1) predation by *Asterias* spp. and *Thais*, (2) competition for space between *Mytilus*, *Balanus*, *Chondrus*, and other algae, (3) herbivory by *L. littorea*, *Acmaea*, and *Strongylocentrotus*, and (4) wave-generated disturbances in the structure of the low intertidal association in New England.

Experimental design

To examine the relative importance of predation, herbivory, and competition for space on the abundance of *Mytilus*, *Balanus*, and *Chondrus*, we performed a variety of experiments. Stainless steel mesh cages (10 × 10 × 5 cm; described in Menge 1975, 1976) were used to include and exclude various combinations of organisms. Treatments included (1) "predator exclusion," i.e., *Thais* and *Asterias* excluded but *L. littorea* enclosed, (2) "herbivore exclusion," i.e., major herbivores (gastropods and sea urchins) excluded but predators included, (3) "exclusion and mussel removal," i.e., predator exclusion and *Mytilus* removed manually and (4) "selective herbivore enclosures," i.e., enclosure of one of *L. littorea*, *L. obtusata*, *Strongylocentrotus*, or *Acmaea* with *Thais* or *Asterias* or both. Controls were stainless steel mesh roofs (to test the effects of shading by the mesh, termed "roofs"), and marked, unmanipulated 10 × 10-cm quadrats (termed "controls"). Since amphipods, isopods, polychaetes, nemerteans, small gastropods, nudibranchs, etc. can easily pass through the mesh, and densities in cages and adjacent controls seemed comparable, the cages do not appear to function as barriers for these organisms. All organisms settling on the cages or roofs during the course of these experiments were removed by scrubbing with a wire brush.

Two types of experiments were initiated. To study factors affecting community establishment, or succession, we initiated either primary or secondary succession by clearing patches or strips ranging in area from ≈0.25–3 m², and then manipulating predator, competitor, and herbivore abundances. Primary succession (succession on completely bare substrata) was begun by removing all organisms with stiff putty knives then repeatedly burning the area with propane torches and scraping with putty knives again until all organisms were thought to be killed. These experiments are termed "denudations." Although we have since discovered that sandblasting is a much more effective way of creating bare substratum, this burning technique is usually effective. Secondary succession (succession on substrata free of all but encrusting organisms) occurs naturally after "clearances" of macroscopic, sessile organisms by storms or other disturbances. To create such new "free space" and

initiate secondary succession. *Chondrus*, *Mytilus*, *Balanus* and other nonencrusting organisms were removed with putty knives. In these clearances, as after storms, encrusting algae (including *Chondrus* holdfasts) remained attached to the rock. These experiments are called "clearances" or "scrapings." Most natural space clearance occurs in winter and early spring and many of the most abundant species in this system settle 1–2 mo later. Hence all experiments were begun from late March to early June to roughly coincide with these natural events. We have not investigated effects of clearances occurring at other times of the year.

To study the factors affecting the persistence of already established communities, we used a second type of experiment. This consisted of manipulating abundances of predators, herbivores, and competitors other than *Chondrus* on preexisting stands of this alga.

All experiments were usually monitored every 2–4 wk by either photographing each treatment, and later estimating percent cover of each species in the laboratory, or by estimating percent cover in the field. Estimates of percent cover from photographs were used only for barnacles and mussels. Percent cover of algae was always estimated directly in the field because, in our experience, percent cover estimates of algae from photographs are inaccurate. All experiments were established at locations which were typical of each study area; unusual locales were avoided.

Various problems were encountered during these experiments. Initially, small *Thais* and *Asterias* persistently invaded many predator exclusion cages which usually led to premature termination of the experiment. This problem was solved by initiating new experiments in which all organisms were cleared from a 1-m² patch around the predator exclusion and predator exclusion-mussel removal cages. Barnacles settled on this newly freed space which created a buffer zone characterized by no canopy and dense prey. This buffer zone apparently reduced the rate at which predators located the experimental cages. In these experiments, controls and roofs were placed near the edge of the cleared patch.

Unfortunately, almost continual severe wave action prevented establishment of low zone cages at Pemaquid Point. Interpretation of community structure dynamics for this area is thus based on extrapolation from experimental results from the low zone cages at other areas, mid zone cages and observations at Pemaquid Point.

Establishment of the low zone community

Chondrus thalli may be removed by (1) severe wave action which removes sheets of *Chondrus* and *Mytilus* bound together (J. Lubchenco, B. A. Menge, *personal observations*, Menge 1976) and perhaps *Chondrus* heavily laden with epiphytes (Prince 1971), (2) ice and

rock scouring (MacFarlane 1952) and (3) humans harvesting Irish moss for carrageenan. A number of investigators have cleared patches of *Chondrus* to observe the rate at which the patch returns to its original level of biomass (MacFarlane 1952, Prince 1971, Ring 1970, Mathieson and Prince 1973). Ring (1970) removed thalli of *Chondrus* and *Gigartina stellata* (a red alga similar to *Chondrus*) in October 1968 and observed a heavy settlement of winter and spring ephemeral algae on the strip. He speculated that these algae were responsible for the slow regrowth of *Chondrus* on the strip. Prince (1971) concluded that the season and reproductive state of *Chondrus* during which removals were done determined how quickly the patch returned to its former state. Most of these experiments involved either removal of the thalli (secondary succession) or of the thalli and basal crusts (primary succession) and subsequent monitoring of regrowth.

In the low zone, the most typical pattern of community development evidently involves secondary succession, since the creation of absolutely bare substratum and initiation of primary succession seem to be rare events. Below, we examine the effects of predation, competition, and herbivory on secondary succession, then consider their influence on primary succession.

Secondary succession: Effect of predation and plant-animal competition.—Recruitment and persistence of *Chondrus* depend heavily on the removal of the competitively superior *Mytilus* and *Balanus* by their predators. This conclusion is indicated by the results of the 8 low intertidal predator exclusion experiments in which predator exclusion was successful. (Eleven other experiments were begun but small predators evaded our control efforts and forced premature termination of these experiments.) Five of the successful experiments were at Little Brewster Cove (results of 2 of these are in Fig. 3); the other 3 occurred at each of the other 3 relatively protected areas.

Following clearance in early spring, community development is initially similar to that in the mid zone (Fig. 3; Menge 1976). Barnacles settle in spring (March to May in Massachusetts, April and May in Maine). (*Balanus crenatus* and *B. balanoides* occasionally settle in the low zone, but the most common barnacle settling in these experiments has been *B. balanoides*.) Whereas in the mid zone *Balanus* often covers 100% of the space (Menge 1976), in the low zone it rarely covers much more than 25% of the space. In the absence of predators, barnacles are rapidly settled upon and overgrown by mussels (Fig. 3c, f). As in mid intertidal experiments, mussels are competitively dominant to barnacles (see below) and will survive in the low intertidal as long as predators are excluded. In the presence of predators (Fig. 3a, b, d, and e), neither barnacles nor mussels usually occupy much space (with exceptions noted below). Rather, in most cases (12 of 16 roofs and controls), *Chondrus* perennates or

TABLE 4. Results of predator exclusion experiments after 1 and 2 growing seasons. Data are given as actual mean percent cover ± 1 standard error (untransformed) and as degrees ± 1 SE (transformed)

Treatment	Taxa	Data format	Mean cover (± 1 SE)	
			After one growing season (n = 8)	After two growing seasons (n = 3)
Control	<i>Balanus</i>	Percent	0	0
		Degrees	(0)	(0)
	<i>Mytilus</i>	Percent	3.5 \pm 3.5	0
		Degrees	(4.0 \pm 4.0)	(0)
	<i>Chondrus</i>	Percent	30.1 \pm 12.9	68.3 \pm 23.7
		Degrees	(28.0 \pm 10.4)	(61.2 \pm 18.0)
Roof	<i>Balanus</i>	Percent	0	0
		Degrees	(0)	(0)
	<i>Mytilus</i>	Percent	1.6 \pm 1.6	0.7 \pm 0.7
		Degrees	(2.6 \pm 2.6)	(2.7 \pm 2.7)
	<i>Chondrus</i>	Percent	28.5 \pm 11.2	75.0 \pm 15.2
		Degrees	(27.4 \pm 8.7)	(62.0 \pm 10.2)
Predator exclusion	<i>Balanus</i>	Percent	1.1 \pm 1.1	0
		Degrees	(2.2 \pm 2.2)	(0)
	<i>Mytilus</i>	Percent	94.9 \pm 5.1	100
		Degrees	(85.0 \pm 5.0)	(90)
	<i>Chondrus</i>	Percent	4.8 \pm 4.8	0
		Degrees	(4.8 \pm 4.8)	(0)
Mussel removal	<i>Balanus</i>	Percent	36.2 \pm 12.7	...
		Degrees	(35.4 \pm 9.6)	...
	<i>Mytilus</i>	Percent	0	...
		Degrees	(0)	...
	<i>Chondrus</i>	Percent	12.3 \pm 12.3	...
		Degrees	(9.7 \pm 9.7)	...

Mytilus were excluded from cleared substrata (Table 5). As shown in Fig. 3, in 3-way competition, *Mytilus* outcompetes *Chondrus* and *Balanus* (Table 5). When mussels are removed and the experiment is begun in spring, barnacles outcompete *Chondrus*, probably by preemption of space and rapid growth (Table 5). In contrast, when *Balanus* does not settle densely (or, presumably, if the experiment was begun in summer or autumn after *Balanus* had settled), *Chondrus* is evidently the "victor." Obviously, this is the same result as that in controls and roofs of the predator exclusions in Fig. 3. Hence, the results in Table 5 suggest that at least when experiments are initiated on newly cleared substrata, the competitive hierarchy in this system is *Mytilus* > *Balanus* > *Chondrus*. The competitive position of ephemeral algae and competitive interactions between settling juveniles and established adults is not revealed by these experiments and will be considered below.

Thus, following clearance of sessile, nonencrusting organisms, *Mytilus* outcompetes *Chondrus* for space in the absence of mussel predators (e.g., at exposed sites). Where mussel predators are present (e.g., calm areas) *Mytilus* is usually prevented from monopolizing space and *Chondrus* can perennate or settle and be-

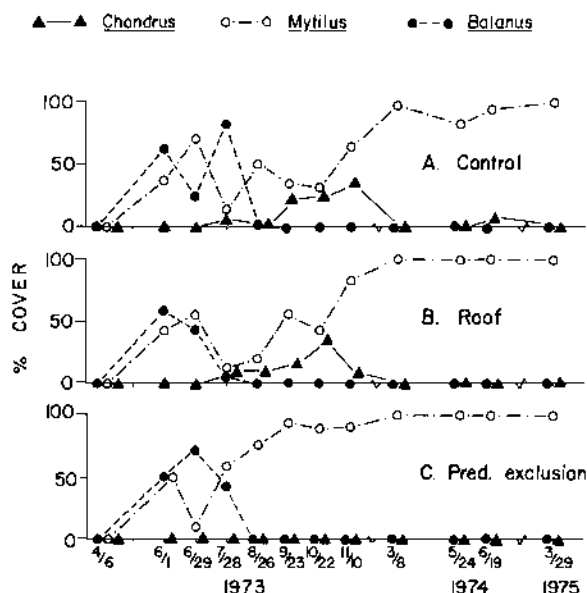


FIG. 4. An escape by *Mytilus* from low zone predators and consequent competitive exclusion of *Chondrus* at Chamberlain (+0.5 m). Data are not transformed.

come established. During colonization episodes, *Chondrus* is apparently a poor competitor for space against both mussels and barnacles.

Secondary succession: Effect of herbivory and plant-plant competition.—1) Substrata covered with encrusting *Chondrus* holdfast. Results of removal of *Chondrus* thallus at 2 sites, 1 with and another without a *L. littorea* population, suggest that the common periwinkle has little direct effect on *Chondrus* but probably determines the abundance of ephemerals (Fig. 5). In turn, ephemerals may slow the rate of return of *Chondrus* thalli. By August 1974, the mean abundance of *Chondrus* with *L. littorea* present and few ephemeral epiphytes was significantly greater than that with abundant epiphytes and no herbivores (Fig. 5b and d; analysis of variance: $F = 23.82$; $df = 1, 18$; $p < .001$).

The effects of herbivores (*L. littorea*, *L. obtusata*, *Acmaea*) following *Chondrus* thallus clearance is shown in Fig. 6. Exclusion of all 3 species resulted in monopolization of secondary space by *Ulva lactuca*, a green ephemeral. In the presence of herbivores (Fig. 6a-e, g, and h) ephemeral algae were eliminated or reduced and *Chondrus* grew to occupy most of the space. Abundance of *Chondrus* in the exclusions (Fig. 6f) is significantly less than that in all other treatments excluding controls (Fig. 6c-e, g, and h; analysis of variance: $F = 78.55$; $df = 1, 6$; $p < .001$). Controls are not included in this statistical analysis because they are not shaded by the mesh, which has a small inhibitory effect on growth rate of *Chondrus*. In April 1975, percent cover of *Chondrus* was significantly inversely correlated to percent cover of ephemeral algae for all treatments (excluding controls; Y [percent cover of

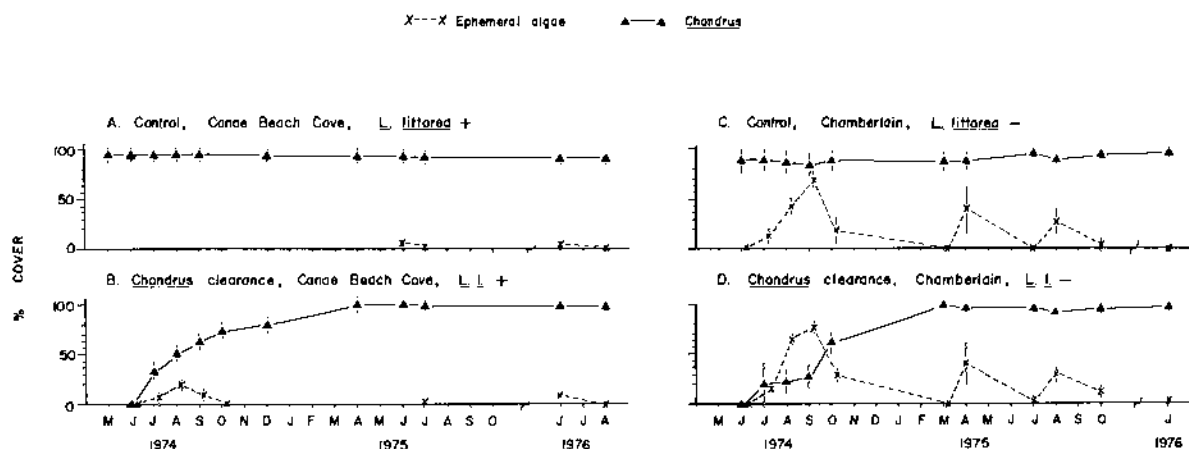
REGROWTH OF *CHONDROS* FOLLOWING THALLUS CLEARANCE

FIG. 5. Recolonization after clearance (B and D) at an area with (Canoe Beach Cove, A and B) and without (Chamberlain, C and D) *L. littorea*. A and C are unmanipulated controls adjacent to B and D. A and B are each 3 m² in area; C and D are each 2 m². Means \pm 95% confidence intervals for 8–12 0.25-m² samples within each treatment are indicated for each date.

Chondrus in degrees] = $68.05 - 0.42 X$ [percent cover of ephemerals in degrees]; $r^2 = .69$).

Acmaea graze marks were observed on the encrusting holdfast of *Chondrus* in the *Acmaea* enclosure (Fig. 6h) but the limpet did not graze enough of this holdfast to adversely affect thallus regrowth. Evidently *Chondrus* thalli perennated faster than *Acmaea* could graze the encrusting holdfast.

At any particular site, only a relatively small percent cover of the encrusting holdfast is necessary for *Chondrus* to perennate successfully and occupy 100% of

the secondary space, because the distal parts of the thalli are branched and bushy and cover a larger area than the holdfast from which they grow. For example, original percent cover of the encrusting holdfast immediately after thallus removal ranged from 12% to 86%, but there was no significant correlation between percent cover of this (X) and of the thallus after 9 mo (Y ; $r^2 = .02$). There is undoubtedly a minimum amount of encrusting holdfast necessary to produce thalli covering 100% secondary space, but this is not revealed by our data.

TABLE 5. Competition between *Mytilus*, *Balanus*, and *Chondrus* in the absence of predators on cleared substrata, i.e., predator exclusion cages. Data are average percent covers in predator exclusion cages (e.g., Fig. 3). Me = *Mytilus edulis*; Bb = *Balanus balanoides*; Cc = *Chondrus crispus*; N is number of treatments for each date.

No. of months (March = 0) ^a	Three-way competition				<i>Mytilus</i> removed			<i>Mytilus</i> removed; <i>Balanus</i> reduced ^b		
	Me	Bb	Cc	N	Bb	Cc	N	Bb	Cc	N
0	0	0	0	8	0	0	3	0	0	4
1	0	1	0	8	0	0	3	2	0	4
2	6	31	2	8	43	2	3	16	0	4
3	34	31	0	8	61	0	3	22	0	4
4	68	11	8	7	66	2	2	27	22	3
5	90	3	6	8	87	0	2	34	44	2
6	97	0	6	7	92	0	2	21	40	2
7	90	1	5	8	92	0	2	27	24	4
8 ^c	94	1	0	7	90	0	2	19	22	4
12	100	0	0	4	18	0	2	7	43	2
13	100	0	0	4	34	0	2	11	42	2
14	100	0	0	4	97	0	2	8	13	1
15	100	0	0	2	79	0	2	50	2	1
16	100	0	0	3	72	0	2	0	19	1
17	100	0	0	3	72	0	2	0	33	1
18	100	0	0	3	51	0	1	0	36	1
19	100	0	0	3	50	0	2	0	65	1

^a Data from 1973–1974 and 1974–1975 were combined. All experiments were begun in March.

^b *Balanus* did not settle as heavily in these treatments.

^c No data could be obtained in December through February.

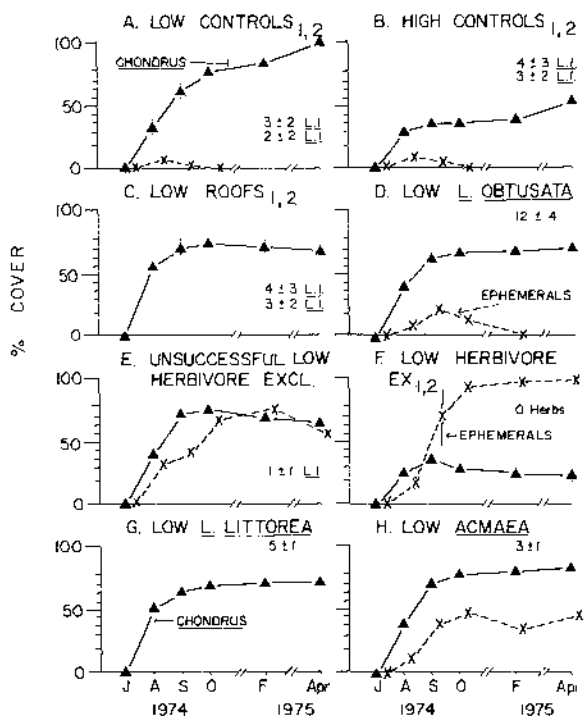


FIG. 6. Effect of herbivores, ephemeral algae, and height in the intertidal on regrowth of *Chondrus* thallus following thallus removal at Canoe Beach Cove. Low treatments are at -0.3 m; high treatments are at $+0.2$ m. In A, B, C, and F symbols indicate means and bars indicate ranges of 2 replicates. Percent cover data are transformed. The number of herbivores ($\bar{X} \pm 95\%$ confidence intervals) are indicated for each treatment. In E, exclusion of herbivores was only partly successful.

Increased height in the intertidal evidently slows regrowth of *Chondrus* (Fig. 6). By April, both low controls (-0.3 m; Fig. 6a) achieved 100% cover of *Chondrus*, while in the 2 high controls ($+0.2$ m; Fig. 6b) *Chondrus* covered only $\approx 50\%$. These differences are significant (analysis of variance: $F = 1,379$; $df = 1,2$; $p < .001$). It seems most likely that the cause of this variation in growth is the difference in immersion time between the 2 tidal levels, though other factors may also have an effect.

In the herbivore exclusion cages (Fig. 6f), ephemeral algae persisted at least through September 1975, at which time they covered 68% and 73% of the area. It is possible that cages, in addition to excluding snails, may also keep ephemeral algae damp or shelter them from effects of wave action, thus allowing them to persist longer. Comparable experiments at Chamberlain, which usually lacks herbivorous snails (Table 2), enabled us to evaluate the biological realism of this persistence. The scarcity of herbivores at this area means that the mesh effect can be tested by comparing controls to the roof and herbivore exclusion cages (Fig. 7a,b). Patterns of colonization and persistence of ephemerals and *Chondrus* are similar in these treat-

REGROWTH OF *CHONDROS* FOLLOWING THALLUS CLEARANCE

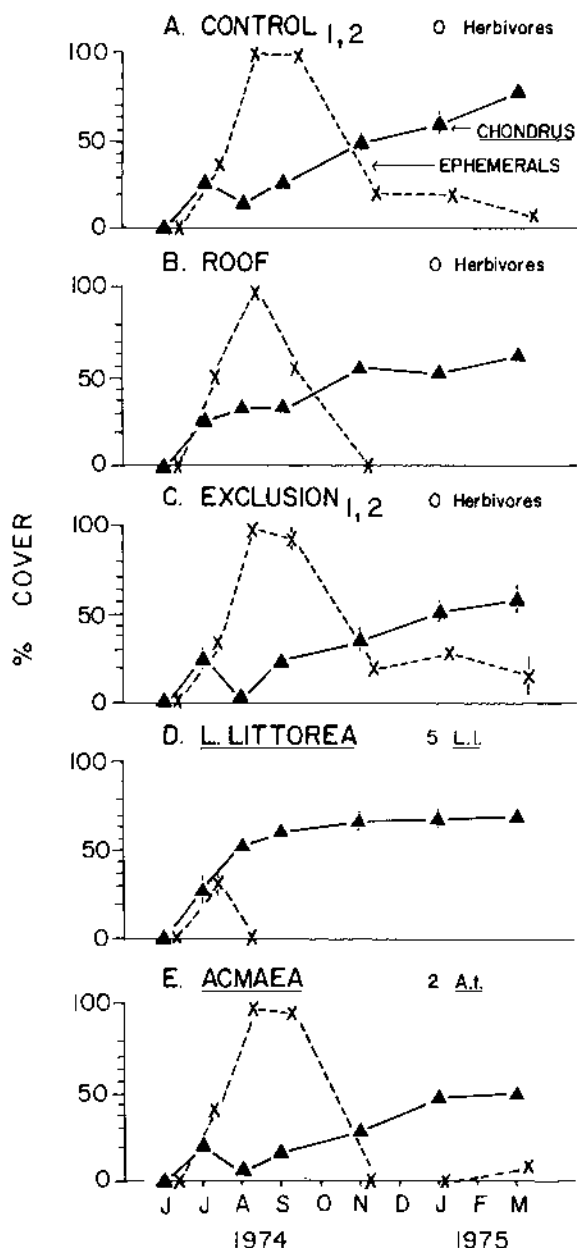


FIG. 7. Effect of herbivores and ephemeral algae on regrowth of *Chondrus* following thallus clearance at Chamberlain (-0.43 m). In A and C, symbols indicate means and bars indicate ranges of the 2 replicates.

ments (Fig. 7a,b,c), suggesting that at least in these experiments, cages and roofs do not have an important effect on survival of ephemerals. At this site, survival in fall and early winter is low. This failure of ephemerals to survive well through winter at Chamberlain

TABLE 6. Effect of herbivores (changes in percent cover) on *Chondrus* prostrate holdfast at Canoe Beach Cove; no ephemeral algae present, cages at Canoe Beach Cove at -0.03 m. HD = high density; LD = low density; LI = *L. littorea*; Lo = *L. obtusata*; At = *Acmaea testudininalis*

Treatment	Cont ₁	Cont ₂	Roof ₁	Roof ₂	Excl ₁	Excl ₂	HD LI	LD LI	HD Lo	LD Lo	HD At	LD At
No. herbivores	2 ± 2LI	2 ± 2LI	5 ± 2LI	4 ± 2LI	0	0	6	3	15	10	2	1
29 Mar 1974	100	92	100	100	88	95	98	83	100	100	100	73
24 Jun 1974	100	93	100	100	91	97	85	84	100	100	41	32
26 Sep 1974	100	92	99	100	98	100	60	81	100	100	0	12
31 Jan 1975	100	91	100	100	97	97	100	83	100	99	0	0
22 Apr 1975	100	91	100	100	97	100	99	82	100	100	0	0
Overall change	0	-1	0	0	+9	+5	+1	-1	0	0	-100	-73

(Figs. 5, 7) but ability to survive well at Canoe Beach Cove (Fig. 6), may be a result of the greater wave shock at the former area relative to the latter.

In the *L. littorea* enclosure (Fig. 7d), ephemerals (*Ceramium* spp., *Petalonia fasciata*, *Enteromorpha intestinalis*, and *Ulva lactuca*) settled densely and were eventually consumed, though they initially swamped the snails. Once the ephemerals were gone, *Chondrus* regrew quickly (Fig. 7d). *Acmaea* was even less able to control ephemeral abundance (Fig. 7e). Thus, in all treatments except the *L. littorea* enclosure, ephemerals were abundant in August and September and growth of *Chondrus* was depressed (Fig. 7). In September percent cover of *Chondrus* thallus was significantly inversely correlated to percent cover of ephemeral algae (Y [percent cover of *Chondrus* in degrees] = $54.32 - 0.38 X$ [percent cover of ephemeral algae in degrees]; $r^2 = .93$). *Ceramium* was the most abundant of these ephemerals, but it and other ephemerals disappeared by winter. *Chondrus* underneath these algae subsequently resumed growth and by March 1975, percent cover of *Chondrus* in the 2 *L. littorea* enclosures was not significantly different from that in the 2 exclusions or the *Acmaea* enclosure (analysis of variance: $F = 2.82$, $df = 1, 3$; $.1 < p < .25$). As in the *Chondrus* thallus clearance at Canoe Beach Cove (Fig. 6), percent cover of *Chondrus* thallus at Chamberlain after 9 mo (March 1975; Fig. 7) was not correlated to the original percent cover of *Chondrus* encrusting holdfast ($r^2 = 0$; original percent cover of *Chondrus* holdfast ranged from 68% to 94%).

To determine the effects of grazers on *Chondrus* holdfast, caging experiments were placed over natural encrusting holdfast at Canoe Beach Cove. Evidently, *Acmaea* can eliminate such holdfasts at artificially high densities (Table 6; see below). Overall change in cover of encrusting holdfast in limpet cages ($\bar{X} = -86.5\%$) is significantly greater than that in controls and roofs ($\bar{X} = -0.25\%$; analysis of variance: $F = 59.63$, $df = 1, 4$; $p < .005$). Abnormally high densities of *L. littorea* can reduce cover of encrusting holdfast during summer but the alga recovers in winter (Table 6), and overall change in cover of holdfast in *L. littorea* enclosures ($\bar{X} = 0\%$) is not significantly different from that in controls and roofs ($\bar{X} = -0.25\%$; analysis of

variance: $F = 1.16$; $df = 1, 4$; $.25 < p < .50$). Because the encrusting holdfast is completely removed in the limpet cages, but a thin cover is left in the *L. littorea* cages, limpets evidently graze closer to the substratum than do periwinkles. Presumably the encrusting holdfast grows back in *L. littorea* enclosures from the thin cover left by the grazers.

Neither normal densities of *L. littorea* nor high or normal densities of *L. obtusata* affect percent cover of encrusting holdfast (Table 6). This may be because these herbivores are either not grazing the holdfast or because it grows as fast as it is consumed. Laboratory feeding experiments discussed above support the former explanation. *Littorina littorea* and *L. obtusata* in short-term (1 mo) laboratory experiments did not eat *Chondrus* holdfast even though no other food was present.

Figures 5b, 6, and 7 indicate that *Chondrus* can perennialize in the presence of periwinkles and limpets. Thus, although these herbivores can remove the encrusting holdfast, they apparently do not affect regrowth of the thallus.

In summary, after clearance ephemerals temporarily impede *Chondrus* perennialization. *Chondrus* returns to previous levels of abundance faster in the presence of *L. littorea* than in its absence, apparently because the limpet quickly consumes the ephemerals. Some ephemerals (e.g., *Ulva*) may persist longer than others (e.g., *Ceramium*), and thus may have different effects on regrowth. However, no epiphytes have been observed to permanently outcompete *Chondrus* except in tide pools (Lubchenco 1978). Thus, the ability of Irish moss to tolerate shade and resume growth once epiphytes are removed seems particularly adaptive. Further, the ability of this alga to quickly regenerate thalli from its encrusting holdfast evidently enhances its ability to occupy space.

2) Substrata covered with encrusting coralline algae. Occasionally space that is cleared in the low zone is covered by encrusting coralline algae, not by encrusting holdfast of *Chondrus*. When this occurs, *Chondrus* can colonize the area only via settlement. The following experiments examine the effects of herbivores on secondary succession on such substrata.

The low intertidal-subtidal interface and shallow

RECOLONIZATION OF AREA CLEARED BY URCHINS

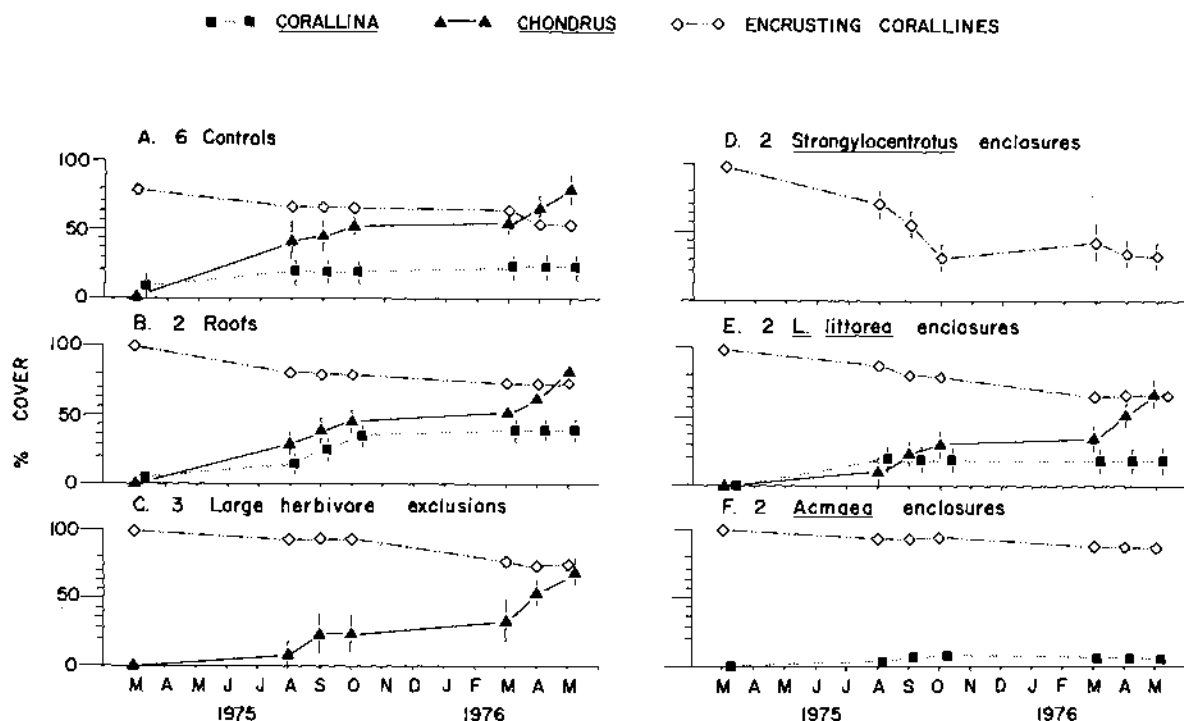


FIG. 8. Effect of herbivores on recolonization of the low zone after sea urchins had removed all macroscopic algae except encrusting corallines (includes *Lithothamnium*, *Lithophyllum*, *Phymatolithon*, *Clathromorphum*, etc.). Mean percent cover and ranges are indicated for 6 replicates in A, 3 in C, and 2 in B, D, E, and F. The "large-herbivore exclusion" kept out large *L. littorea*, large *Acmaea* and *Strongylocentrotus*; many small (<3 mm in length) herbivores (*Margarites*, *Lacuna*, small *L. littorea* and small *Acmaea*) invaded the cage.

subtidal zone (-0.61 to -1.23 m) at Grindstone Neck was characterized by a high cover of encrusting coralline algae, a moderate canopy (mostly the annual kelp *Alaria*) from spring to autumn, and little *Chondrus* (2-3%; Table 7). Sea urchins were abundant at this site from July 1974 to winter 1974-75. They remained under the edges of large boulders during daytime low tides and foraged out from the boulders during high tide. In contrast, the low intertidal-subtidal interface at another site, Canoe Beach Cove, has a dense *Chondrus* bed and lacks urchins (96% cover; Table 7). For unknown reasons, the urchins disappeared from Grindstone Neck during winter 1974-75. Herbivore enclosure and exclusion cages were established the following spring to assess the effect of herbivores (sea urchins, limpets, and periwinkles) on recolonization of this area. All cages were placed on substrata completely covered by encrusting coralline algae (Fig. 8).

As expected, the effect of *L. littorea* on settlement and growth of perennial algae was minor. *Chondrus* settles and gradually becomes the most abundant occupier of space in *L. littorea* enclosures, large herbivore exclusions (exclusion of *L. littorea* and *Acmaea*), controls, and roofs (Fig. 8a-c, e). No ephemeral algae

appear in the large herbivore exclusions even though they appeared in low zone herbivore exclusion cages nearby. It was impossible to exclude small snails (*Margarites*, *Lacuna*, and small *L. littorea*) from the herbivore exclusion cage and they may have grazed settling ephemeral algae.

Strongylocentrotus (Fig. 8d) and *Acmaea* (Fig. 8f) have major effects on algal colonization and growth. Limpets essentially maintained the same algal composition throughout the duration of the experiment (mostly the encrusting corallines such as *Lithothamnium*, *Clathromorphum*, etc.). Sea urchins not only prevent colonization by *Chondrus*, but also consume some of the encrusting coralline algae (Fig. 8d). However, this effect probably occurs only at high urchin densities.

The effects of limpets in these and earlier experiments are probably an exaggeration. Enclosure of even a single limpet in a 10 × 10-cm cage results in a density which is equivalent to 100/m². In comparison, normal mean limpet densities range from 0.4/m² to 15.7/m² at the different areas (Table 2) and individual 0.25 m² quadrats had densities reaching 58 limpets/m², or about half the experimental density. In addition, caged limpets were usually relatively large individuals

RECOLONIZATION AFTER COMPLETE DENUDATION

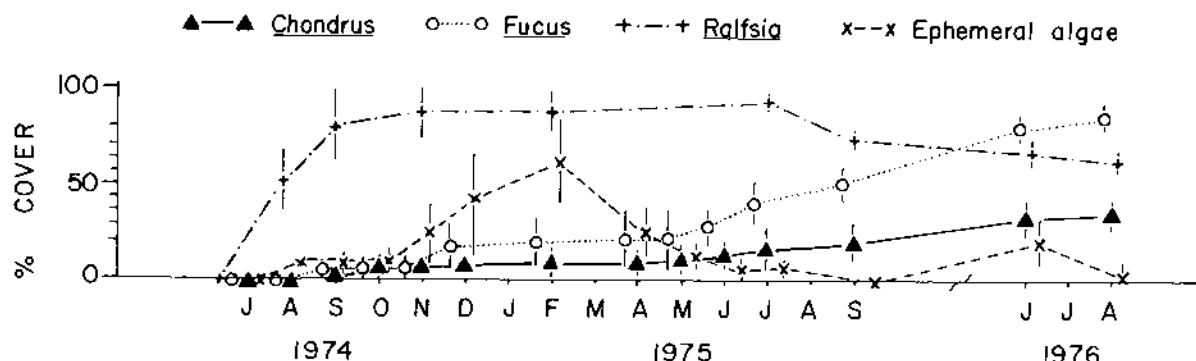


FIG. 9. Percent cover of organisms recolonizing a denuded 3-m² patch 16–18 July 1974 at Canoe Beach Cove. *Chondrus* covered 91% of the patch in July prior to denudation. Points represent means \pm 95% confidence intervals for eight 0.25-m² quadrats at each date.

(1.5–2.0 cm long compared to mean individual size and 9% confidence intervals at the study sites ranging from 0.67 ± 0.04 cm to 1.29 ± 0.05 cm long), making the biomass enclosed even greater than densities indicate. Thus, results of limpet enclosures must be interpreted cautiously.

In summary, only 2 herbivores appear to be capable of preventing *Chondrus* from becoming established. Limpets (when enclosed in cages, Fig. 8f) and sea urchins (enclosed, Fig. 8d; or not enclosed, Table 7) can evidently maintain bare or encrusting coralline-covered space. However, these two herbivores are usually scarce (limpets) or absent (urchins) in the low zone; herbivores that are usually present (i.e., *L. lit-*

torea; Table 2) cannot prevent establishment of *Chondrus* thalli on either encrusting coralline algae or from encrusting holdfasts.

Primary succession.—To initiate primary succession in the low zone, a 3-m² patch of *Chondrus* was cleared and burned in May 1974 at Canoe Beach Cove. Prior to clearance, Irish moss occupied virtually all of the area ($\bar{X} \pm 95\%$ confidence intervals = $90.6 \pm 12.3\%$, $n = 8$) and *L. littorea* was abundant ($649/\text{m}^2$ or $162.2 \pm 53.1/0.25 \text{ m}^2$). Two week after burning, herbivore enclosure and enclosure cages, roofs, and controls were placed in the patch to evaluate effects of herbivores on colonization events. Cages and controls were placed adjacent to the eight 0.25-m² quadrats used

TABLE 7. Percent of algae and density of herbivores in low intertidal and shallow subtidal zones, July 1974, at 1 area with and 1 area without sea urchins. Percent cover = mean \pm 95% confidence intervals; density = mean \pm 95% confidence intervals per 0.25 m² for *L. littorea* and *Acmaea*; density of *Lacuna* and *Margarites* was taken in .01 m², so is given first in numbers per 0.25 m², then as $\bar{X} \pm 95\%$ CI/.01 m² in parentheses. $N = 10$ quadrats for each height. Subtidal transects were done with SCUBA equipment

Parameters	Grindstone Neck			Canoe Beach Cove	
	Low intertidal (-0.15 m)	Low intertidal-subtidal interface (-0.61 m)	Shallow subtidal (-1.23 m)	Low intertidal (-0.15 m)	Low intertidal-subtidal interface (-0.61 m)
Percent cover					
Crusts	11 \pm 13	65 \pm 4	94 \pm 4	40 \pm 32	20 \pm 7
Bare	8 \pm 12	15 \pm 19	3 \pm 2	13 \pm 4	2 \pm 3
Algal holdfasts	24 \pm 24	4 \pm 4	3 \pm 4	33 \pm 13	73 \pm 6
<i>Chondrus</i>	68 \pm 20	2 \pm 1	3 \pm 4	87 \pm 5	96 \pm 3
Ephemeral algae	0	2 \pm 2	7 \pm 9	0	0
<i>Alaria</i>	0	54 \pm 16	20 \pm 9	0	0
<i>Laminaria saccharina</i>	0	2 \pm 1	4 \pm 5	0	1 \pm 2
Density					
<i>Littorina littorea</i>	18.8 \pm 5.3	1.6 \pm 1.6	5.0 \pm 2.5	163.9 \pm 49.7	83.8 \pm 24.5
<i>Acmaea</i>	1.5 \pm 1.4	2.7 \pm 2.7	6.3 \pm 3.2	0	0
<i>Lacuna</i>	15 (0.6 \pm 0.7)	47 (1.9 \pm 1.3)	440 (17.6 \pm 23.5)	10 (0.4 \pm 0.5)	233 (9.3 \pm 2)
<i>Margarites</i>	7.5 (0.3 \pm 0.5)	6 (0.2 \pm 0.3)	15 (0.6 \pm 0.8)	0	0
<i>Strongylocentrotus</i>	no	abundant	abundant	no	no

to monitor the large patch. Predator exclusion cages were not established in these experiments, but it seems likely that their effects are the same as above. Both *Thais* and *Asterias* were present in the general area (Table 2) and as usual were included in cages.

Results are shown in Figs. 9 and 10. Colonization in the large 3-m² patch (Fig. 9) was mirrored by that in the controls and roof (Fig. 10a, b). Following denudation, the encrusting brown alga *Ralfsia* settled and quickly occupied most of the rock surface. In September, germlings of *Fucus vesiculosus*, normally a mid zone perennial brown alga, settled. Most of these were eaten by *L. littorea*, but those in crevices were often missed or inaccessible to this snail. The stand of *Fucus* which eventually developed in these experiments arose from these escaped germlings. Once *Fucus* attains a length of 3–5 cm, periwinkles usually do not graze them (Menge 1975). Hence, *Fucus* germlings have a potential spatial refuge (crevices) and older individuals have a refuge in size from periwinkles (Menge 1975). Those *Fucus* with holdfasts in crevices became established, continued to grow and after 2 yr occupied 95% of the canopy space (Figs. 9 and 10). *Fucus* did not become established in controls and roof until winter, but then grew quickly to dominate canopy space in the 2 controls and the roof which had crevices (Fig. 10). The importance of a refuge in initial establishment of *Fucus* is indicated by the failure of *Fucus* to become established in 1 control which lacked a crevice.

In controls, roofs, and the large patch, ephemeral algae (*Enteromorpha*, *Ulva*, *Scytosiphon*, *Petalonia*, *Dumontia*, *Spongomorpha*, *Rhizoclonium*) became abundant during the winter (when *L. littorea* was inactive) and then declined in abundance in the spring, summer, and fall (Figs. 9, 10a, b). In addition to these ephemerals, *Chondrus* appeared in these treatments. In all cases, this alga grew from encrusting holdfasts in crevices. Evidently, either our denudations were not completely successful, or new plants settled or survived only in crevices. After 2 yr *Chondrus* occupied 30% of the secondary space (Fig. 9). The decline in abundance of *Ralfsia* may be due to competition with *Chondrus* holdfasts, newly settled encrusting coralline algae, or to shading by *Fucus*.

In herbivore exclusion cages, *Ralfsia* initially settled and covered 21% of the substratum, grew quickly and occupied 100% of the primary space, then decreased in abundance rapidly as ephemeral algae increased in abundance, suggesting ephemerals outcompeted *Ralfsia*. As in secondary succession experiments, ephemerals persist in the absence of *L. littorea* and evidently prevent invasion by *Chondrus* (Fig. 10).

Before enclosure of *L. littorea* in cages, a thin cover of *Ralfsia* occupied ≈60% of the primary space. After enclosure of periwinkles, *Ralfsia* disappeared and eventually *Chondrus* invaded and grew (Fig. 10d). Evidently a high density of periwinkles (4 in each en-

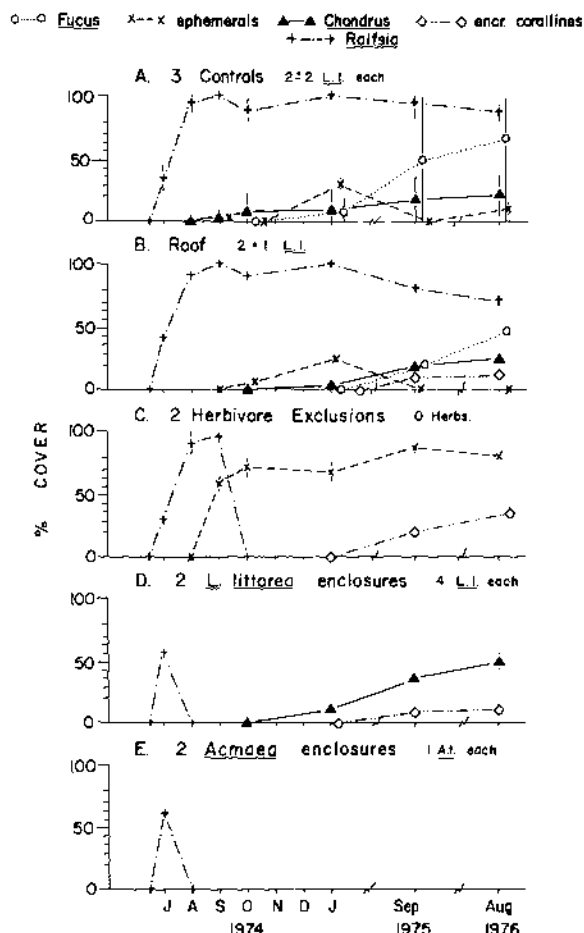


FIG. 10. Effects of herbivores on recolonization of completely denuded space in the low zone. Mean percent cover and ranges are indicated for 3 replicates in A, 2 in C, D, and E. The mean number of grazers per treatment is indicated for each date at the top of each treatment.

sure cage) eliminates *Ralfsia* and slows but does not prevent colonization by *Chondrus* (compare Figs. 10c and d). This interpretation is supported by laboratory experiments which indicate that *L. littorea* will graze *Ralfsia* (but only if it is a thin layer: Menge 1975), and by results in the controls and roof (Fig. 10a, b) which had normal *L. littorea* densities.

The effect of *L. littorea* on succession in these experiments seems determined by littorine density and the attractiveness of the different colonizers as food. Thus, at normal densities (controls and roof in Figs. 9, 10a, b), periwinkles appear to remove ephemeral algae, sporelings and germlings (i.e., consume highly preferred food). High periwinkle densities (i.e., when enclosed in cages; Fig. 10d) appear to force snails to consume less-preferred food (e.g., *Ralfsia*). Thus, only nonedible plants (*Chondrus*, encrusting corallines) successfully colonize *L. littorea* cages. Although *L. littorea* in even higher densities (6/0.1 m² or 600/m²) can decrease abundance of encrusting holdfasts of

Chondrus for a short time (Table 6), they do not appear to adversely affect the recolonization of *Chondrus* thalli (Fig. 10a, b, d). Irish moss grows from crevices in the *L. littorea* enclosure as in the roof and controls, suggesting periwinkles may eliminate *Chondrus* holdfast if it is thin (as they do for *Ralfsia*) and not in crevices. Hence, like *Fucus*, young *Chondrus* plants may require a spatial refuge. However, this recruitment results more probably from perennation by holdfasts in crevices which were not destroyed by burning.

Limpets (Fig. 10e) evidently also quickly graze all *Ralfsia* present and prevent further algal colonization. Despite the presence of appropriate looking crevices in limpet enclosures, no *Fucus* or *Chondrus* have become established. *Acmaea* is known to graze *Chondrus* holdfast (Table 6) and *Fucus* germlings (Menge 1975) and apparently prevents establishment of these algae by removing any holdfast or germlings that are present. However, as noted above, this effect may occur only at artificially high densities.

The primary succession experiments were initiated only once in the early summer. Since different ephemeral algae settle during different seasons (Menge 1975), there would undoubtedly be differences in species of algae colonizing if denudations were done at different times of the year. However, since *L. littorea* consumes most intertidal ephemeral algae (Menge 1975, Lubchenco 1978), this herbivore should have the same effect on colonization events during most of the year except winter when it is inactive. The rate at which perennial species become established would probably depend on when they settle and how fast they grow, both season-related events. Although we would expect the general results and effects of herbivores on primary successional events to be similar regardless of the time of initiation of experiments, this interpretation needs experimental verification.

Two years after denudation of *Chondrus*, *Fucus* occupies 95% of the canopy space and is the dominant member of the community (Fig. 9; August 1976). *Chondrus* abundance is slowly increasing. Normal densities of periwinkles apparently remove ephemeral epiphytes that slow down or prevent the recolonization of *Fucus* and *Chondrus* (compare Fig. 10c to 10a, b, d). However, with intense *L. littorea* grazing, *Fucus* does not become established, but *Chondrus* does recolonize and grow slowly. Limpets seem to be more effective grazers, because they can prevent colonization of both *Fucus* and *Chondrus* and hence maintain bare space.

Thus, *L. littorea* actually has a positive effect on recolonization of *Chondrus* by removing ephemeral algae which either inhibit or prevent colonization of the perennials, *Chondrus* and *Fucus*. That is, foraging by periwinkles seems to increase the rate of succession. Similar results have been obtained in the mid

intertidal (Menge 1975, B. A. Menge and J. Lubchenco, personal observations).

The overall effect of herbivores on establishment and development of the low zone community seems as follows. When abundant, periwinkles can increase the rate at which *Chondrus* colonizes an area (either *de novo* or by perennation from encrusting holdfasts) by preferentially consuming ephemeral algae that delay recruitment or growth of *Chondrus*. When herbivores are absent or scarce, ephemeral algae become seasonally abundant and delay the rate at which *Chondrus* dominates an area. Two herbivores that can graze either encrusting holdfasts (limpets) or holdfasts and thalli (sea urchins) are either not abundant or not usually present. Thus, *Chondrus* has apparently escaped control by herbivores; the latter actually have a positive effect on abundance of this alga.

Persistence of the low zone community

Previous sections indicate that (1) mussel predators are crucial to the establishment of *Chondrus* beds and (2) low zone herbivores increase the rate at which this alga becomes established. In this section we examine factors affecting the persistence of established *Chondrus*. Again, both mussel predators and herbivores are important.

Effect of predation and animal-plant competition.—Predator exclusion experiments placed on stands of *Chondrus* indicate that exclusion of predators results in the gradual replacement of *Chondrus* by *Mytilus* (Fig. 11). In one experiment (at Little Brewster Cove, Fig. 11c), initial *Chondrus* cover was 20% and increased to 40% before *Mytilus* began outcompeting both algae and barnacles (max cover = 28%). By August, *Mytilus* covered 100% of available space in this treatment. The second experiment (at Grindstone Neck, Fig. 11f) started with a 100% cover of *Chondrus*. Although it took longer, *Mytilus* eventually replaced the alga.

The roofs and controls (Fig. 11a, b, d, e) show that *Chondrus* persists when predators are present but that mussels appear quite frequently and sometimes nearly outcompete *Chondrus* before being discovered and eaten by predators. This latter observation again suggests that escapes from predators by mussels occasionally occur in the low zone.

When both predators and mussels are excluded, *Chondrus* appears able to maintain its occupancy of space against potential invasion by barnacles. In two experiments run from March 1973 to April 1974, *Chondrus* maintained a mean cover ranging between 58% and 95% whereas barnacle cover ranged from 0% to 4%. Thus, the competitive hierarchy given earlier is relevant only on cleared substratum in spring. If *Chondrus* already occupies the substratum, barnacle larvae are evidently unable to, or do not, penetrate between the blades of this alga and recruit.

In summary, these results indicate predators play a

EFFECT OF PREDATION, COMPETITION ON ESTABLISHED STANDS OF *CHONDRUS* - LOW INTERTIDAL

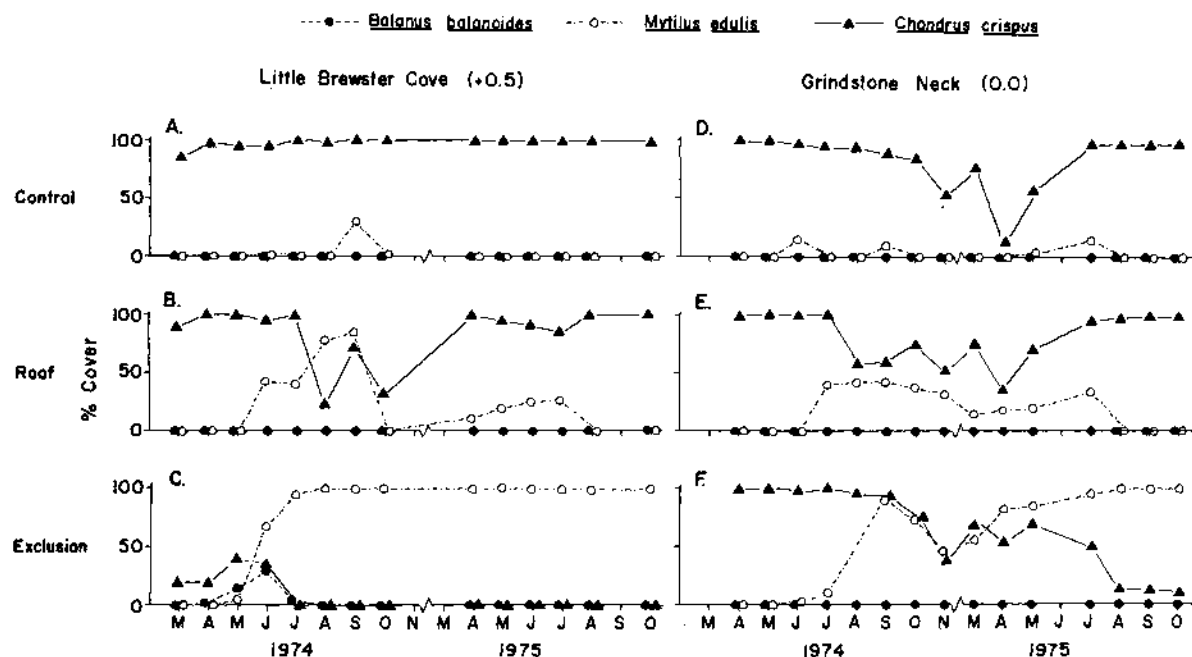


FIG. 11. Effects of competition from *Mytilus* and predation by starfish and whelks on the persistence of *Chondrus* at +0.15 m (+0.5 ft) at Little Brewster (A through C) and at 0 m (0 ft) at Grindstone Neck (D through F).

crucial role in the persistence of *Chondrus* in that they prevent *Mytilus* from outcompeting the alga. At protected areas, if there were no predators, *Chondrus* would be eliminated by *Mytilus*. In fact, this probably explains the dominance of mussels in the low zone at Pemaquid Point; predators are scarce and/or ineffective in controlling these bivalves.

Effect of herbivory and plant-plant competition.—As shown in Fig. 2, abundance of ephemeral algae in the low zone is seasonal at all but the most protected area, being most abundant in the late spring. When algae are most abundant at such sites, *Chondrus* abundance is relatively low (e.g., Grindstone Neck and Chamberlain, Fig. 1). These algae settle epiphytically on *Chondrus*, on free space, or on mussels and barnacles. Note that at the most protected site (Canoe Beach Cove), where ephemerals are least abundant (Fig. 2), *L. littorea* is most abundant (Table 2). Excluding the data point from a very exposed area (VE in Fig. 12), percent of *Chondrus* covered by epiphytes at different areas in June 1974 is significantly inversely correlated with the density of *L. littorea* (Y [cover in degrees] = $74.76 - 0.18X$ [$L. littorea/m^2$], $r^2 = .82$; Fig. 12). This correlation suggests that the effectiveness of *L. littorea* in removing epiphytes from *Chondrus* is at least partly related to its density. Where *L. littorea* is absent (i.e., at moderately exposed sites like Chamberlain; Table 2), epiphytes remain for longer

periods of time than where *L. littorea* is present (e.g., 6 vs. 3 mo, Menge 1975). At more exposed sites, wave action frequently removes epiphytes from *Chondrus* as does *L. littorea* at protected areas. Thus, the highest density of ephemerals on *Chondrus* probably occurs at areas that are exposed enough to exclude *L. littorea* but not so exposed that ephemeral algae are continually torn loose (Fig. 12).

To evaluate direct effects of ephemerals, and both direct and indirect effects of *L. littorea* on persistence of *Chondrus*, we initiated standard sets of herbivore exclusion experiments on stands of this alga. At Grindstone Neck periwinkles remove all ephemerals from *Chondrus* in the *L. littorea* enclosure, the 2 controls and the roof, but as usual do not affect *Chondrus* directly (Fig. 13a, b, d). In contrast, in herbivore exclusions various ephemerals (including *Ulva lactuca*, *Enteromorpha intestinalis*, *Porphyra* sp., *Rhizoclonium tortuosum*, and *Spongomorpha spinescens*) increase in abundance and persist for at least 13 mo.

Chondrus thalli appear to be adversely affected by shading by the mesh. The drop in percent cover of *Chondrus* in the 2 controls is significantly less than the drop in percent cover of *Chondrus* under both the roof and the *L. littorea* enclosure cage (Fig. 13; analysis of variance: $F = 3481$, $df = 1,2$; $p < .001$). Similar results were obtained in an experiment in a high zone tide pool at Chamberlain (Fig. 14). No epiphytes were

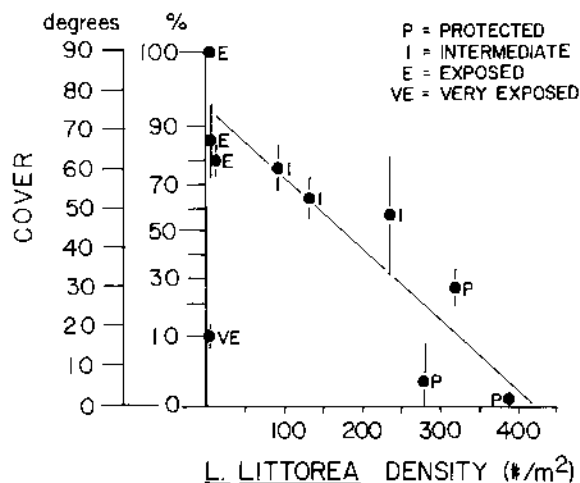


FIG. 12. Relationship between abundance of epiphytic ephemerals on *Chondrus* and density of *L. littorea* at 10 different areas. Bars indicate 95% confidence intervals for means of ten 0.25-m² quadrats at each area. Means and confidence intervals are in degrees. Percent cover axis is also shown for easier interpretation of transformed data.

present in any of the treatments from July 1973 to March 1974, perhaps because of the relatively infrequent exposure of this pool to settling gametes and spores. The effects of the shading by the mesh without any complication of epiphytes can be seen clearly here. Relative to controls, there is a significant decrease in percent cover of *Chondrus* thallus from July 1973 to March 1974 in all mesh-covered treatments (analysis of variance: $F = 17.19$; $df = 1,5$; $p < 0.001$). Thus, shading by the mesh can cause a decrease in percent cover of *Chondrus* thallus.

Despite this effect and the high level of the pools in Fig. 14, these experiments (Figs. 13 and 14) again indicate that ephemeral algae can shade *Chondrus* and slow down or prevent its growth. In Fig. 13, the abundance of *Chondrus* in exclusion cages (with epiphytes present) at the termination of the experiment (August 1973; $t = 13$ mo) is significantly less than in any other treatment (with epiphytes removed; analysis of variance: $F = 31.33$; $df = 1,4$; $p = .005$). In the high pools, the ephemeral *Enteromorpha* persisted only in the herbivore exclusion cage, though it settled in all treatments (Fig. 14). As a result, *Chondrus* declined in abundance and the entire thallus (but not the hold-fast) disappeared by July. Thus, as also reported elsewhere, *Enteromorpha* can evidently outcompete *Chondrus* in pools (Lubchenco 1978). However, since most epiphytic algae do not persist outside tide pools indefinitely, even in the absence of herbivores (Menge 1975), declines in abundance of *Chondrus* in the low zone are probably normally short term. Only if different epiphytes continually replace one another would *Chondrus* be permanently outcompeted (this in fact occurs in high tide pools that lack herbivores; see Lubchenco 1978).

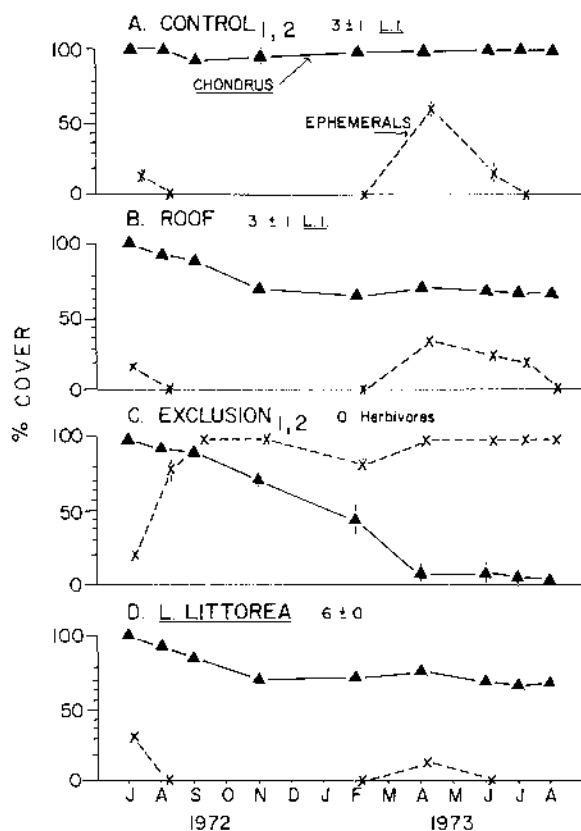


FIG. 13. Effect of *L. littorea* on persistence of *Chondrus* at -0.15 m at Grindstone Neck. In A and C symbols indicate the means and bars the ranges of the 2 replicates.

Finally, another possible adverse effect of epiphytes on *Chondrus* (besides shading) suggested by Prince (1971) is that *Chondrus* with a heavy load of epiphytes may be removed during storms, much as one of us has shown for fucoids (Menge 1975).

In summary, our experiments suggest that the development and persistence of the extensive stands of *Chondrus* occurring in the low zone throughout much of the Atlantic coast of North America is dependent primarily on 2 processes, predation and herbivory. The former, by removing the dominant competitor in the system (*Mytilus edulis*) frees *Chondrus* from competition with these bivalves. (Presumably the mechanism involves interference by shading and smothering effects.) The herbivores, by removing ephemerals, release *Chondrus* from inhibition by these short-lived algae. In addition, Irish moss appears to outcompete other perennial algae for primary space (Fig. 5 and Menge 1975). Thus, survival and abundance of *Chondrus* is essentially a by-product of the foraging activities of the 2 types of consumers and its own competitive abilities. Although both consumers are clearly important in allowing *Chondrus* to persist, the predator-mussel interaction would seem the more important, because mussels are both longer-lived than

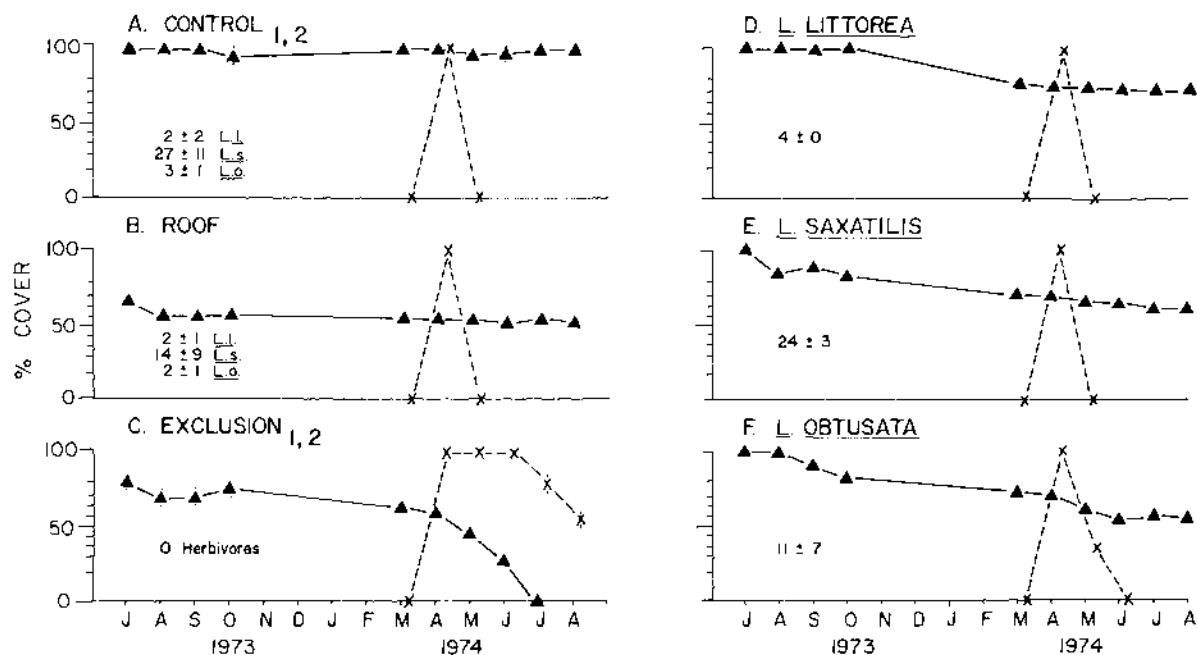


FIG. 14. Effect of the ephemeral alga *Enteromorpha* and littorines on persistence of tide pool *Chondrus* at $\approx +3.68$ m at Chamberlain. In A and C, symbols indicate means and bars ranges of the 2 replicates in each.

ephemerals, and can outcompete them for space (Menge 1976, personal observations).

DISCUSSION

Organization of the low zone community

The structure and organization of the low zone community is summarized in Table 8. Our data indicate that this system has 3 characteristic states of structural dominance and persistence which are correlated to the degree of wave shock (Fig. 1, Tables 1, 8). These are (1) *Mytilus* alone, which has low persistence (Pemaquid Point), (2) *Chondrus* and *Mytilus* with intermediate persistence (Chamberlain, Little Brewster Cove, and Grindstone Neck), and (3) *Chondrus* alone with high persistence (Canoe Beach Cove). Abundance of ephemeral algae declines with decreasing exposure to waves and tends to be seasonal at all but the most protected site (Fig. 2, Table 8). Consumer abundances are less clearly related to a wave shock gradient. Herbivores occur only at the 3 most protected sites while predators occur at all sites (Table 2). However, starfish and *Thais* abundances vary among sites with no obvious correlation to a wave shock gradient (with the exception that starfish do not occur at exposed sites) or to each other (Table 2).

Our experiments and observations indicate that the organization of the low zone community is dependent on several general processes, including consumer-prey interactions, physical disturbances, and competition for space. At exposed headlands, the lack of effectiveness of predators in controlling mussels, wave shock, and life history characteristics of mussels and

Chondrus evidently explains both the complete domination of space by mussels and the low persistence stability observed at these sites. Though predators (mostly *Thais*) are present at exposed sites, they are apparently restricted to crevices and other shelter by wave shock as in the mid intertidal zone (Menge 1978a) and probably have no effect on mussel abundance. Mussels at exposed sites have apparently completely escaped control by predators and dominate low zone space by virtue of their good recruitment, fast growth, early maturation, and dominant status as competitors for space (Table 9). Cleared space is quickly colonized and dominated by mussels. Because predators are ineffective in controlling mussels, growth in the mussel bed eventually becomes constrained by crowding. Continued growth loosens patches of mussels and eventually large sheets of *Mytilus* are torn loose and washed away by winter storms. This leaves small clumps of mussels on large areas of free space each spring (Tables 8 and 9). Extensive beds of mussels usually develop by August but persist for a relatively short time. This pattern of clearance of space by storms, settlement, intense competition for space (primarily between barnacles and mussels) leading to a mussel monopoly of low persistence is more or less an annual event and suggests these communities possess high adjustment stability. *Chondrus* is scarce (Fig. 1) and seems unable to take advantage of the resources freed by these disturbances, probably because space is available only briefly each spring and *Chondrus* recruits slowly (Table 9).

At sites of intermediate exposure to waves, preda-

TABLE 8. Summary of the organization of the low intertidal community in New England

Characteristic	Areas			
	Pemaquid Point	Chamberlain	Little Brewster Cove, Grindstone Neck	Canoe Beach Cove
Wave exposure	Exposed	Relatively exposed	Relatively protected	Protected
Structurally dominant species	<i>Mytilus</i>	<i>Chondrus</i> and <i>Mytilus</i>	<i>Chondrus</i> and <i>Mytilus</i>	<i>Chondrus</i>
Ephemeral algae	Very abundant, seasonal	Abundant, seasonal	Abundant, seasonal	Scarce
Persistence of dominant species	Low	Intermediate	Intermediate	High
Importance of:				
A. Predation	Low (ineffective)	Intermediate (control <i>Mytilus</i> with occasional escapes)	Low: Direct effect = none Indirect effect = variable control of ephemeral algae	High (control <i>Mytilus</i> with no escapes)
B. Herbivory	Unimportant (no herbivores)	Unimportant (no herbivores)		Intermediate: Direct effect = none Indirect effect = control ephemeral algae
C. Interspecific competition for primary space:				
1. Plant-animal	High (<i>Mytilus</i> dominates space, resistant to invasion by all species)	Intermediate (<i>Chondrus</i> and <i>Mytilus</i> coexist due to occasional escapes by <i>Mytilus</i> from predators)		Low (<i>Mytilus</i> eaten)
2. Plant-plant	Low (<i>Mytilus</i> dominates)	Intermediate (<i>Chondrus</i> dominates when <i>Mytilus</i> is scarce)		High (<i>Chondrus</i> dominates space because <i>Mytilus</i> eliminated; resistant to invasion by other plants)
D. Epiphytes	Probably low	Intermediate (induce variation in abundance of <i>Chondrus</i>)		Low (eaten by herbivores)
E. Physical disturbance				
1. Wave shock	High (clears extensive areas of space frequently)	Intermediate (clears patches of space by removing mussels; removes ephemerals)	Intermediate (clears patches of space by removing mussels)	Low
2. Cobble scour	Low (none present)	Low (none present)	Intermediate (clears space in winter)	Relatively Low (clears space infrequently)

tors, and disturbance from either wave shock or cobble scour or both seem to control the *Chondrus-Mytilus* codominance and patterns of stability observed at these sites. Predators usually control mussels, which allows *Chondrus* sufficient time to settle, grow, and monopolize space (Table 8). However, the effectiveness of predators varies in both space and time and often large patches of mussels occur in a matrix of *Chondrus* and may have 3 fates. First, they may be eventually discovered by predators, in which case *Mytilus* is eaten and the thalli of *Chondrus* persist. Second, patches of both *Chondrus* and *Mytilus* may be torn loose by waves (usually in late winter) in which case only the encrusting holdfast of *Chondrus* remains. This crust then grows new thalli which develop into a *Chondrus* bed by late fall to early winter (depending on herbivore effectiveness in controlling epiphytic ephemeral algae). *Mytilus* may settle in this *Chondrus* bed and the cycle begins again. Third, both

mussels and *Chondrus* may be crushed by cobbles in which case (a) neither persists or (b) the encrusting holdfast of *Chondrus* remains. Escapes by mussels and removal of *Chondrus* occur irregularly and usually at time periods >1 yr. Hence at intermediate sites persistence seems greater than that observed at exposed sites (Table 8). Adjustment stability seems less at intermediate sites because patches do not return to a predisturbance state for ≈ 6 mo following spring clearances vs. ≈ 3 mo at exposed sites.

The effect of herbivores (primarily *L. littorea*) at intermediate sites is also variable. They are absent at some sites (Chamberlain; Table 8) and have no effect. At slightly less exposed intermediate sites (e.g., Grindstone Neck), they are abundant but have no direct controlling effect on *Chondrus*. Rather, they control the abundance of ephemeral epiphytic algae which can shade *Chondrus* and suppress its growth (Figs. 6, 7, 10, Table 8). However, ephemeral algae escape con-

TABLE 9. Life history and survival characteristics of major space occupants in low zone

Characteristic	Space occupant			
	<i>Mytilus</i>	<i>Balanus</i>	<i>Chondrus</i>	Ephemeral algae
A. Recruitment	Good Apr-Oct	Good Mar-Jun	Poor Sep-Nov	Good all year
B. Growth	Rapid	Rapid	Slow	Rapid
C. Maturation age	≈ 1 yr	≈ 1 yr	?	≈ weeks
D. Approximate average longevity	Intermediate (1-2 yr)	Intermediate (1-2 yr)	Long (?)	Short (months)
E. Asexual reproduction (animals) or Perennation (plants)	No	No	Yes	No
F. Interspecific competition for primary space				
1. Ability when colonization is simultaneous (rank)	1	2	3 ^a	4 ^a
2. Ability when colonization is asynchronous				
(a) As invader	Invades all	Rarely invades	Rarely invades	Rarely invades
(b) Against invasion	Resists all	Resists all but <i>Mytilus</i> ^b	Resists <i>Balanus</i> and ephemerals but not <i>Mytilus</i>	Resists <i>Balanus</i> and <i>Chondrus</i> but not <i>Mytilus</i>
G. Resistance to consumers	Low	Low	High	Low
H. Resistance to physical perturbations	Low	Intermediate	High	Low

^a See text for short term interactions.^b Resistance to invasion by *Chondrus* not clear.

trol by herbivores during winter and spring so that ephemerals probably contribute to some variation in abundance of *Chondrus*.

At protected sites, the dominance of *Chondrus* and the patterns of stability seem regulated by consumer-prey interactions and life history and competitive characteristics of *Chondrus*. Predators are consistently efficient at eliminating mussels (and barnacles) and as a result *Chondrus* stands are highly persistent and experience few hindrances to regrowth following a disturbance (Tables 8 and 9). Moreover, our experiments on secondary succession suggest low zone communities possess relatively high adjustment stability though it is less than that at exposed headlands. Such resilience seems due to the rapid perennation of *Chondrus* from its encrusting holdfast, the rate of which is further enhanced by the dense populations of herbivores which are active much of the year. Ephemeral epiphytes are rapidly located and cropped and are apparently never abundant enough to suppress *Chondrus* growth (Fig. 2, Table 8).

The general ecological significance of several features of this system deserves special emphasis. First, the role of consumers in determining the pattern followed during community development, or succession, seems of overriding importance. Although competitive interactions clearly occur and are important during any particular successional sequence, the sequence followed is clearly regulated by the predators of the competitive dominant organism, mussels (Fig. 3, Table 8). Predator effectiveness evidently varies approximately inversely with the level of wave shock. At the poles of this wave shock gradient, monopolies of mus-

sels (exposed) or *Chondrus* (protected) form. At intermediate sites these two species are codominants, apparently due in part to the variable effectiveness of predators. A mussel monopoly clearly results in the absence of predators. The development of a *Chondrus* monopoly is more complex and results from the combined effects of the removal of *Mytilus* by predators, the highly effective escape by *Chondrus* from all co-existing consumers, and the apparent competitive dominance of *Chondrus* to other plants. Although they have no direct controlling effect, the herbivores play a subtle but important role of damping variation (i.e., increasing persistence) and influencing rates of succession. This effect does not seem to have been demonstrated previously but as our experiments suggest is potentially quite important. The high level of persistence stability of *Chondrus* at protected sites seems strongly affected by the efficient control of epiphytes by *L. littorea* (Table 8).

Second, the structural dominance of *Chondrus* at protected areas seems to depend on several key characteristics of this alga. Probably the most important of these is the ability of this species to perennate or grow vegetatively from its extensive encrusting holdfast (Table 9). This is evidently the key factor allowing a rapid return to a predisturbance state in secondary succession. For example, our experiments (Fig. 5) show that during secondary succession *Chondrus* returned to 50% of its maximum abundance (100% at Canoe Beach Cove and 98% at Chamberlain) in 2-3.5 mo, respectively, after clearance in June 1974. In contrast, during primary succession at Canoe Beach Cove, at least 30 mo are required for *Chondrus* to

reach 50% of its maximum abundance (assuming that maximum abundance = 100%; Fig. 9). The importance of perennation is further emphasized by other results of these experiments. During primary succession, *Chondrus* must regain space by dispersal and recruitment rather than regrowth. It appears that the slow recruitment observed in these experiments (Fig. 9) is partly a consequence of the fact that more opportunistic species, for example, *Ralfsia* (<1 mo to 50% of maximum abundance of 95%), ephemeral algae (5 mo to 50% of maximum abundance of 65%), and especially *Fucus vesiculosus* (15 mo to 50% of maximum abundance of 90%) acquire and dominate space relatively rapidly. This presumably slows recruitment and growth of *Chondrus* greatly. Thus, the tenacious holdfast enables *Chondrus* to (1) be less susceptible to disturbance, i.e., have a greater persistence than other abundant organisms and (2) recover faster from disturbances which remove just the thalli than can organism that must rely on recruitment to recolonize a disturbed area.

Third, physical disturbance from wave shock or cobble scour plays a major role by clearing space (which initiates succession) and hence inducing variation in abundance of space occupiers and reducing persistence stability. This effect is most marked at the more exposed areas and has probably been a major force in shaping both the dynamics of the low zone community and in the evolution of the life cycle of populations of mussels on exposed headlands. This mechanism probably also has an important but longer-term effect at more protected sites. *Chondrus* apparently cannot persist in sites with frequent disturbance (because it is outcompeted by mussels) but can persist where perturbations are less frequent. Several aspects of the life history of *Chondrus*, especially its perennation abilities, appear to be important adaptations which lead to both relatively high persistence and adjustment stability in the face of relatively less frequent but still major disturbances.

Organization of the New England rocky intertidal community

There are 3 major findings that this study has in common with investigations of the high and mid intertidal zones in New England (Menge 1976, Menge and Sutherland 1976). One of these is the increased importance of predator-prey interactions in structuring the community with decreased environmental harshness. In habitats of relatively low harshness, predators control the abundance of the functionally dominant competitor (*Mytilus*) and allow algae to colonize and persist. Competitive interactions between algae result, with a single competitive dominant (*Chondrus*) usually monopolizing most of the space. In harsh habitats, mussels eliminate all competitors because predators are ineffective. Presumably this explains the extensive monospecific beds of mussels ob-

served in both mid and low zones on rocky shores at exposed headlands.

The competitive interactions occurring between the most abundant species appear complex and depend in part on (1) the relative age or size of the organisms and (2) the time span observed. Mussels clearly out-compete barnacles and Irish moss for primary space. The outcome of barnacle-Irish moss competition appears to depend on which species colonizes first. If either is well established, the other does not usually settle or grow. Results of plant-plant competition are different over a short time period than a long time period. Various ephemeral algae can temporarily out-compete *Chondrus* but eventually die, are eaten, or removed by waves. *Chondrus* can become established then but is susceptible to future invasions by ephemeral algae. *Fucus* can settle on bare space and out-compete *Chondrus* until *Fucus* dies or is removed at which time *Chondrus* takes over permanently and prevents future recolonization by *Fucus* (J. Lubchenco, *personal observation*). In both cases, early successional species can delay the rate at which later successional species appear. Since herbivores preferentially graze the earlier species, they increase the rate of succession.

Thus, the most abundant space occupiers in this system do not form a strict competitive hierarchy (i.e., A always outcompetes B which always outcompetes C), nor do they form networks (A outcompetes B which outcompetes C, but C outcompetes A; see Jackson and Buss 1975). Instead, results of adult-adult interactions differ from adult-juvenile or larval and larval-larval interactions such that what appears to be a simple hierarchy between adults is in fact most complex (as Woodin 1976 and Sutherland 1974 describe for soft sediment and hard substratum communities, respectively). Our system has a top competitor (*Mytilus*) but perhaps network-like interactions between other competitors.

A second parallel between high, mid, and low community organization is the fact that even though predators are present at exposed headlands (Table 2) they are ineffective in controlling mussels. This lack of effectiveness is apparently the result of increasing risks experienced by predators in foraging with increased wave activity (Menge 1978a). Thus, predator density alone does not provide an adequate measure of predation intensity. Variations in effectiveness of predators or herbivores in controlling their prey seems to be a key to understanding both local and geographic patterns of community structure (Connell 1975, Menge and Sutherland 1976, Menge 1978a, 1978b).

A third, closely related theme is the importance of escapes from consumers by animal or plant prey. In the low zone mussels occasionally escape control by predators (as also reported for the mid zone; Menge 1976). This apparently accounts for the occasional abundance of mussels at sites of intermediate expo-

sure to waves (Fig. 1). Evidently, the probability of any particular intertidal locale being searched for prey by predators is uneven over space as well as time (predators are inactive in the intertidal zone during the winter). That is, predation intensity seems spatially heterogeneous.

Escape by plants from their enemies appears to be a particularly significant phenomenon in determining observed patterns of community structure in nature (Connell 1971, Dayton 1975a, 1975b, Menge 1975, Paine and Vadas 1969). In this study we find that low zone herbivores are ineffective in controlling *Chondrus* recruitment, growth, or abundance. In fact, from the point of view of the alga, the feeding of the most abundant herbivore (periwinkles) primarily serves an antifouling function. This effect occurs in the mid zone as well where fucoid algae escape the control of this same periwinkle but have epiphytic algae removed by the grazers (Menge 1975, *personal observation*).

The structural dominance of this New England system by either 1 species (*Mytilus* at most exposed sites, *Chondrus* at most protected) or 2 (both mussels and Irish moss at intermediate sites) contrasts rather strongly with the observed structure in many other systems. The low intertidal zone on the Pacific Coast of North America is characterized by high animal and plant diversity, even though there appear to be 1 or 2 dominant alga(e) at specific sites (e.g., Dayton 1975a). Similar high diversities occur in low intertidal zones in the Bay of Fundy and the Atlantic shores of Europe (J. Lubchenco 1978, Lewis 1964). Prominent contributors to the high diversity in these low zones are kelps, other large algae and both sessile and vagile animals. Although the low zone of New England has a variety of animals and numerous species of small, usually epiphytic ephemeral algae (see Appendix 1), it apparently lacks both kelps (except for *Alaria* at exposed sites) and other large, long-lived algae attached to the substratum as well as the diversity of animals found elsewhere. Our study suggests that protected sites in New England differ from the above in having a low zone characterized primarily by 1 algal species, *Chondrus*. Although this alga occurs elsewhere (e.g., Bay of Fundy, European shores) it is usually found primarily in mixed stands in these regions.

The causes of these differences are not entirely clear. Experiments with the normally scarce sea urchins and limpets, coupled with the results of other studies on the effects of herbivores (e.g., Kitching and Ebling 1961, Jones and Kain 1967, Vadas, 1968, Paine and Vadas 1969, Dayton 1975a) suggest the scarcity of sea urchins and limpets is partly responsible for the escape and monopolization of space by *Chondrus*. That is, the herbivore guild in the low zone may be too simple (consisting essentially of browsing snails) to cope with a variety of morphological and other characteristics of plants. Historical effects would seem unimportant since considerable differences in struc-

ture occur between the faunistically similar, adjacent low zones of New England and the Bay of Fundy (Lubchenco 1978, J. Lubchenco and B. A. Menge *personal observation*). Moreover, *Chondrus* or *Chondrus*-like species (e.g., *Gigartina*) occur in, but do not dominate the more distant, but still taxonomically similar intertidal regions of the British Isles (Lewis 1964). Thus, we are left with the question of why there are no herbivores in New England that can control the dominant alga.

Succession and stability

Results in this paper and other studies in marine systems (Vadas 1968, Paine and Vadas 1969, Dayton 1971, 1975a, Sutherland 1974, Foster 1975a, 1975b) suggest that predators and herbivores can determine the form of the ultimate state (so-called "climax") of the system. Thus, starfish and predaceous snails determine whether mussels or Irish moss will be the ultimate "stable node" achieved in the low zone of New England. On the west coast of North America, several studies indicate the key role herbivores can play in regulating algal composition of low intertidal (Paine and Vadas 1969, Dayton 1975a) and subtidal algal associations (Vadas 1968, Foster 1975b). Consumers may also regulate the "trajectory" taken by the system in approaching this state by operating as filters on young stages. This mechanism was suggested by both Connell (1971) and Janzen (1970) to be important in structuring tropical forest communities. Our study indicates that though herbivores do not affect *Chondrus* directly, they determine how rapidly a *Chondrus*-dominated state is achieved by grazing the early dominant organisms in succession, ephemeral algae, which can delay the rate at which later species become established (Figs. 6, 7, 10). On the west coast, abundance of low zone algae appears to be determined primarily by sea urchins (Dayton 1975a). Individual plants in this system can escape control from herbivores and competition between adult plants seems of great importance in regulating algal composition in this association (Dayton 1975a). Numerous herbivore species other than urchins are present in this system (limpets, other gastropods, chitons) and it seems possible that the low zone herbivore guild may strongly influence recruitment and so indirectly influence the composition of the macroscopic algal association. Studies on the food and effects of limpets (Southward 1964, Dayton 1971, Nicotri 1977) indicate that these grazers concentrate on microscopic plants but that some algae, mostly fucoids, occasionally escape control by limpets and form a canopy. Our experiments indicate that though limpets can have a similar effect in New England, they are usually too scarce to have any widespread effect.

Thus, effects of consumers in this system are critical in determining both the final state and the rate at which

that state is reached. Furthermore, the life history characteristics of the organisms appear to be in phase with the rate of disturbances and affect both how resistant the community is to perturbation and how quickly it rebounds following a disturbance. The increasing numbers of reports on the influence consumers have on community structure in nonmarine systems (e.g., Harper 1969, Connell 1971, Maguire 1971, Sprules 1972, Brooks and Dodson 1974, Platt 1975) suggests such effects may be widespread and of great potential significance in both community development and persistence.

ACKNOWLEDGMENTS

We thank M. Cohen, M. L. Lubchenco, C. Hibbard, S. Riggs, P. McKie, B. Walker, D. Spero, and many others for field assistance. We particularly acknowledge Steve Garrity, whose tireless and devoted assistance in the field and laboratory we greatly appreciate. The reviewers and especially J. P. Sutherland and D. Wethey read the manuscript and gave us numerous constructive criticisms. We thank N. Riser, Director of Northeastern University's Marine Science Institute, for continued access to the Canoe Beach Cove site and to laboratory facilities. We acknowledge the Coast Guard personnel at Boston Light on Little Brewster Island for cheerfully tolerating our frequent invasions of their shores. This research was supported by University of Massachusetts Faculty Growth Grants, NSF Grants GA-35617 and DES72-01578 A01 (to B.A.M.) and NSF Doctoral Dissertation Grant GA-40003 (to J.L.). This paper is contribution no. 47 from the Marine Science Institute, Northeastern University, Nahant, Massachusetts.

LITERATURE CITED

- Brooks, J. L., and S. J. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150:28-35.
- Connell, J. H. 1961a. Effect of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31:61-104.
- . 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723.
- . 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* 40:49-78.
- . 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Proceedings of Advanced Study Institute Dynamics Numbers Population*. Pages 298-312 in P. J. Den Boer and G. R. Gradwell, editors, *Dynamics of populations*. Oosterbeek 1970, Centre for agricultural publications and documentation (Wageningen).
- . 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* 3:169-192.
- . 1975. Some mechanisms producing structure in natural communities: A model and some evidence from field experiments. Pages 460-490 in M. L. Cody and J. Diamond, editors, *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts, USA.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119-1144.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351-389.
- . 1975a. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45:137-159.
- . 1975b. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. *Fisheries Bulletin* 73:230-237.
- Dodson, S. I. 1974. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. *Ecology* 55:605-613.
- Drury, W. H., and I. C. T. Nisbet. 1973. Succession. J. Arnold Arbor. 54:331-368. Harvard University, Cambridge, Massachusetts, USA.
- Ebling, F. J., J. A. Kitching, L. Muntz, and C. M. Taylor. 1964. The ecology of Lough Ine. XIII. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *Journal of Animal Ecology* 33:78-83.
- Foster, M. S. 1975a. Algal succession in a *Macrocystis pyrifera* forest. *Marine Biology* 32:313-329.
- . 1975b. Regulation of algal community development in a *Macrocystis pyrifera* forest. *Marine Biology* 32:331-342.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. *Quarterly Review Biology* 50:237-266.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* 15:839-928.
- Harper, J. L. 1969. The role of predation in vegetational diversity. *Brookhaven Symposia in Biology* 22:48-61.
- Horn, H. S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, New Jersey, USA.
- . 1975a. Forest succession. *Scientific American* 232(5):90-98.
- . 1975b. Markovian properties of forest succession. Pages 196-211 in M. L. Cody and J. Diamond, editors, *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts, USA.
- Hurd, L. E., and L. L. Wolf. 1975. Stability in relation to nutrient enrichment in arthropod consumers of old field successional ecosystems. *Ecological Monographs* 44:465-482.
- Jackson, J. B. C., and L. Buss. 1975. Allelopathy and spatial competition among coral reef invertebrates. *Proceedings of the National Academy of Sciences, USA* 72:5160-5163.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-528.
- Jones, N. S., and J. M. Kain. 1967. Subtidal colonization following the removal of *Echinus*. *Helgolander Wissenschaftliche Meeresuntersuchungen* 15:460-466.
- Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecological Monographs* 20:229-250.
- Kitching, J. A., and F. J. Ebling. 1961. The ecology of Lough Ine. XI. The control of algae by *Paracentrotus lividus* (Echinoidea). *Journal Animal Ecology* 30:373-383.
- Lewis, J. R. 1964. The ecology of rocky shores. The English Universities Press, Limited, London, England.
- Lubchenco, J. (formerly Menge, J. Lubchenco). 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23-39.
- MacFarlane, C. I. 1952. A survey of certain seaweeds of commercial importance in southwest Nova Scotia. *Canadian Journal of Botany* 30:78-97.
- Maguire, B., Jr. 1971. Phytotelmata: Biota and community structure in plant-held waters. *Annual Review of Ecology and Systematics* 2:439-464.
- Margalef, R. 1969. Diversity and stability: A practical pro-

- posals and a model of interdependence. Brookhaven Symposium in Biology 22:25-37.
- Mathieson, A. C., and J. S. Prince. 1973. Ecology of *Chondrus crispus* Stackhouse. Pages 53-79 in M. J. Harvey and J. McLachlan, editors. *Chondrus crispus*. Nova Scotia Institute of Science, Halifax, Nova Scotia.
- Mauzey, K. P. 1966. Feeding behavior and reproductive cycles in *Pisaster ochraceus*. Biological Bulletin 131:127-144.
- Mauzey, K. P., C. E. Birkeland, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49:603-619.
- Menge, B. A. 1972a. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecological Monographs 42:25-50.
- . 1972b. Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecology 53:635-644.
- . 1973. Effect of predation and environmental patchiness on the body size of a tropical pulmonate limpet. Veliger 16:87-92.
- . 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355-393.
- . 1978a. Predation intensity in a rocky intertidal community: Relation between predator foraging activity and environmental harshness. Oecologia 33 (in press).
- . 1978b. Predation intensity in a rocky intertidal community: Effect of an algal canopy, wave action and desiccation on predator foraging rates. Oecologia 33 (in press).
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition and temporal heterogeneity. American Naturalist 110:351-369.
- Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. Oecologia 17:293-317.
- . 1975. Effect of herbivores on community structure of the New England rocky intertidal region: Distribution, abundance and diversity of algae. Doctoral thesis. Harvard University, Cambridge, Massachusetts, USA.
- Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology 58:1020-1032.
- Orians, G. H. 1975. Diversity, stability and maturity in natural ecosystems. Pages 139-150 in W. H. van Dobben and R. H. Lowe-McConnell, editors. Unifying concepts in ecology. Dr. W. Junk, The Hague, Netherlands.
- Osman, R. W. 1977. The establishment and development of a marine epifauna community. Ecological Monographs 47:37-63.
- Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.
- . 1969. The *Pisaster-Tegula* interaction: Prey patches, predator food preference and intertidal community structure. Ecology 50:950-961.
- . 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52:1096-1106.
- . 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.
- . 1976. Size-limited predation: An observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57:858-873.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography 14:710-719.
- Pickett, S. T. A. 1976. Succession: An evolutionary interpretation. American Naturalist 110:107-119.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs 45:285-305.
- Prince, J. S. 1971. An ecological study of the marine red alga *Chondrus crispus* in the waters off Plymouth, Massachusetts. Doctoral thesis. Cornell University, Ithaca, New York, USA.
- Rex, M. R. 1976. Biological accommodation in the deep-sea benthos: Comparative evidence on the importance of predation and productivity. Deep-Sea Research 23:975-987.
- Ring, P. D. 1970. Developmental and ecophysiological studies of *Chondrus crispus* (L.) Stackhouse. Master's thesis. University of Maine, Orono, Maine, USA.
- Root, R. B. 1973. Organization of a plant arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-124.
- Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamelli-branchiata) on exposed rocky shores. II. Growth and mortality. Oecologia 3:317-350.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company, San Francisco, California, USA.
- Southward, A. J. 1964. Limpet grazing and the control of vegetation on rocky shores. Pages 265-273 in D. J. Crisp, editors. Grazing in terrestrial and marine environments. Blackwell Press, Oxford, England.
- Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375-386.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. American Naturalist 108:859-873.
- Vadas, R. L. 1968. The ecology of *Agarum* and the kelp bed. Doctoral thesis. University of Washington, Seattle, Washington, USA.
- Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: The importance of biological interactions. Ecological Monographs 44:171-187.
- . 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. Journal of Marine Research 34:25-41.

APPENDIX I.

A. EPHEMERAL ALGAE. Those species which usually persist for short periods of time during the year in the low zone are:

Chlorophyta	Phaeophyta
<i>Cladophora</i> sp.	<i>Ectocarpus</i> sp.
<i>Chaetomorpha linum</i>	<i>Elachistea fucicola</i>
<i>Enteromorpha</i> spp.	<i>Petalonia fasciata</i>
<i>Monostroma</i> sp.	<i>Pilayella littoralis</i>
<i>Rhizoclonium tortuosum</i>	<i>Scytosiphon lomentaria</i>
<i>Spongomorpha arcata</i>	
<i>S. lanosa</i>	Rhodophyta
<i>S. spinescens</i>	<i>Bangia fuscopurpurea</i>
<i>Ulothrix flacca</i>	<i>Ceramium</i> spp.
<i>Ulva lactuca</i>	<i>Dumontia incrassata</i>
	<i>Polysiphonia</i> spp. other than <i>lanosa</i>
	<i>Porphyra</i> spp.

B. OTHER SPACE OCCUPANTS. Various plants and animals other than *Balanus balanoides*, *Chondrus*, and *Mytilus* occupy space in the low zone. These usually represent a total of <5% cover (Figs. 1, 2, Table I). The more common of these species are listed below. This list is not exhaustive nor is it meant to be a checklist. We include these names merely to indicate the presence of organisms often found in transects but actually occupying little space.

PLANTS

Lichens
Verrucaria mucosa

Algae	Rhodophyta
Phaeophyta	<i>Ahnfeltia plicata</i>
<i>Chordaria flagelliformis</i>	<i>Alaria esculenta</i>
<i>Dictyosiphon foenicularceus</i>	<i>Callophyllis cristata</i>
<i>Fucus distichus</i>	<i>Clathromorphum</i> sp.
<i>F. vesiculosus</i>	<i>Corallina officinalis</i>
<i>Ralfsia clavata</i>	<i>Cystoclonium purpureum</i>
	<i>Gigartina stellata</i>
	<i>Halosaccion ramentaceum</i>
	<i>Hildenbrandia rubra</i>
	<i>Laminaria digitata</i>
	<i>L. saccharina</i>
	<i>Lithothamnion</i> spp.
	<i>Palmaria palmata</i>
	<i>Petrocelis middendorffii</i>
	<i>Phycodrys rubens</i>
	<i>Phymatolithon</i> sp.
	<i>Polyides rotundus</i>
	<i>Psilota plumosa</i>

ANIMALS

Porifera	Mollusca
<i>Halichondria</i> sp.	<i>Anomia</i> sp.
<i>Halictona</i> sp.	<i>Modiolus modiolus</i>
<i>Leucoselenia botryoides</i>	<i>Saxicava</i>
Cnidaria	Annelida
<i>Metridium senile</i>	<i>Spirorbis borealis</i>
<i>Obelia</i> sp.	
<i>Sertularia pumila</i>	Arthropoda
<i>Tubularia</i> sp.	<i>Balanus balanoides</i>
	<i>B. crenatus</i>
Ectoprocta	Chordata
<i>Electra pilosa</i>	<i>Amaroucium</i> spp.
<i>Flustrellidra hispida</i>	<i>Botryllus schlosseri</i>