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Author(s): Craig R. Johnson and Kenneth H. Mann

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## DIVERSITY, PATTERNS OF ADAPTATION, AND STABILITY OF NOVA SCOTIAN KELP BEDS<sup>1</sup>

CRAIG R. JOHNSON<sup>2</sup>

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

AND

KENNETH H. MANN

Department of Fisheries and Oceans, Marine Ecology Laboratory,  
Bedford Institute of Oceanography, P.O. Box 1006,  
Dartmouth, Nova Scotia, Canada B2Y 4A2

**Abstract.** There are two alternate community states in the rocky subtidal of the Atlantic coast of Nova Scotia, an unproductive sea urchin/coralline alga community, and highly productive kelp beds dominated by *Laminaria longicruris*. Disease-induced mortality of the sea urchins (*Strongylocentrotus droebachiensis*) triggered a switch from the first state to the second and provided a unique opportunity to study (1) the ability of *L. longicruris* to recover its former dominant status, and (2) its stability when competing with other seaweeds and when perturbed by storms and grazers other than urchins. Rates of recolonization of *L. longicruris* depended on the proximity of a refugial source of spores. When reproductive plants were nearby, a closed canopy developed within 18 mo of urchin mortality. When a reproductive population was several kilometres away, there was sparse recolonization for 3 yr, then a massive recruitment occurred with closure of the canopy in the 4th yr.

*Laminaria* is clearly the competitive dominant in the seaweed community. Manipulative experiments showed that the kelp limits the abundance of several understory species, but there was no evidence that the abundant annual seaweeds limited kelp recruitment. When sea urchins were rare, the density and growth rates of *Laminaria* were influenced mostly by intraspecific competition. When the canopy of adult plants was removed there was a dramatic increase in kelp recruitment, but the recruits that grew in dense patches in the clearings were significantly smaller than those of a similar age that grew more sparsely beneath the canopy. Once the kelp recovered from destructive grazing and formed a mature forest, it was able to maintain its dominance, even in habitats subject to severe nutrient stress for 8 mo of the year. For most of the year mortality and erosion of laminae outweighed the effects of recruitment and growth, and the canopy declined, especially during winter when storms were frequent. Erosion was exacerbated by grazing of the gastropod *Lacuna vincta*. However, in late winter and early spring, recruitment and rapid growth restored the canopy. When severe storm damage was simulated by completely removing *Laminaria* in patches, the kelp rapidly recolonized and soon outgrew other seaweeds.

Unlike the competitive dominants in kelp bed systems in the northeast Pacific, *L. longicruris* in Nova Scotia manifests multiple patterns of adaptation that enable it to dominate early and late stages of succession in a range of habitats of different levels of nutrient stress and of disturbance from storms and grazers. The principal threat to the stability of the kelp beds is destructive grazing by sea urchins. We suggest that the considerable differences between the dynamics of kelp beds in Nova Scotia and those of the northeast Pacific, and the high degree of stability of *L. longicruris* stands in Nova Scotia, is attributable to the low diversity of kelps and therefore low levels of competition in Nova Scotia, and to the multiple adaptations of *L. longicruris* that enable it to tolerate several stresses and disturbances.

We argue that the dynamics of community organization, and therefore the stability properties of this system are determined primarily by biological interactions and not by physical variables. This differs from the kelp communities in the northeast Pacific, in which both biological and physical factors influence dynamics significantly at a primary level. We offer a qualitative model of the dynamics of community structure in Nova Scotia that

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<sup>2</sup> Present address: Australian Institute of Marine Science, PMB No. 3, Townsville MC, Queensland 4810, Australia.

may be viewed as a set of deterministic "subroutines," in which each subroutine describes the outcome of a particular biological interaction. The subroutine(s) that predominate at one point in time and space are probably determined mostly by physical hydrographic variables that have a large stochastic component.

*Key words:* community structure; competition; disturbance; diversity; kelp; *Laminaria*; multiple adaptations; Nova Scotia; sea urchins; stability; stress; succession.

## INTRODUCTION

Community structure and its dynamics can be described in terms of the successional processes and stability properties that prevail in a community. Notions of community stability (Holling 1973, Sutherland 1981, Yodzis 1981, Pimm 1982, 1984, Connell and Sousa 1983, Dayton et al. 1984) and succession (Connell and Slayter 1977, Horn 1981) share a common underlying basis in that they relate to the manner in which species respond to biological and physical stresses and disturbances in the environment. To understand these community processes and properties at a finer scale of resolution, we need information on the population biology, life history, physiological, and behavioral characteristics of the component species. In this paper, we examine the response of the kelp *Laminaria longicruris* to large- and small-scale disturbances, and its interactions with other seaweeds, at two sites in eastern Canada. From considering some of its ecological, life history, and physiological traits we identify multiple patterns of adaptation in the kelp, and relate this and the low diversity of kelp species in Nova Scotia to the stability of the seaweed community in which *L. longicruris* dominates.

Of the multiplicity of definitions that have been applied to aspects of stability (e.g., Holling 1973, Connell and Sousa 1983), we adopt the terminology of Dayton et al. (1984), who suggested that community stability may be separated into three parts: (1) persistence, referring to a community having approximately constant composition through more than one turnover of the dominant species, (2) resistance, referring to the resistance of a community to disturbance or displacement by other species, and (3) resilience, which refers to the ability of a community to return to its original composition following perturbation and invasion by new species. These definitions can be equated with the constructs of Sutherland (1981) and Pimm (1984). We expand the meaning of resilience to embody situations in which a community returns to its original composition following a perturbation that changes markedly the relative abundance of species (which may include local extinctions), but where new species do not colonize. Also, we differ from Dayton et al. (1984) in assessing persistence in terms of turnover (see Connell and Sousa 1983) and not generation time.

The rocky subtidal of the Atlantic coast of Nova Scotia has two contrasting community configurations, either of which may span decades in time and extend along hundreds of kilometres of coastline. In the absence of high densities of sea urchins, the hard sub-

stratum supports dense and highly productive seaweed beds that grow in a more or less continuous band around the coast and are dominated by *L. longicruris* to a depth of 15–20 m (MacFarlane and Bell 1933, MacFarlane 1952, Edelstein et al. 1969, Mann 1972a, Novacek and McLachlan 1986). The biological and physical structure of these seaweed communities is three-tiered and relatively simple; *Laminaria* forms a closed canopy over smaller perennial and ephemeral algae that may grow to 0.01–0.5 m above the bottom, and there is a basal layer of encrusting coralline algae (Johnson and Mann 1986a, Novacek and McLachlan (1986). However, grazing by sea urchins (*Strongylocentrotus droebachiensis*) can convert the seaweed beds into unproductive sea urchin/coralline alga communities that are largely devoid of noncalcareous algae (Mann 1977, Chapman 1981, Wharton and Mann 1981). In the area of our study sites the unproductive state persisted from the late 1960's, but mass mortalities of the sea urchins in 1980–1983 (Miller and Colodey 1983, Scheibling and Stephenson 1984) attributed to an amoeboid pathogen (Jones 1985, Jones et al. 1985, Jones and Scheibling 1985) provided a unique "natural experiment" and opportunity to study the processes of recovery of the seaweed beds. We examined the ability of *Laminaria longicruris* to (1) recover its former dominant status following removal of the dense population of sea urchins, and (2) maintain this dominance when subject to storms, grazers other than sea urchins, and competition from other species. Considering the results of the present investigation together with those of previous studies, we construct a qualitative model of the dynamics and structure of the community as a whole, and compare the dynamics of kelp beds in Nova Scotia with those of the northeast Pacific, paying attention to differences in the diversity of kelps and the patterns of adaptation of the dominant species.

## METHODS

### Site description

Field work was conducted at Paul Pt. (44°34'21" N, 63°56'01" W) and at Mill Cove (44°35'30" N, 64°03'42" W) in St. Margaret's Bay on the Atlantic coast of Nova Scotia. Both sites are moderately exposed, with a boulder substratum to a depth of ≈ 15–17 m that is covered by encrusting coralline algae (Johnson and Mann 1986a). Mass mortality of sea urchins occurred at Paul Pt. in the autumn months of 1980, but a healthy population of urchins persisted at Mill Cove for another year until September 1981. (The exact time of urchin

mortality at Paul Pt. is not known, but we observed complete mortality at a site  $\approx 0.7$  km away by November of 1980. When Paul Pt. was first visited, the bottom was littered with the spines and tests of dead urchins.) The mortality of the urchins allowed seaweeds to recover (Johnson 1984), and at the time of the investigation, Paul Pt. supported a dense stand of *Laminaria longicuris*, which formed a closed canopy over an understory predominately of filamentous and foliose red and brown algae. In contrast, algal cover at Mill Cove comprised mostly small foliose and filamentous species with sparse kelp cover. All manipulations were conducted at  $\approx 10$  m depth; this is the middle of the bathymetric range of *L. longicuris* in St. Margaret's Bay recorded by Mann (1972a).

#### Identification of algae

Algae were identified according to the keys of South and Hooper (1980). Species of *Antithamnion* and *Antithamnionella* were pooled under the generic assemblage *Antithamnion* spp., species of *Callithamnion* spp. and *Seirospora seirosperma* (see Bird and Johnson 1984) were grouped under the assemblage *Callithamnion* spp., species of *Ectocarpus* and *Pilayella littoralis* were collectively referred to as ectocarpoids, and the species pairs *Polysiphonia nigrescens* and *P. flexicaulis*, and *Sphacelaria furcigera* and *S. cirrosa*, were not differentiated and were referred to as *P. nigrescens* and *S. furcigera*, respectively (detailed analysis of destructive samples showed that *Seirospora seirosperma* and *P. flexicaulis* were rare during the period of study; C. R. Johnson, *personal observation*). Throughout the paper we use the term "annual species" to include "aspect annuals" (i.e., plants in which a minute basal portion survives throughout the winter to grow again in the spring), since aspect annuals and annuals *sensu stricto* are likely to have similar ecological effects at the macroscopic level.

#### Measurement of *Laminaria* canopy cover

The extent of *Laminaria* cover was expressed as an index of lamina area (total shade area of *Laminaria* laminae/m<sup>2</sup> of bottom). The index was calculated from estimates of the shade area of individual laminae, obtained by converting in situ measurements of blade dimensions to shade area with regression functions calculated from measurements of 184 plants collected from the Paul Pt. site (details in Johnson and Mann 1986b). Note that the estimates were of shade area and not surface area of the laminae; because the margins of *L. longicuris* are convoluted the surface area of one side of a plant is much greater than its shade area. Also, since laminae overlap and do not lie exactly horizontal in the field, the index overestimates the actual shade area cast by the canopy and can exceed the area of the bottom to which the plants are attached. In unmanipulated areas the index was estimated by measuring kelps

		DOMINANT PERENNIAL SEAWEEDS	
		Present	Removed
DOMINANT ANNUAL SEAWEEDS	Present	Treatment A plots 1 & 2	Treatment B plots 3 & 4
	Removed	Treatment C plots 5 & 6	Treatment D plots 7 & 8

FIG. 1. Design of experiment to determine effect of dominant perennial and annual seaweeds on abundances of other algae. Removal of seaweeds was undertaken in both 1982 and 1983 at both sites, and details of these manipulations are presented in Table 1. The four treatments were also maintained clear of chitons, limpets, and sea urchins; thus the only difference between the control plots (treatment A) and the surrounding nonexperimental area was in the manipulation of grazers.

within 10 randomly positioned  $1 \times 2$  m quadrats on each sampling occasion.

#### Partitioning the changes in *Laminaria* canopy cover

The lamina area index was also determined in four experimental plots at Paul Pt. (plots 1, 2, 5, and 6, Fig. 1). Within each plot, *Laminaria* plants of lamina length  $\geq 0.2$  m were tagged and numbered. On each sampling occasion the dimensions of all tagged plants were measured (for calculation of the lamina area index), notes made of plants lost since the previous sampling, and new plants attaining a blade length of 0.2 m were recorded as recruits and tagged and measured. These data enabled partitioning of the change in lamina area index between samplings into components that increase canopy area (net growth of existing plants and recruitment) and those serving to reduce canopy area (net loss of lamina tissue and mortality). Considering the four plots as replicates, each component was expressed as a mean rate of change of the lamina area index per 30-d period.

#### Influence of dominant annual and perennial seaweeds on structure of understory

To test the null hypotheses that the most abundant perennial and annual seaweeds have no influence on the structure of the understory algal assemblage, manipulation experiments were conducted at both sites from May 1982 through October 1983 (design given in Fig. 1). The experiments consisted of eight  $4 \times 4$  m randomly positioned plots (four treatments by two replicates each), but sampling was restricted to a  $2 \times 2$  m area within each plot to avoid edge effects. This design is a compromise between increased probability of Type 2 error (through low replication) and an attempt to minimize edge effects and the problem of misreading small-scale stochastic variation in species abundances by using large manipulation areas. To avoid damaging plants when working in the experimental plots, divers

TABLE 1. Details of manipulations of algae. Note that *Anthithamnion* spp. includes species *Anthithamnionella*, and *Polysiphonia nigrescens* includes both *P. nigrescens* and *P. flexicaulis*; however both *Anthithamnionella* and *P. flexicaulis* were rare components of the community.

Species	Date of removal			
	Paul Pt.		Mill Cove	
	1982	1983	1982	1983
<b>Perennial dominants</b>				
<i>Laminaria longicurvis</i>	1, 5, 12 July	24, 25 May	27 Aug	2 May
<i>Desmarestia aculeata</i>	1, 5, 12 July	...	27 Aug	...
<b>Annual dominants</b>				
<i>Acrothrix novae-angliae</i>	...	...	27 Aug	...
<i>Anthithamnion</i> spp.	5, 6 Aug	1, 4, 6 June	...	2, 5, 6 May
<i>Ceramium rubrum</i>	5, 6 Aug	...	...	2, 5, 6 May
<i>Polysiphonia nigrescens</i>	...	...	28, 29 Aug	...
<i>Polysiphonia urceolata</i>	5, 6 Aug	1, 4, 6 June	28, 29 Aug	2, 5, 6 May

always lay on and worked through a moveable aluminum frame (2.5 × 2.5 m with 0.4-m legs).

Details of all manipulations of algae are given in Table 1. Annual dominants were identified as those species of percentage cover ≥ 15% in the surrounding undisturbed area at the time of manipulation. Because the abundances of annual species varied from year to year, different species were removed in each year of the experiment. Perennial species were removed by tearing the holdfast from the substratum, but annual species were removed with forceps and suction lifts. Initially both *Laminaria longicurvis* and *Desmarestia aculeata* were classed as perennial dominants, but because the cover of *D. aculeata* dropped rapidly soon after the experiment began and remained at low levels for the duration of the experiment, it was not manipulated in the 2nd yr, and responses to removal of "perennial dominants" may be attributed to the influence of the *Laminaria* canopy alone. While *Bonnemaisonia hamifera* may be viewed as a perennial dominant in terms of its percentage cover, no attempt was made to manipulate this species, since it forms a low filamentous turf 2–4 cm high or is epiphytic on other seaweeds and cannot be removed effectively.

The responses of understory algae to the manipulations, and their abundances in the surrounding unmanipulated area, were assessed in terms of percentage cover, which was estimated by dropping thin brass rods through 30 randomly chosen holes of a possible 100 drilled in a thick plexiglass tablet, and recording the species that each rod touched or through whose canopy the rods penetrated. The 100 holes were equidistant within a 0.125 m<sup>2</sup> area, and the plexiglass quadrat was raised off the substratum by three adjustable legs. On each sampling occasion 5 randomly positioned quadrats were assessed in each of the experimental plots, and samples of 10 randomly positioned quadrats were made in the surrounding undisturbed community.

All plots were also maintained clear of chitons (*Tonicella rubra*), limpets (*Notoacmaea testudinalis*), and newly recruited sea urchins (*Strongylocentrotus droe-*

*bachiensis*). Removal of grazers was performed initially in July 1982 at Paul Pt. and in August 1982 at Mill Cove, and since migration into the sites was negligible, it was unnecessary to clear grazers again until March–April 1983 after new recruits appeared. Some animals close to the rock/sediment interface and all those below it could not be removed. It was not possible to maintain the manipulation plots free of the gastropod grazer *Lacuna vineta* (Montagu), which was present in high densities during the winter and spring months, but at 10 m depth grazing by *Lacuna* was restricted largely to *Laminaria* blades (see Johnson and Mann 1986b). Note that the only difference between the experimental plots designated as "controls" and the surrounding undisturbed community (hereafter referred to as the "nonexperimental area") was in the manipulation of grazers. Densities of grazers in the surrounding community were not monitored.

#### Recruitment of *Laminaria*

A census was made of small plants in two size classes (≥ 0.1 m and ≥ 0.2 m lamina length) in May 1983 at both sites, ≈ 3 mo after the winter recruitment and 9–10 mo after the first manipulations. The results were taken as indications of rates of recruitment, although strictly speaking they were influenced both by recruitment and differential survival of recruits. Complete censuses were made within the experimental plots, and in addition recruitment in the nonexperimental area was estimated from 10 random 2-m<sup>2</sup> quadrats. Also in May 1983 at Paul Pt., the size (estimated shade area of laminae) of recruits in plots from which *Laminaria* had been removed was compared with those of a similar age growing beneath the canopy.

Differences in recruitment rates at the two sites were examined by comparing plots from which perennial dominants had been removed (this comparison excluded shading effects that might result from the different canopy densities at the two sites). By comparing the treated plots and the nonexperimental area in various combinations, it was possible to assess the influ-

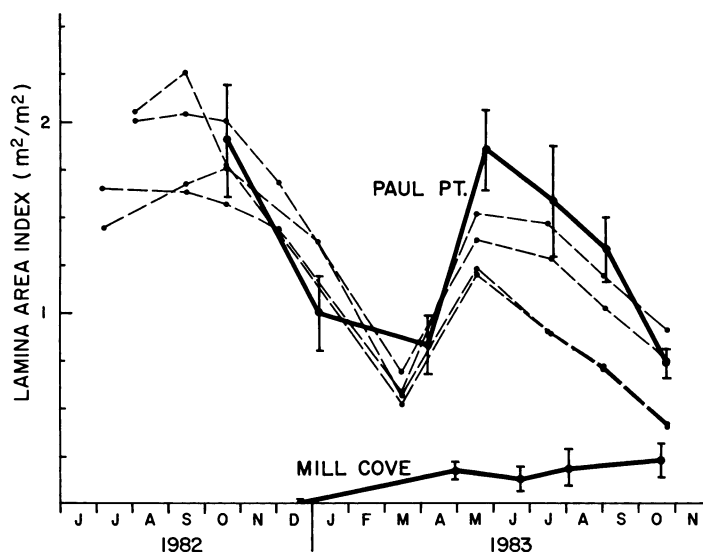


FIG. 2. Cover of *Laminaria longicurvis* canopy relative to substratum area (lamina area index) at Paul Pt. and Mill Cove. Solid heavy lines are untreated areas (data are means  $\pm$  SE), dashed lines give results of censuses of all plants within 4-m<sup>2</sup> experimental plots at Paul Pt. (treatments in which canopy was not manipulated; see Fig. 1). Note that the mass mortality of sea urchins occurred at Paul Pt. in October-November 1980, but at Mill Cove a healthy population of urchins was present until September 1981.

ence of the dominant annuals and perennials on *Laminaria* recruitment within sites. It was valid to compare recruitment in the manipulated sites with the nonexperimental area, since we showed earlier that at Paul Pt. there was no evidence of recruitment of *Laminaria* being influenced by the grazing of limpets, chitons, and juvenile urchins (Johnson and Mann 1986b).

#### Statistics

For most parametric tests, data usually required transformation to achieve homoscedasticity and a normal distribution of error terms. The principal exceptions were the *t* tests, which did not assume equality in variances. In the text, transformations are described in terms of the untransformed variate, *Y*, e.g., *Y* was transformed to  $\ln(Y + 1)$ . For the multivariate analyses of variance (MANOVA), several changes were made to the raw data to minimize heteroscedasticity in dispersion matrices and nonnormality of residuals. First, rare species (peak abundance  $\leq 4.0\%$  cover) were excluded from the analysis. Second, dimensionality was reduced further by conducting a principal components analysis (PCA) on the within-cells correlation matrix. The MANOVA was conducted on the first several transformed principal components that accounted for most of the total variance. It was valid to apply a unique transformation to each principal component, since the principal components were approximately uncorrelated (see Press 1972).

In analyzing the contribution of individual components of increase and decrease in the rate of change in the lamina area index in the experimental plots, a three-way (component  $\times$  date  $\times$  plot) mixed model ANOVA

with repeated measures was used, since the same plants were measured repeatedly through time.

In examining the response of nonmanipulated understory species to removals of perennial and annual seaweeds, the ANOVA and MANOVA models were date effect  $\times$  annual effect  $\times$  perennial effect  $\times$  plot effect (nested within annual  $\times$  perennial), including all interactions, where the effects of date, annual, and perennial treatments were fixed, and the plot effect was random. (Since the area that was sampled within a plot was much smaller than the total area of each plot, it was assumed that dates were independent.) Obviously, understory species that were manipulated could not be included in the complete analysis, but they were tested for response to removal of perennial species. The appropriate ANOVA model in these cases was date effect  $\times$  perennial effect  $\times$  plot effect (nested within perennial effect), including interactions. In all cases when species responses were examined individually, the Bonferroni adjustment was applied to the probability of Type 1 error, otherwise  $\alpha = .05$ .

## RESULTS

### Rate of recovery of *Laminaria* canopy

Comparing the two sites, there was no consistent relationship between the amount of *Laminaria* cover and time since mortality of the sea urchins (Fig. 2). The lamina area index at Paul Pt.  $\approx 18$  mo after urchin mortality was an order of magnitude greater than that at Mill Cove after an equivalent period free of urchin grazing. Similarly, in 1983 *Laminaria* recruitment in the plots at Paul Pt. in which the kelp canopy was

TABLE 2. Recruitment of *Laminaria longicuris* in experimental plots and in the surrounding nonexperimental area at Paul Pt. and Mill Cove, assessed in May 1983 after the 1982–1983 winter recruitment. a = one-tailed, b = two-tailed test. Experimental treatments were removal of dominant annual (Ann) and perennial (Per; mostly *L. longicuris*) seaweeds.\*

Treatment	Treatments separate	Results of <i>t</i> tests	Pooling within "perennial" treatments*	Results of <i>t</i> tests
Number of recruits/m <sup>2</sup> ( $\bar{X} \pm \text{SE}$ )				
<b>A. Paul Pt.</b>				
a. Recruits with lamina length $\geq 0.1$ m				
–Per + Ann	41.50 $\pm$ 12.25	$P = .762^b$	Kelps removed; 45.00 $\pm$ 7.55	$P = .008^a$
–Per – Ann	48.50 $\pm$ 12.99		Nonexp. area; 6.25 $\pm$ 1.60	
Nonexp. area	6.25 $\pm$ 1.60			
b. Recruits with lamina length $\geq 0.2$ m				
–Per + Ann	18.50 $\pm$ 3.01	$P = .556^b$	Kelps removed; 23.38 $\pm$ 5.50	$P = .022^a$
–Per – Ann	28.25 $\pm$ 11.24		Kelps not removed; 2.94 $\pm$ 1.07	
+Per + Ann	3.63 $\pm$ 2.37	$P = .672^b$	Nonexp. area; 4.10 $\pm$ 2.23	
+Per – Ann	2.25 $\pm$ 0.50			
Nonexp. area	4.10 $\pm$ 2.23			
<b>B. Mill Cove</b>				
a. Recruits with lamina length $> 0.1$ m				
–Per + Ann	0.38 $\pm$ 0.13		Kelps removed; 0.19 $\pm$ 0.12	
–Per – Ann	0.00 $\pm$ 0.00		Nonexp. area; 0.25 $\pm$ 0.13	
Nonexp. area	0.25 $\pm$ 0.13			
b. Recruits with lamina length $> 0.2$ m				
–Per + Ann	0.25 $\pm$ 0.25		Kelps removed; 0.13 $\pm$ 0.13	
–Per – Ann	0.00 $\pm$ 0.00		Kelps not removed; 0.00 $\pm$ 0.00	
+Per + Ann	0.00 $\pm$ 0.00		Nonexp. area; 0.25 $\pm$ 0.13	
+Per – Ann	0.00 $\pm$ 0.00			
Nonexp. area	0.25 $\pm$ 0.13			

\* Since recruitment was similar in plots with the same "perennial" treatment (results of *t* tests in table) whether annual species were removed or not, data within "perennial" treatments were pooled as shown. At Paul Pt. recruitment of plants  $\geq 0.1$  m lamina length was significantly greater in the removal plots than in the nonexperimental area, and significantly more plants  $\geq 0.2$  m lamina length recruited in the removal areas than in the nonremoval plots and the surrounding area. The difference in recruitment of plants  $\geq 0.2$  m lamina length in the nonremoval and nonexperimental areas was not significant. Recruitment in plots from which kelps were removed showed that recruitment was significantly greater at Paul Pt. than at Mill Cove (one-tailed *t* tests; for recruits  $\geq 0.2$  m blade length  $P = .012$ , for recruits  $\geq 0.1$  m blade length  $P = .005$ ).

removed was about two orders of magnitude greater than in similar plots at Mill Cove (Table 2). However, during the winter of 1984–1985 there was a large recruitment of kelp at Mill Cove, so that by midsummer 1985 the canopy was closed. In November 1985 the lamina area index at Mill Cove ( $\bar{X} \pm \text{SE}$ ) was estimated at  $1.75 \pm 0.28$  m<sup>2</sup>/m<sup>2</sup> of substratum, which was not significantly different (two-tailed *t* test,  $P = .84$ ) from the estimate of cover at Paul Pt. at this time ( $1.83$  m<sup>2</sup>/m<sup>2</sup> of substratum,  $\text{SE} = 0.64$ ). Clearly, the growth of understory species at Mill Cove for the 3 yr when kelp cover was low was insufficient to prevent the massive recruitment of *Laminaria*.

#### Components of seasonal variation in *Laminaria* cover

The fully developed *Laminaria* cover at Paul Pt. exhibited significant seasonal variation in cover (Fig. 2; one-way (with date) ANOVA, transformation =  $Y^{0.4}$ ,  $F = 5.47$ ,  $\text{df} = 6, 63$ ,  $P \ll .001$ ). The canopy steadily deteriorated from midsummer until early spring, at which time recovery was dramatic over a 6–8 wk period. In the decline phase the lamina area index fell to less than half of its springtime value.

When the changes in canopy cover in the four plots at Paul Pt. in which *Laminaria* was not manipulated were decomposed into components of recruitment, mortality, and net increases and decreases in individual lamina size, it was clear that there were highly significant differences in the contribution of each component to the net change in canopy area, depending on time of year (Fig. 3; three-way [component  $\times$  date  $\times$  plot] mixed model ANOVA with repeated measures showed significant date  $\times$  component interaction,  $F = 5.76$ ,  $\text{df} = 21, 63$ ,  $P \ll .001$ ). For most of the year mortality of larger plants and erosion of laminae exceeded the combined effects of blade growth and recruitment of new individuals to the population, and the *Laminaria* canopy declined. Mortality and loss of lamina tissue was particularly high through the stormy months October–February. Restoration of the canopy during March through mid-May was due largely to increased growth rates of already established plants; growth has been measured in St. Margaret's Bay at this time of year at  $\approx 10$  mm/day (Chapman and Craigie 1977, Gagné et al. 1982). Few plants were lost or exhibited a net decrease in blade size during this period. Recruitment of plants of 0.2 m minimum lamina length

was also greatest during the period mid-March through mid-May, but because of the small size of individuals recruited over any 2–3 mo period, their contribution to increasing the canopy was minimal.

Several observations indicated that the behavior of the kelp canopy within these four plots was representative of *Laminaria* beds in the area. The lamina area index in all plots did not differ significantly from that estimated in the surrounding nonexperimental area (two-tailed *t* tests,  $P \gg .3$  for all plots at all sampling dates; see Fig. 2). Also, the differences in the rates of recruitment of *Laminaria* in these plots (treatments A and C), and in the surrounding area were not significant (one-way [with treatment] ANOVA,  $F = 0.17$ ,  $df = 2, 11$ ,  $P = .85$ , transformation not required; see Table 2).

#### *Influence of dominant annuals and the kelp canopy on Laminaria recruitment*

There was no evidence from the experiments at either site that removal of the dominant annual species had any effect on kelp recruitment (Table 2). In contrast, recruitment of *L. longicruris* beneath a canopy of adult conspecifics was much lower than in plots where the canopy had been removed. These responses were unambiguous and we have no reason to suppose that the inability of the dominant annuals to influence kelp recruitment might stem from low replication in the experimental design. At Paul Pt., the number of *Laminaria* recruits attaining a blade length of  $\geq 0.1$  m was significantly greater in the clearings than in the nonexperimental area (Table 2). Similarly, the number of recruits of minimum lamina length 0.2 m was significantly greater in these plots than in those where dominant perennial species were not removed and in the nonexperimental area (Table 2). Recruitment in the nonremoval (control) experimental plots was not significantly different from that in the nonexperimental area. We interpret these responses to removal of "perennial dominants" at Paul Pt. as attributable primarily to removal of the *Laminaria* canopy, since the cover of *D. aculeata* declined rapidly soon after the start of the experiment and remained at low levels (Fig. 4). The recruitment response of *Laminaria* following removal of the canopy was probably due to increased light levels, since substratum space at Paul Pt. was not limiting (Fig. 5). Several studies have shown that irradiance levels beneath canopies of *Laminaria* (Kain 1979 and references) and other kelps (Anderson and North 1969, Pearse and Hines 1979, Dean and Jacobsen 1984, Gerard 1984b, Reed and Foster 1984) are much lower than surface values and are frequently limiting for plant recruitment and growth. We saw no evidence of *L. longicruris* limiting locally the recruitment of conspecifics (or any other species) by physical abrasion of kelp fronds sweeping the substratum, such as has been observed in other kelps (Black 1974, Dayton 1975a, Velimirov and Griffiths 1979, Duggins 1980, Kirkman

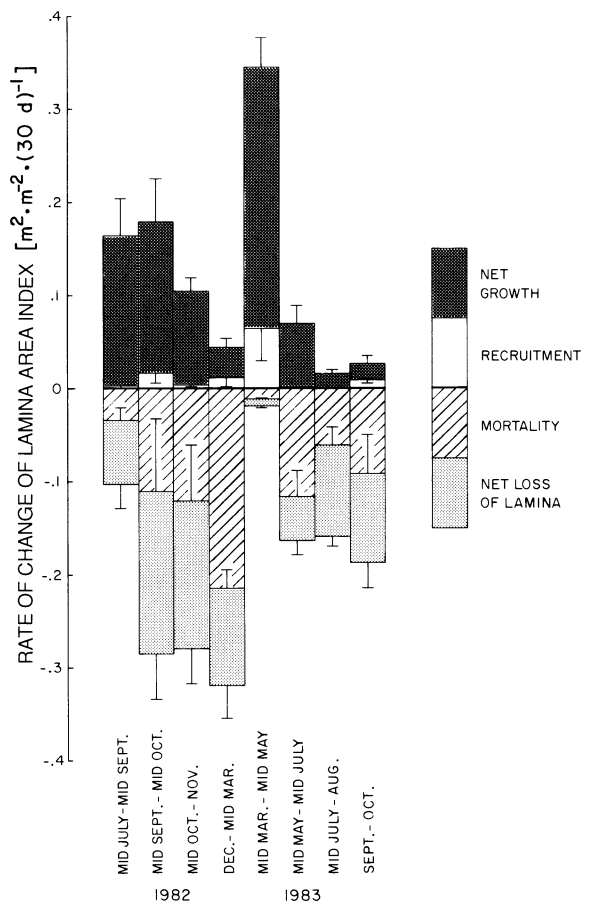


FIG. 3. Partitioning of rate of change in cover of *Laminaria longicruris* canopy relative to substratum area (lamina area index) in four experimental plots at Paul Pt. into components of recruitment, mortality, and net growth and net loss of laminae. Data are means  $\pm$  SE.

1981). The distal one-third of the lamina of *L. longicruris* may rest on the substratum, but only in calm conditions.

Although a greater number of *Laminaria* recruits grew in the kelp removal plots at Paul Pt., these plants grew in dense patches and were significantly smaller than recruits of a similar age in the nonexperimental area and in experimental plots in which the kelp canopy was left intact (Table 3), suggesting that growth has a density-dependent component. The difference in the size of the *Laminaria* recruits in the nonremoval plots and the surrounding area was not significant.

#### *Relative influence of Laminaria canopy and dominant annual seaweeds on understory*

Of the 23 unmanipulated understory species encountered at Paul Pt., only 7 attained a peak cover of  $\geq 4\%$ ; these 7 were included in the analysis to test for response to removal of dominant annual and perennial seaweeds (see Appendix). Among these 7, in cases



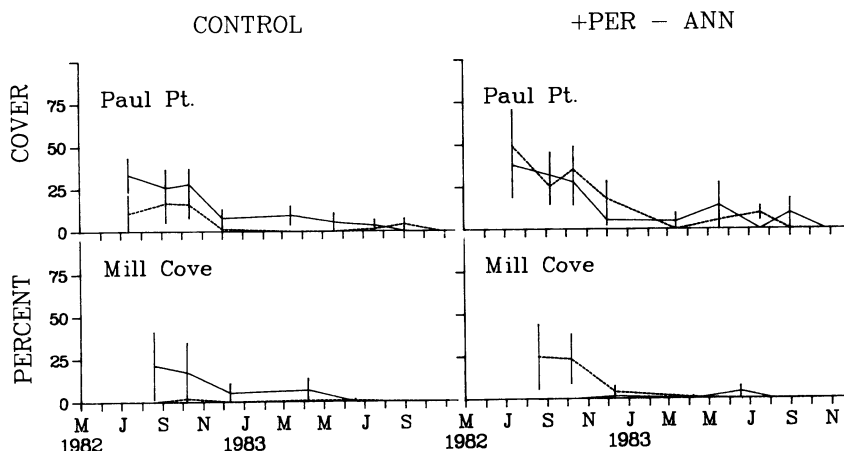


FIG. 4. Percentage cover of *Desmarestia aculeata* in experimental plots at Paul Pt. and Mill Cove showing the decline of this species during the experiment (two replicate plots per treatment at each site). Data are means  $\pm$  SE.

in which the response to the treatments was consistent, most exhibited increased abundances when the *Laminaria* canopy was removed. Only the ectocarpoids showed a significant response to manipulation of annual understory species.

A MANOVA of the first four principal components generated from a PCA of the within-cells correlation matrix of these seven species showed significant interactions between (1) perennial and annual removal treatments, indicating that effects of the kelp canopy were modified by the abundance of dominant annual species, and (2) between season (date), and removal of perennials, showing that removal of kelp affected the composition of the understory mostly during spring and summer, but not at other times of the year when understory cover was uniformly low. It also showed that seasonal variation (date) in seaweed cover and spatial variation among replicate plots is highly significant (Table 4). However, not all species followed this overall pattern. When analyzed individually, it was revealed that all species experienced significant seasonal changes in cover (cover being lowest during winter and early spring), and that variability in cover among replicate plots was high at least for part of the year in four of the seven species, but the responses to the re-

moval treatments were dissimilar (Table 5 and Fig. 6). During the months when they were most abundant, the cover of *Callithamnion* spp., *Desmarestia viridis*, and *Saccorhiza dermatodea* increased significantly relative to controls in plots in which the kelp canopy was removed, but showed no significant response to removal of annuals. Although ectocarpoids were never abundant, their cover increased significantly during the summer months in response to the removal of both annual and perennial species. In contrast, *Bonnemaisonia hamifera* showed no significant response to either removal treatment. Since substratum space was not limiting (Fig. 5), it seems likely that all of the significant changes in seaweed cover that were attributed to manipulations were responses to changes in light levels. Because changes in cover of the understory as a consequence of canopy removal occurred only in late spring and summer, it was not surprising that in winter the meager and slow-growing understory in the nonexperimental area did not respond to the reduced kelp canopy at this time.

The behavior of the perennials *Polysiphonia nigrescens* and *Rhodomela confervoides* was more complex, and they demonstrated a significant interaction of the annual and perennial removal treatments. Overall,

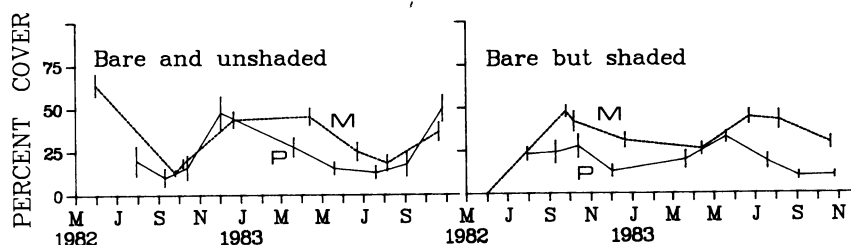


FIG. 5. Percentage of rock substratum that was bare and unshaded, and bare but shaded by fleshy understory algae, in the nonexperimental area at Paul Pt. (P) and Mill Cove (M). Note that "bare" refers only to bare of fleshy algae, and should not be taken to mean absence of encrusting corallines, which covered most of the rock substratum. Data are means  $\pm$  SE.

TABLE 3. Size (estimated shade area of lamina,  $\bar{X} \pm \text{SE}$ ) of *Laminaria longicuris* recruits in kelp removal plots, in nonremoval plots, and in the nonexperimental area at Paul Pt., assessed in May 1983 after the 1982–1983 winter recruitment.\*

Treatment	Shade area (cm <sup>2</sup> )	N
(A) Recruits with $\geq 0.1$ m lamina length		
Removal plots	122.9 ( $\pm 5.9$ )	766
Nonexperimental area	260.4 ( $\pm 30.5$ )	125
(B) Recruits with $\geq 0.2$ m lamina length		
Removal plots	218.3 ( $\pm 9.8$ )	374
Nonremoval plots	503.5 ( $\pm 48.0$ )	47
Nonexperimental area	375.7 ( $\pm 41.1$ )	82

\* Results of one (\*) and two-tailed (°) *t* tests comparing mean plant sizes showed that for (A) recruits with  $\geq 0.1$  m lamina length, plants in the removal plots were significantly smaller than those in the nonexperimental area ( $P < .001^*$ ), and (B) recruits with  $\geq 0.2$  m blade length, the difference in size of plants in the nonremoval plots and in the nonexperimental area was not significant ( $P > .05^b$ ), but plants in the removal plots were significantly smaller than those in either the nonremoval plots or the surrounding nonexperimental area (for both,  $P < .001^*$ ).

cover of *P. nigrescens* was significantly lower in plots from which annual species only were removed, but no other treatment differed from the control. For *R. confervoides*, cover was significantly lower in plots from which either annuals or *Laminaria* had been removed, but its cover in plots where both annuals and kelp were removed was not significantly different from the control plots. Since these two species are perennial, these enigmatic results may not be real responses to the treatments, but probably arise from differences in cover among treatments at the beginning of the experiment. Their “responses” correlate with their initial cover in

TABLE 4. Effect of removal of dominant perennial and annual seaweeds on understory assemblage at Paul Pt. (assessed from July 1982–Oct 1983 in terms of percentage cover; removals began in July 1982).

Source	Denominator Mean square for <i>F</i>	<i>P</i> *
<i>P</i> (removal of perennials)	Error 1	.433
<i>A</i> (removal of annuals)	Error 1	.151
<i>D</i> (date)	Error 2	$< .001$
<i>D</i> $\times$ <i>P</i>	Error 2	$< .001$
<i>D</i> $\times$ <i>A</i>	Error 2	.924
<i>P</i> $\times$ <i>A</i>	Within cells	$< .001$
<i>D</i> $\times$ <i>P</i> $\times$ <i>A</i>	Within cells	.215
Plot nested within ( <i>P</i> $\times$ <i>A</i> ) = error 1	Within cells	$< .001$
<i>D</i> $\times$ plot nested within ( <i>P</i> $\times$ <i>A</i> ) = error 2	Within cells	.052

\* Results of MANOVA (Pillai's statistic) of first four principal components (PC's) obtained from PCA of within-cells correlation matrix of seven most abundant unmanipulated species (PC's 1–4 absorbed 74.0% of total dispersion). Transformations: PC1 and PC3 not transformed;  $\ln(Y + 50)$  for PC2;  $\ln|Y - 45|$  for PC4.

that the average initial cover of *P. nigrescens* and of *R. confervoides* in both the “– annuals” and “– perennials” treatments was only  $\approx 20$  and 39%, respectively, of that in the control plots (Fig. 6). These large differences in initial cover are not significant (two-way nested ANOVA (treatment  $\times$  plot, plot within treatment), transformation =  $\ln(Y + 1)$ ; *P. nigrescens*,  $F = 1.11$ ,  $df = 3, 4$ ,  $P = .44$ ; *R. confervoides*,  $F = 0.44$ ,  $df = 3, 4$ ,  $P = .74$ ), but statistical power in these tests was low (high variances and low replication).

When the percentage cover of the manipulated annual species in the control plots at Paul Pt. was com-

TABLE 5. Effect of removal of dominant perennial (mostly *Laminaria*) and annual seaweeds on understory assemblage at Paul Pt. (assessed from July 1982–October 1983 in terms of percentage cover; removals began in July 1982).\*

Source	Understory species						
	<i>Bon-nemai-sonia hamifera</i>	<i>Polysiphonia nigrescens</i>	<i>Rhodomela confervoides</i>	<i>Callithamnion</i> spp.	<i>Desmarestia viridis</i>	<i>Saccorhiza dermatodea</i>	Ectocarpoids
<i>P</i> (removal of perennials)	NS	NS	NS	NS	NS	NS	†
<i>A</i> (removal of annuals)	NS	NS	NS	NS	NS	NS	†
<i>D</i> (date)	§	§	‡	§	§	§	§
<i>D</i> $\times$ <i>P</i>	NS	NS	NS	§	†	§	§
<i>D</i> $\times$ <i>A</i>	NS	NS	NS	NS	NS	NS	§
<i>P</i> $\times$ <i>A</i>	NS	‡	§	NS	NS	NS	NS
<i>D</i> $\times$ <i>P</i> $\times$ <i>A</i>	NS	NS	NS	NS	NS	NS	NS
Plot nested within ( <i>P</i> $\times$ <i>A</i> ) = error 1	NS	§	§	†	§	NS	NS
<i>D</i> $\times$ plot nested within ( <i>P</i> $\times$ <i>A</i> ) = error 2	NS	NS	NS	NS	‡	NS	NS
Transformations	not required	arcsin <i>Y</i>	$\ln(Y + 1)$	$\ln(Y + 1)$	$(Y + 2)^{0.019}$	$\ln(Y + 1)$	$(Y + 2)^{-0.060}$

\* Data give results of ANOVAs of abundances of common unmanipulated understory species. Denominator mean squares for *F* tests are as given in Table 4. Levels of significance (after Bonferroni adjustments) are: NS =  $P \geq .0071$ ; † .0014  $< P < .0071$ ; § .00014  $< P \leq .0014$ ; ‡  $P < .00014$ .

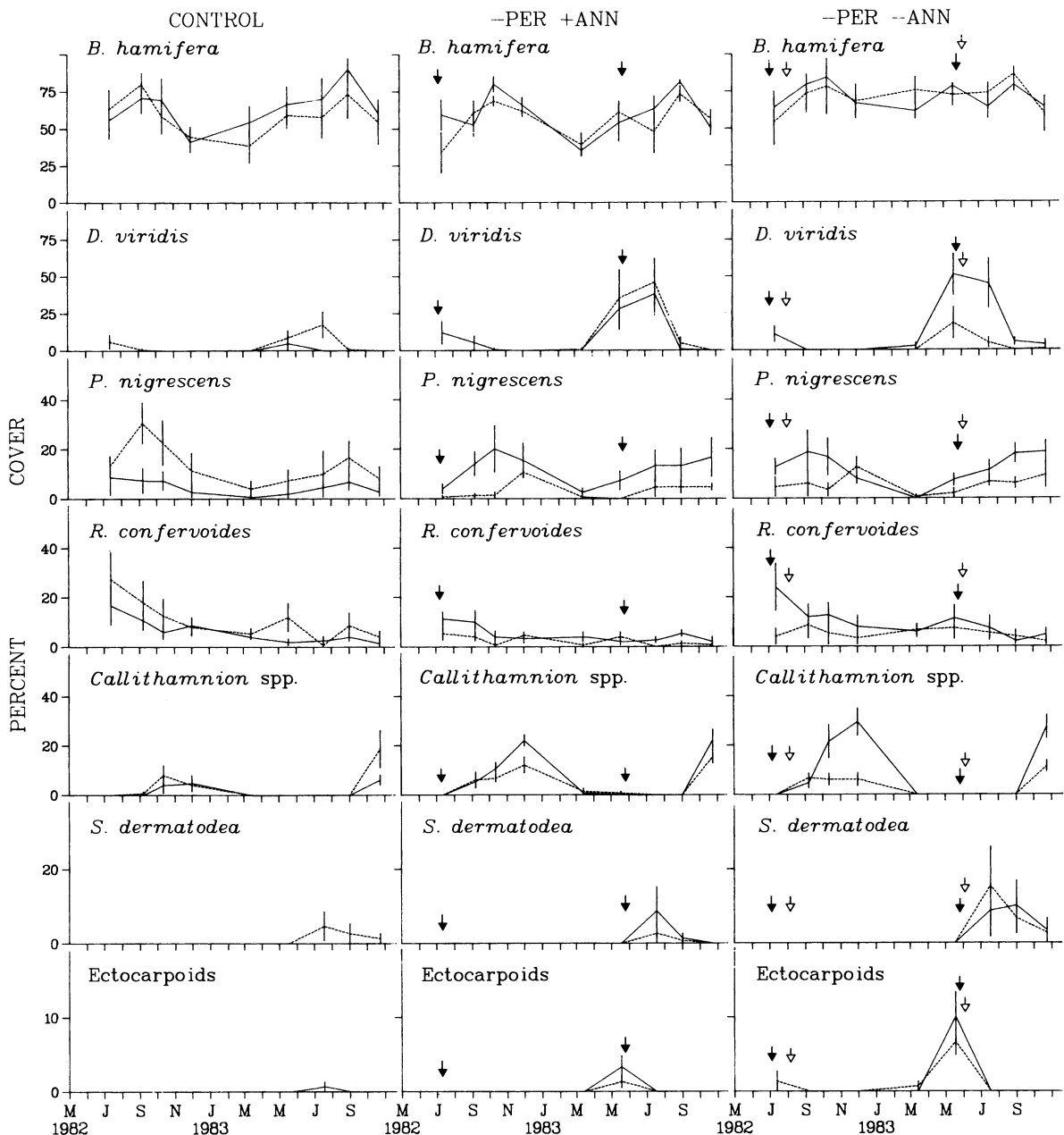


FIG. 6. Effect of removal of dominant perennial (PER, mostly *Laminaria*) and annual (ANN) seaweeds on understory algae at Paul Pt.; data show percentage cover of common unmanipulated species in the four treatments (two 16-m<sup>2</sup> plots per treatment). Solid arrows indicate date of removal of perennial dominants and subsequent removal of recruits, open arrows show dates of removal of dominant annual seaweeds. Generic names are given in the Appendix. Data are means  $\pm$  SE.

pared with plots from which *Laminaria* had been removed, only *Ceramium rubrum* showed a significant increase in cover in response to absence of the canopy (Table 6 and Fig. 7). The increased cover of *Polysiphonia urceolata* and reduced cover of *Antithamnion* spp. in 1983 in the canopy removal plots relative to the control areas was not significant.

It is noteworthy that at Mill Cove where *L. longi-*

*cruris* was rare, the cover of understory species was greater than at Paul Pt.; however, it is possible that differences in the two sites other than the extent of kelp cover could influence the extent of the understory. Over the period 30 July 1982–20 October 1983, the total cover of all understory species was on average 17.1% higher in the nonexperimental area at Mill Cove than at Paul Pt. When only the larger species were consid-

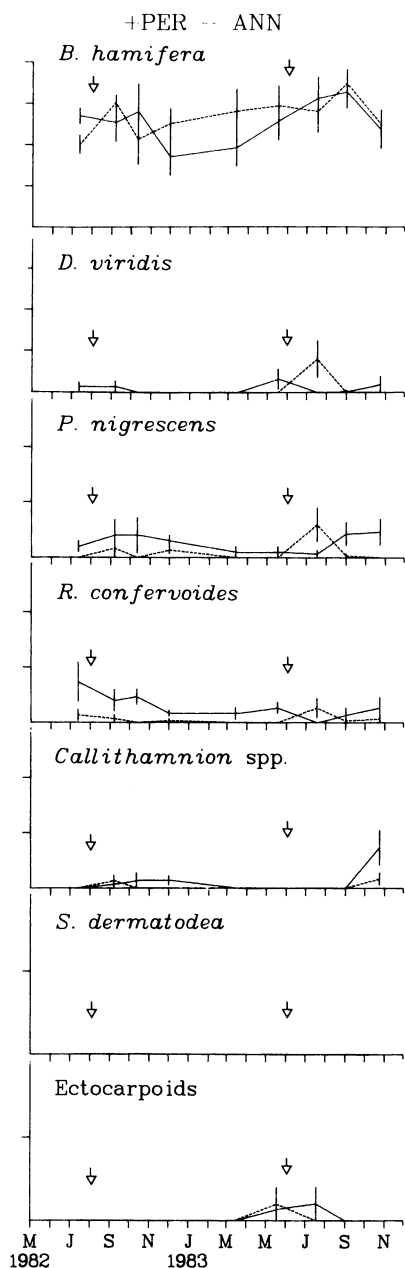


FIG. 6. Continued.

ered (i.e., ignoring the short filamentous turf of *Bonnemaisonia hamifera*), this difference was increased to 55.1%.

*Effect of abundant annual seaweeds on understory when kelp cover is low*

At Mill Cove most of the seaweeds were small and cover of both *Laminaria longicruris* and *Desmarestia*

*aculeata* was low. Among those species whose behavior was palpable, none responded significantly to removal of either the annual dominants or the few large perennial plants, and only *Callithamnion* spp. demonstrated a significant response to the combined removal of both guilds of dominants. Thirty species were recorded at Mill Cove, but only five of the unmanipulated understory algae attained a peak percentage cover  $\geq 4\%$  and were included in tests for response to manipulations (Appendix). The combined response of these five species showed significant variation in cover among seasons (dates) and among replicate plots, and identified significant perennial  $\times$  annual, and date  $\times$  annual, interactions (Table 7).

Examining species individually (Table 8 and Fig. 8) indicated that all five exhibited significant seasonal changes in cover, with cover declining during late autumn or winter, and most showed significant variance in cover between replicate plots within treatments. Neither *Desmarestia viridis* or *Sphacelaria plumosa* showed a significant response to any of the treatments, but in early winter 1983 cover of *Callithamnion* spp. was significantly greater in plots from which both annual and perennial dominants were removed than in the control plots. Changes in cover of the perennial species were not so readily interpreted, and like the observations at Paul Pt., differences in cover of *Rhodomela* among treatments probably stems from dissimilar initial abundances among treatments rather than being real responses to removals. Cover of this species was significantly greater in all treatments in which annuals were removed, but only in 1982. At the beginning of the experiment, mean cover of *Rhodomela* in the “- annual, - perennial” and in the “- annual, + perennial” treatment plots was 138 and 314% greater, respectively, than cover of this plant in the control areas, although these differences were not significant (two-way nested ANOVA (treatment  $\times$  plot, plot within treatment), transformation =  $Y^{0.316}$ ,  $F = 3.77$ ,  $df = 3, 4$ ,  $P = .12$ ). However, the significance of the perennial  $\times$  date interaction for *Bonnemaisonia hamifera* cannot be attributable to differences in abundance at the beginning of the experiment. The decline in cover of this species over the 1982–1983 winter was less in plots from which the few large perennials were removed, but the reason for this is unclear.

None of the annual species that were manipulated at Mill Cove showed a significant response to removal of perennials relative to the control plots (Table 9, Fig. 9).

## DISCUSSION

### *Stability of Laminaria beds*

It is important to consider appropriate scales in time and space when referring to community stability (Sutherland 1981, Connell and Sousa 1983, Dayton et al. 1984). Here we discuss detailed observations made at

TABLE 6. Effect of removal of dominant perennial seaweeds (mostly *Laminaria*) on understory species at Paul Pt. (assessed from July 1982–Oct 1983 in terms of percentage cover; removals began July 1982).\*

Source	Denominator mean square	Understory species		
		<i>Polysiphonia urceolata</i>	<i>Ceramium rubrum</i>	<i>Antithamnion</i> spp.
D (date)	Error 2	§	§	§
P (removal of perennials)	Error 1	NS	NS	NS
$D \times P$	Error 2	NS	†	NS
Plot nested within $P = \text{error 1}$	Within cells	NS	NS	NS
$D \times \text{plot nested within } P = \text{error 2}$	Within cells	NS	NS	†
Transformations		$(Y)^{0.242}$	$(Y + 2)^{0.058}$	$\ln(Y + 1)$

\* Data give results of nested ANOVAs of abundance of manipulated understory species. Denominator mean square for  $F$  tests are indicated. Levels of significance (after Bonferroni adjustments) are : NS =  $P \geq .0167$ , †  $.0033 < P < .0167$ , §  $P \leq .00033$ .

specific sites on a meso scale (from 10 to  $10^4$  m<sup>2</sup>), and consider these with the results of larger scale but more general surveys to comment on the stability properties of *Laminaria* beds on the Atlantic coast of Nova Scotia in general. We refer to disturbance as loss of plant biomass whether biologically or physically induced, and stress as physiological constraints on production imposed by resource limitation.

**Persistence.**—There is ample qualitative evidence of persistence stability of *Laminaria* beds in Nova Scotia. Although *L. longicuris* usually lives for  $\approx 2$  yr (Chapman 1984, Smith 1985; C. R. Johnson, *personal observation*) and may occasionally survive for 4 yr (Chapman 1986), stands of this kelp are known to have persisted for 3–18 yr in several locations in Nova Scotia. We observed little change in the cover of *Laminaria* at Paul Pt. from 1981–1986, a constant canopy of *L. longicuris* at nearby Boutilier's Pt. has been noted since 1968 (see Mann 1972a, Bernstein et al. 1981, C. R. Johnson, *personal observation*), and open stands of species of *Laminaria* have been persistent for at least 8 yr at Pubnico in the south and at Sandy Cove in the

Bay of Fundy (A. R. O. Chapman, *personal observation*).

Detailed data on the composition of the understory assemblage in other Nova Scotia kelp beds are few, but our measurements at Paul Pt. and Mill Cove suggest that with the possible exception of *Desmarestia aculeata*, the cover of understory perennials does not fluctuate greatly from year to year. In contrast, although the same species of annual plants grew in the understory each year, their abundances were not consistent among years and are probably influenced greatly by stochastic events that affect their recruitment. High yearly variability underscores patterns of abundance in many ephemeral plants (Jernakoff 1985, see also Hoffmann and Ugarte 1985), but this does not imply poor persistence of the community as a whole.

The coralline algae that form the basal layer of the seaweed community are ostensibly the most persistent of all the algal guilds. They cover nearly all of the primary hard substratum in both the sea urchin- and *Laminaria*-dominated communities (Johnson and Mann 1986a). Encrusting coralline algae are well adapted to intense grazing (e.g., Steneck 1983, 1986, Padilla 1984), and in Nova Scotia they are the only macrophytes that survive intense grazing by the urchins, but they also survive being overgrown by other algae even when all grazers are absent, partly due to their innate antifouling ability (Johnson and Mann 1986a). We add the caveat that it may be inappropriate to assess the persistence of the coralline guild in terms of turnover. Because their longevity is potentially unlimited, it is impractical if not irrelevant to consider turnover, although their generation time may be as little as 2–3 yr. Paine et al. (1985) have also emphasized the problems of assessing the stability of clonal and other very long-lived organisms.

**Resistance.**—The greatest threat to the persistence of the *Laminaria* beds is grazing by sea urchins. When they occur in high densities the urchins decimate the kelps and fleshy understory species, and excepting shallow areas where wave action prevents their feeding, their devastation may extend over hundreds of square

TABLE 7. Effect of removal of dominant perennial (mostly *Laminaria*) and annual seaweeds on understory assemblage at Mill Cove (assessed from August 1982–Oct 1983 in terms of percentage cover; removals began August 1982).

Source	$P^*$
P (removal of perennials)	.316
A (removal of annuals)	.469
D (date)	$\leq .001$
$D \times P$	.081
$D \times A$	.002
$P \times A$	$< .001$
$D \times P \times A$	.098
Plot nested within $(P \times A) = \text{error 1}$	$\leq .001$
$D \times \text{plot nested within } (P \times A) = \text{error 2}$	.619

\* Results of MANOVA (Pillai's statistic) of first four principal components (PC's) obtained from PCA of within-cells correlation matrix of five most abundant unmanipulated species (PC's 1–4 absorbed 89.7% of total dispersion). Transformations: PC1 and PC4 not transformed;  $\ln|Y - 15|$  for PC2;  $\ln(Y + 10)$  for PC3. Denominator mean squares for  $F$  test are as given in Table 4.

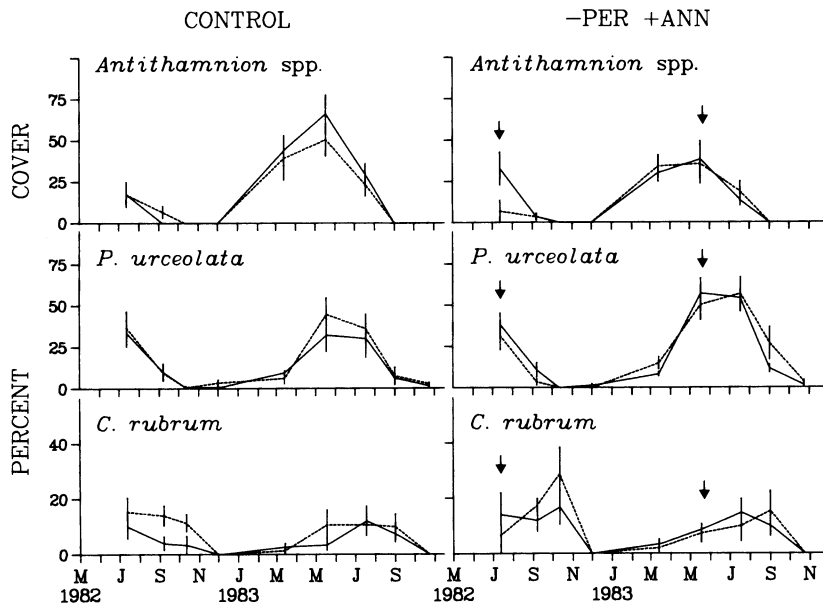


FIG. 7. Effect of removal of dominant perennial (mostly *Laminaria*) seaweeds on understory algae at Paul Pt.; data show percentage cover of dominant annual species in the two treatments in which dominant annuals were not manipulated (two 16-m<sup>2</sup> plots per treatment). Symbols and notes as in Fig. 6.

kilometres (Wharton and Mann 1981). However, when sea urchin numbers are low, *Laminaria* shows considerable resistance to deterioration from winter storms, high densities of nonechinoid grazers, and severe nutrient stress. The kelp is phenotypically plastic in its response to water movement, and develops more strengthening tissue but grows more slowly as exposure increases, so that plants at exposed sites have short stipes, thick strap-like blades, and minimal development of the lateral frill (Gerard and Mann 1979). The large plants with long stipes, wide lateral frills, and high growth rates that are found in sheltered areas are easily destroyed by wave action (see also Chapman 1974).

*Laminaria* is also resistant to grazing by the gastropod *Lacuna vineta*, which replaces sea urchins as the principal grazer of the macroscopic sporophyte when urchin numbers are low. Although *Lacuna* shows preference for *Laminaria* and its densities can exceed 4000 individuals/m<sup>2</sup>, the kelp is well defended against their grazing, ostensibly by its toughness and high concentrations of polyphenols in the meristematic region, so that although the snails promote erosion of the lateral portions of laminae they do not contribute to kelp mortality (Johnson and Mann 1986b).

*L. longicruris* is also tolerant of nutrient stress. For 8 mo of the year, excepting December–March, nitrogen

TABLE 8. Effect of removal of dominant perennial (mostly *Laminaria*) and annual seaweeds on understory assemblage at Mill Cove (assessed from August 1982–October 1983 in terms of percentage cover; removals began August 1982).\*

Source	Understory species				
	<i>Bonnemai- sonia hamifera</i>	<i>Rhodomela confervoides</i>	<i>Callitham- nion spp.</i>	<i>Desmarestia viridis</i>	<i>Sphacelaria plumosa</i>
P (removal of perennials)	NS	NS	NS	NS	NS
A (removal of annuals)	NS	NS	NS	NS	NS
D (date)	§	‡	§	§	‡
$D \times P$	†	NS	NS	NS	NS
$D \times A$	NS	§	NS	NS	NS
$P \times A$	NS	NS	‡	NS	NS
$D \times P \times A$	NS	NS	NS	NS	NS
Plot nested within ( $P \times A$ ) = error 1	‡	NS	§	NS	§
$D \times$ plot nested within ( $P \times A$ ) = error 2	NS	NS	§	NS	NS
Transformations	not required	(Y) <sup>0.402</sup>	(Y) <sup>0.287</sup>	ln(Y + 1)	(Y) <sup>0.006</sup>

\* Data give results of nested ANOVAs of common unmanipulated understory species. Denominator mean squares for *F* tests are as given in Table 4. Levels of significance (after Bonferroni adjustments) are NS =  $P \geq .01$ , † .002 <  $P$  < .01, ‡ .0002 <  $P$  ≤ .002, §  $P$  ≤ .0002.

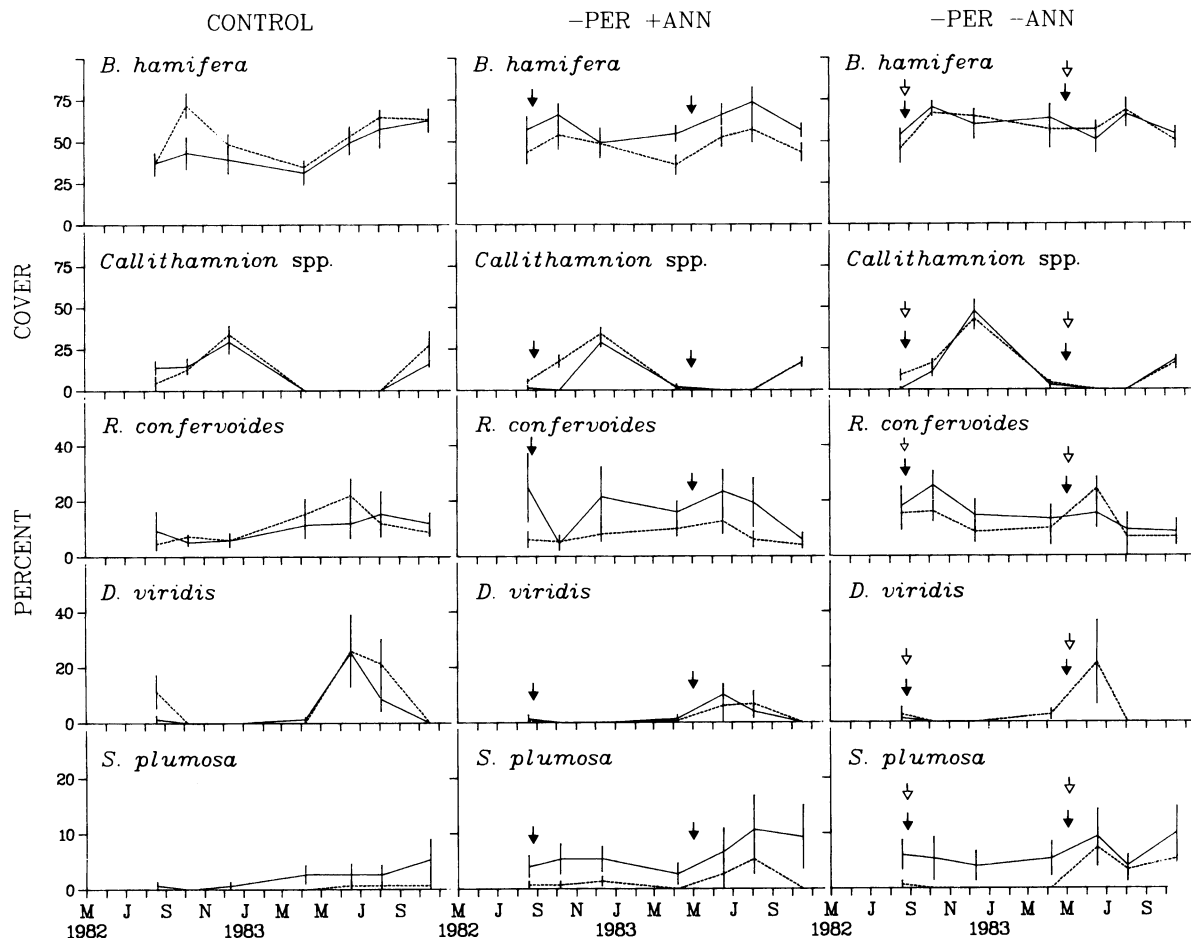


FIG. 8. Effect of removal of dominant perennial (mostly *Laminaria*) and annual seaweeds on understory algae at Mill Cove; data show percentage cover of common unmanipulated species in the four treatments (two 16-m<sup>2</sup> plots per treatment). Symbols and notes as in Fig. 6.

levels in St. Margaret's Bay are extremely low (Chapman and Craigie 1977, Gagné et al. 1982). The kelp accumulates nitrogen from the water when levels are high during winter, and uses this internal reserve to achieve high growth rates in the spring when light conditions are favorable but available nitrogen virtually absent in the water (Chapman and Craigie 1977, Gagné et al. 1982, Espinoza and Chapman 1983). It is noteworthy that *L. longicruris* also forms an extensive and closed canopy and is clearly the dominant seaweed on the west coast of Nova Scotia in the Bay of Fundy (J. Gagné, *personal communication*) where upwelling provides an abundance of nitrogen year round (Gagné et al. 1982).

Another requirement for resistance stability is the persistence of a community despite challenges from species that can potentially displace residents. At Paul Pt. there was no suggestion that the dominant ephemeral plants, which comprise a large portion of the understory subcanopy in summer, inhibited *Laminaria* recruitment or could displace the kelps. Instead, like

many other canopy-forming kelps (e.g., Dayton 1975a, b, Foster 1975b, Pearse and Hines 1979, Moreno and Sutherland 1982, Dayton et al. 1984, Reed and Foster 1984), *L. longicruris* overgrew and limited the abundance of several of the dominant ephemeral plants. The principal factor limiting recruitment and the growth rates of new recruits of *Laminaria* was competition for light with conspecifics. Reduction of recruitment by a canopy of adult conspecifics has been reported in many other kelps (Anderson and North 1969, Pearse and Hines 1979, Santelices et al. 1980, Kimura and Foster 1984, Reed and Foster 1984, Santelices and Ojeda 1984a, b), including *Laminaria groenlandica* (Duggins 1980). In contrast, the negative effect of density on growth rates that we observed is less often recorded in natural populations of seaweeds (but see Black 1974, Cousens and Hutchings 1983, Santelices and Ojeda 1984b), and is the reverse of what is found in some species (Schiel 1985).

Our observations differ from Chapman's (1984), who found that recruitment of visible plants of *Laminaria*

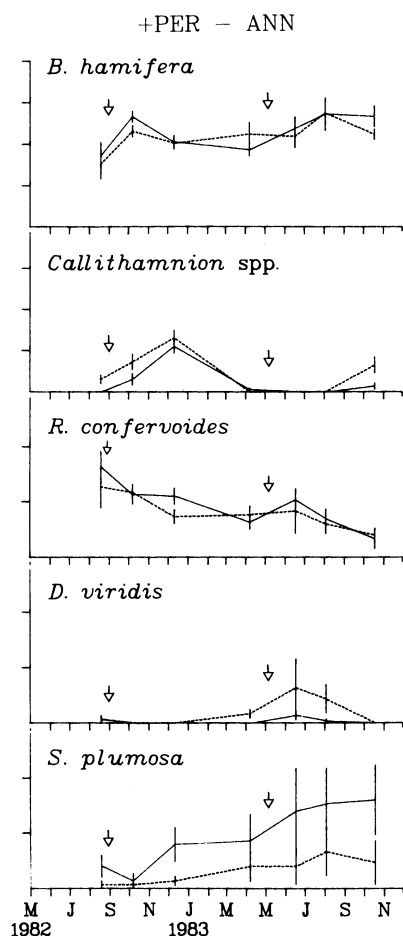


FIG. 8. Continued.

spp. was not affected by removal of kelps in a mixed stand of *L. longicuris* and *L. digitata* at Pubnico on the south shore of Nova Scotia, but that removal of a red algal turf led to a 10-fold increase in *Laminaria* recruitment. This contradiction is explained in part by the kelp cover at Pubnico being much less than at Paul

Pt., but it also raises an important query concerning differences between the understory guilds on the east coast (facing the open Atlantic) and south coasts of Nova Scotia. Why don't extensive and dense turfs of perennial red algae (mainly *Chondrus crispus* and *Phyllophora truncata*) that limit kelp recruitment in the southwest (Chapman 1984, Smith 1985) grow on the east coast, where, instead, a large portion of the understory are ephemeral plants that have no detectable effect on kelp recruitment? Even when understory species at Mill Cove grew unchecked by a kelp canopy for 3 yr, their cover was unable to prevent strong recruitment of *L. longicuris*. A starting hypothesis is that disturbance from grazing by sea urchins (which are always rare in the south) is sufficiently frequent on the east coast to prevent these slow-growing plants (Mathieson and Prince 1973 and references) from forming turfs, i.e., that grazing breaks inhibition (sensu Connell and Slayter 1977) by the turfs. Mann's (1972a) observation that *Chondrus* sometimes dominates in shallow water ( $\approx 2$  m depth) at exposed sites on the Atlantic coast where wave action prevents sea urchins feeding is consistent with this idea, and Lubchenco and Menge (1978) showed experimentally that grazing by urchins prevented the competitively superior (Lubchenco 1980) *Chondrus* from extending into the shallow subtidal. If dense and long-lived perennial turfs could establish widely in the understory on the east coast of Nova Scotia, this would likely have far-reaching effects on the resistance stability of the *Laminaria* beds by displacing them as they do on the south coast.

On the east coast the only two kelps that potentially compete with *L. longicuris* are *Laminaria digitata* and *Agarum cribrosum*, which are also perennial laminarians. With increasing exposure to wave action from moderate levels upward, *L. longicuris* often coexists with *L. digitata*, but only in shallow water ( $< 5$  m) at sites of extreme exposure is the latter found in monospecific stands (MacFarlane 1952, Edelstein et al. 1969, Mann 1972a, Scheibling 1986; C. R. Johnson, *personal observation*). *L. longicuris* dominates over the range from low to high exposure to wave action. A partial explanation for these observations is that digitate kelps

TABLE 9. Effect of removal of dominant perennial seaweeds (mostly *Laminaria*) on understory assemblage at Mill Cove (assessed from August 1982–October 1983 in terms of percentage cover; removals began August 1982).\*

Source	Understory species				
	<i>Polysiphonia uaeolata</i>	<i>Polysiphonia nigrescens</i>	<i>Ceramium rubrum</i>	<i>Antithamnion</i> spp.	<i>Acrothrix novae-angliae</i>
D (date)	\$	\$	\$	\$	\$
P (removal of perennials)	NS	NS	NS	NS	NS
$D \times P$	NS	NS	NS	NS	NS
Plot nested within P = error 1	NS	\$	NS	‡	NS
$D \times$ plot nested within P = error 2	NS	NS	NS	NS	NS
Transformations	(Y) <sup>0.188</sup>	$\ln(Y + 1)$	$\ln(Y + 1)$	$\ln(Y + 1)$	$\ln(Y + 1)$

\* Data give results of nested ANOVAs of manipulated understory species. Denominator mean squares for F tests are as given in Table 6. Levels of significance (after Bonferroni adjustments) are NS:  $= P \geq .01$ , ‡:  $.0002 < P \leq .002$ , \$:  $P \leq .0002$ .



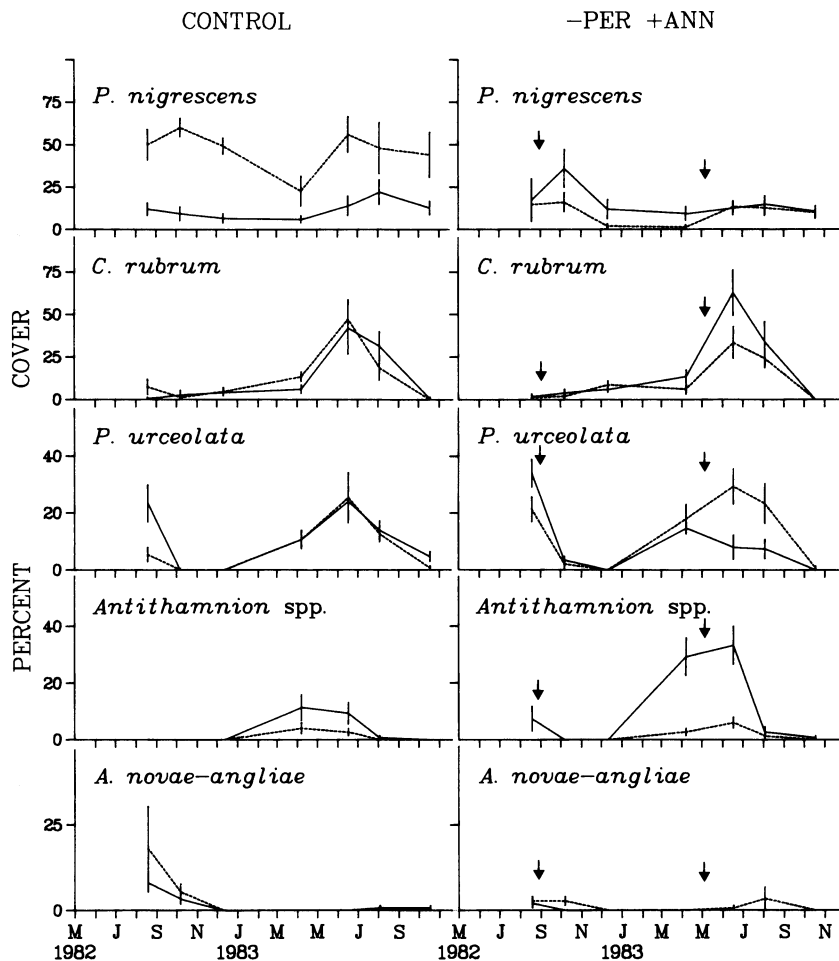


FIG. 9. Effect of removal of dominant perennial (mostly *Laminaria*) seaweeds on understory algae at Mill Cove; data show percentage cover of dominant annual species in the two treatments in which dominant annuals were not manipulated (two 16-m<sup>2</sup> plots per treatment). Symbols and notes as in Fig. 6.

are more tolerant of wave stress than are wide single-blade morphologies (Dring 1982, Lobban et al. 1985); however, the exact nature of the competitive interaction between these congeners, and whether this interaction is modified by wave action, is unclear. At our St. Margaret's Bay sites, only one specimen of *L. digitata* was found at Paul Pt.

More is known of the interaction of *Agarum* with *Laminaria* species. When sea urchins are rare, *Agarum* normally replaces *Laminaria* spp. with increasing depth on hard substratum (Edelstein et al. 1969, Mann 1972a, Tremblay and Chapman 1980, Novaczek and McLachlan 1986), but the depth of the changeover zone can vary from  $\approx 10$ –20 m (C. R. Johnson, *personal observation*). Keats et al. (1982) reported that similar numbers of *Laminaria* and *Agarum* grew at 20 m depth at an urchin-free site in Newfoundland, but they gave no indication of the relative sizes of the plants. In Nova Scotia *L. longicruris* grows much larger than *Agarum*.

*Agarum* does sometimes grow in the understory of *Laminaria* beds in Nova Scotia (C. R. Johnson, *personal observation*) and Newfoundland (Keats et al. 1982), but while it may coexist, there is no evidence of it outcompeting the larger *Laminaria* species that have higher growth and recruitment rates. These untested conclusions are supported by the work of Vadas (1968) and Dayton (1975b) in the Pacific, who examined the interactions of *Agarum* species with several species of *Laminaria* and other large kelps, and concluded that *Agarum* was unable to compete with the larger, faster growing species. Vadas (1968) found that only when sea urchins were abundant could *Agarum* dominate, since it was mostly avoided by the urchins who fed selectively on other kelps.

In summary, notwithstanding the hiatus in the data that address displacement of *Laminaria* by other seaweeds, it seems that on the Atlantic coast of Nova Scotia, threats to the persistence of stands of *L. lon-*

*gicuris* from invasion by other algae are of secondary importance relative to disturbance from storms and especially grazing by sea urchins.

**Resilience.**—Large-scale destruction of *L. longicuris* beds by sea urchins and small-scale localized disturbance from storms that erode laminae and tear away whole plants is countered by the considerable ability of *Laminaria* to recover from perturbations. The presence of a dense stand of *L. longicuris* at Paul Pt., when the site was first visited only 18 mo after urchin mortality, demonstrates the kelp's impressive potential to recolonize and form a closed canopy, and is indicative of its high growth rates and prodigious reproductive output. Chapman (1984) estimated a production of  $\approx 1.5 \times 10^7$  spores/cm<sup>2</sup> of sorus in a population at Pubnico in Nova Scotia, and although this stand was relatively sparse ( $\approx 10$  times less dense than that at Paul Pt.), this amounted to a peak spore production of  $\approx 5.25 \times 10^9$  spores/m<sup>2</sup> substratum. This large-scale recovery parallels the behavior of *Laminaria* reported in earlier studies. Chapman (1981) noted that in an artificially cleared area regeneration occurred almost immediately, while Breen and Mann (1976) found that after removal of urchins from an urchin-dominated site, a closed canopy formed within 4–5 mo.

Why did a closed *Laminaria* canopy not develop at Mill Cove until 1985, nearly 4 yr following urchin mortality at this site? The difference in the rate of recovery of kelp at the two sites correlates with the distance from the nearest spore source. A large refugial population (14 400 m<sup>2</sup>, A. R. O. Chapman, *personal observation*) of reproductive plants that had persisted throughout the urchin/coralline-dominated period was only  $\approx 0.7$  km upstream from Paul Pt. on an outgoing tide. At the height of the ebb, tidal currents in the area attain 0.5–0.8 m/s (1–1.5 knots). In contrast, the closest refugial population to the Mill Cove site grew on a breakwater  $\approx 1.1$  km to the south but was not reproductive, and currents in the area are much less than at Paul Pt. We suggest that initial colonization at Mill Cove was slow, since spore release was dependent on the arrival of sorus-bearing drift plants from populations considerably farther afield than 1.1 km, but that once a base population became established and a threshold density was reached, spore release by local plants resulted in an exponential increase in recruitment in the 1984–1985 winter, enabling the kelp canopy to close by the latter half of 1985. Our observations are consistent with measurements made of other laminarian species, showing that spore dispersal from the parent sorus is very limited (Anderson and North 1966, Dayton 1973, Paine 1979, Dayton et al. 1984). For these kelps, long-distance dispersal relies on the drifting of reproductive plants or plant pieces. However, as a general case the absence of a nearby kelp refugium at Mill Cove was anomalous. Along most of this coast, refuge populations protected from urchin grazing by

wave action persisted as a narrow band in the low intertidal and shallow subtidal throughout the urchin–coralline period. In light of the results of Chapman's (1981) experimental clearings and our observations in St. Margaret's Bay, it seems that the rapid and widespread recovery of *Laminaria* along the entire coast following the demise of the sea urchins (Moore and Miller 1983, Miller 1985a, Novacek and McLachlan 1986, Scheibling 1986) is due largely to the inoculation of contiguous subtidal areas with spores from these infralittoral refugia.

Having regained dominance, *Laminaria* also responds quickly to disturbances that partially or wholly destroy plants in local patches, and is thus able to maintain its dominance. Much of the decline in canopy cover during autumn and winter storms is from erosion of laminae, but since the intercalary meristem is situated at the base of the blade, plants can rejuvenate if as little as 10–20 mm of their lamina remains (C. R. Johnson, *personal observation*). If entire plants are destroyed and holes made in the canopy, recruitment of visible *Laminaria* sporophytes increases dramatically. Moreover, the removal experiments at Paul Pt. showed that despite crowding by conspecifics that retards growth in dense patches of new recruits, the new plants of *L. longicuris* soon dominate and outgrow the developing summer annuals. In similar experiments on the south shore of Nova Scotia, Smith (1985) also recorded higher recruitment of *L. longicuris* in plots totally harvested of kelp, and he and MacFarlane (1952) found it took only 1 yr for the kelp to recover to pre-removal biomass. Furthermore, it seems that recovery and dominance by *Laminaria* would be the outcome regardless of the season of canopy removal. Even if summer annuals formed a closed stratum following removal of *Laminaria* early in summer after the kelp's recruitment period, this "canopy" would disappear in the autumn and *Laminaria* could be expected to dominate by the following spring. Reed and Foster (1984) also found that the time of canopy removal had little effect on the composition of subsequent colonizers, but this contrasts with many intertidal (Hay and South 1979, Sousa et al. 1981) and subtidal communities (Foster 1975a, Sutherland and Karlson 1977, Peckol and Searles 1983), in which the season that a limiting resource becomes available may have profound impact on the composition of the ensuing community.

#### *Comparison with kelp bed systems in the northeast Pacific*

Are there commonalities or generalizations that apply to the stability properties, and therefore to the dynamics, of different kelp bed systems? The well-studied kelp communities on the west coast of North America provide a suitable basis for comparison with those on the east coast in Nova Scotia, and may be divided conveniently into two regions; central and southern

TABLE 10. Comparison in terms of stability of the dynamics of kelp beds in Nova Scotia with those in the northeastern Pacific. Superscript numbers refer to literature references given in footnote.

Nova Scotia	California	Northern northeastern Pacific
<b>Persistence</b>		
<i>Laminaria longicuris</i> grows in extensive homogeneous stands that may persist for several turnovers (1, 30).	Kelps appear as dynamic mosaic of patches (cf. 10, 39, 40, 41).	Kelps appear as dynamic mosaic of patches (8, 17, 20, 42).
Coralline algae abundant beneath seaweed cover and in areas of intensive grazing by urchins (27).	Coralline algae abundant beneath seaweed cover and in areas of intensive grazing by urchins (26, 32, 40).	Coralline algae abundant beneath seaweed cover and in areas of intensive grazing by urchins (4, 34).
<b>Resistance</b>		
<i>L. longicuris</i> recruitment unaffected by dominant annuals (but limited by canopy of conspecific adults: 1).	Some canopy-forming kelps can be displaced by invasion of other species (10, 40) (several limit their own recruitment: 10, 39, 40, 41).	Some canopy-forming kelps can be displaced by invasion of other species (8, 17, 20, 38, 42) (several limit their own recruitment: 12, 17).
<i>L. longicuris</i> relatively well adapted to wave action (1, 25).	<i>Macrocystis pyrifera</i> vulnerable to wave action (7, 9, 10, 11, 33, 41).	<i>M. integrifolia</i> (14, 16), <i>Pterygophora californica</i> (12), and <i>Laminaria</i> spp. vulnerable to wave action.
<i>L. longicuris</i> able to store nitrogen and is tolerant of nutrient stress (6, 19, 22).	<i>M. pyrifera</i> has poor capacity for nitrogen storage and is vulnerable to nutrient stress (24, 36).	
<i>L. longicuris</i> and other fleshy seaweeds vulnerable to destructive grazing by sea urchins (31, 43). Change in urchins' behavior from passive detritivore to active destruction of seaweed related to increase in density of urchins and not to change in density of kelp (31, 43).	<i>M. pyrifera</i> and other fleshy seaweeds vulnerable to destructive grazing by sea urchins (7, 13, 26, 29, 35, 38). Change in urchins' behavior in some areas induced by change in density of kelp and unrelated to density of urchins (26, see also 13, 32). In other areas destructive grazing may be caused by increase in urchin density (29, 35, 39).	Kelps and other fleshy macroalgae vulnerable to destructive grazing by sea urchins (4, 8, 17, 20, 21, 37, 38), but some species may attain refuge in size (18, 37). Destructive grazing appears to be induced by an increase in urchin density (4, 9, 17, 20, 21, 37, 38).
<i>L. longicuris</i> resistant to grazing by gastropods at high densities (28).		
Many understory species increase in abundance following canopy removal (1).	Many understory species increase in abundance following canopy removal (7, 39, 40).	Many understory species increase in abundance following canopy removal (8, 15) but some decrease their cover (8).
<b>Resilience</b>		
<i>L. longicuris</i> usually quick to respond to small and large scale disturbances and dominates early and late stages of succession (1, 3, 5).	<i>M. pyrifera</i> colonizes soon after disturbance only if reproductive conspecifics are nearby (39, 40), otherwise other kelps can establish which may preempt superior competitors and other species (2, 10).	Following disturbance, abundant early colonizers are not usually competitive dominants (8, 17, 42).
Sequence of succession relatively invariant; factors affecting sequence in other systems affect only rate of succession (1, 3, 5).	Sequence of succession affected by timing and scale of disturbance, proximity to spore source, dispersal ability, and season of spore production (10).	
Endpoint of succession nearly always <i>L. longicuris</i> over wide range of wave exposure and nutrient stress (1, 3, 5; J. Gagné, personal communication).	Endpoint of succession modified by disturbance (10, 40).	Endpoint of succession modified by disturbance (8, 20, 42).

<sup>1</sup> This paper, <sup>2</sup> Ambrose and Nelson 1982, <sup>3</sup> Breen and Mann 1976, <sup>4</sup> Breen et al. 1982, <sup>5</sup> Chapman 1981; <sup>6</sup> Chapman and Craigie 1977, <sup>7</sup> Cowen et al. 1982, <sup>8</sup> Dayton 1975b, <sup>9</sup> Dayton 1985, <sup>10</sup> Dayton et al. 1984, <sup>11</sup> Dayton and Tegner 1984, <sup>12</sup> De Wreede 1984, <sup>13</sup> Dean et al. 1984, <sup>14</sup> Druehl 1978, <sup>15</sup> Druehl and Breen 1986, <sup>16</sup> Druehl and Wheeler 1986, <sup>17</sup> Duggins 1980, <sup>18</sup> Duggins 1981, <sup>19</sup> Espinoza and Chapman 1983, <sup>20</sup> Estes et al. 1978, <sup>21</sup> Foreman 1977, <sup>22</sup> Gagné et al. 1982, <sup>23</sup> Gerard 1982, <sup>24</sup> Gerard 1984a, <sup>25</sup> Gerard and Mann 1979, <sup>26</sup> Harrold and Reed 1985, <sup>27</sup> Johnson and Mann 1986a, <sup>28</sup> Johnson and Mann 1986b, <sup>29</sup> Leighton 1971, <sup>30</sup> Mann 1972a, <sup>31</sup> Mann 1977, <sup>32</sup> Mattison et al. 1977, <sup>33</sup> Moreno and Sutherland 1982, <sup>34</sup> Neushul 1967, <sup>35</sup> North and Pearse 1969, <sup>36</sup> North and Zimmerman 1984, <sup>37</sup> Pace 1981, <sup>38</sup> Paine and Vadas 1969, <sup>39</sup> Pearse and Hines 1979, <sup>40</sup> Reed and Foster 1984, <sup>41</sup> Rosenthal et al. 1974, <sup>42</sup> Vadas 1968, <sup>43</sup> Wharton and Mann 1981.

California, and the region to the north from Washington through British Columbia and Alaska (see Table 10 for summary of comparison).

In Nova Scotia *L. longicruris* grows in a more or less continuous band around the coast where suitable substratum exists (cf. present study, MacFarlane 1952, Edelstein et al. 1969, Mann 1972a, Tremblay and Chapman 1980, Moore and Miller 1983, Miller 1985a, Novacek and McLachlan 1986, Scheibling 1986), but in California the kelp beds are a complex mosaic of patches of many species that are dynamic in time and space (Dayton et al. 1984; see also Pearse and Hines 1979, Reed and Foster 1984). The competitive dominant in this community (*Macrocystis pyrifera*) develops a dense surface canopy that monopolizes the light resource and effectively resists invasion by other kelps, but only if stress and disturbance are at low levels (Pearse and Hines 1979, Dayton et al. 1984, Reed and Foster 1984). Unlike *L. longicruris*, because it is a much larger plant that forms a surface canopy, *M. pyrifera* is notoriously susceptible to damage and destruction from wave action (Rosenthal et al. 1974, Cowen et al. 1982, Moreno and Sutherland 1982, Dayton and Tegner 1984, Dayton et al. 1984, Reed and Foster 1984, Dayton 1985), and it has minimal capacity for nitrogen storage (Gerard 1982) so that plants in southern California deteriorate greatly during summer periods of nutrient stress (Gerard 1984a, North and Zimmerman 1984). If small patches of *M. pyrifera* are destroyed and there are reproductive conspecific nearby, provided the frequency of disturbance is low, *M. pyrifera* is normally among the early macroalgal colonizers and is able to develop a canopy and regain dominance quickly (Rosenthal et al. 1974, Pearse and Hines 1979, Dayton et al. 1984, Reed and Foster 1984). In contrast, when large-scale destruction occurs, *M. pyrifera* shows resilience, and other smaller kelps are able to colonize and dominate in patches (Dayton et al. 1984, Reed and Foster 1984). These patches resist invasion of other seaweeds by limiting their recruitment, but it is in exposed areas where wave stress prevents *M. pyrifera* from establishing at all that the smaller kelps are most prolific. As in Nova Scotia, destructive grazing by sea urchins is the primary agent of disturbance that can destroy all kelp patches and leave areas barren of any fleshy seaweeds (North and Pearse 1969, Pearse and Hines 1979, Cowen et al. 1982, Dean et al. 1984, Harrold and Reed 1985). However, the mechanism that activates the change in behavior of the urchins from passive detritivore (feeding on drift algae) to active grazer (feeding on attached algae) may be different from that which induces destructive grazing in Nova Scotia. There is strong evidence to show that in some areas in California intensive grazing of kelp occurs primarily as a result of a change in the density of kelp and is unrelated to the density of urchins. In these areas, if the density of attached algae declines, so does the availability of drift algae, and the

urchins leave the shelter of cracks and crevices to forage actively (see also Mattison et al. 1977, Dean et al. 1984, Harrold and Reed 1985). However, in other areas in California the decimation of kelps has been associated with high densities of urchins (e.g., North and Pearse 1969, Pearse and Hines 1979), although in situations in which intensive grazing occurred as a consequence of urchins forming large feeding aggregations (e.g., Leighton 1971, Dean et al. 1984), it is not clear whether the aggregations were simply the result of high densities, or of mobile animals grouping at a food source (see Dean et al. 1984). In Nova Scotia there is no evidence of a causative link between kelp density and onset of destructive grazing, and although the mechanism(s) that induce sea urchins at high density to aggregate remains a controversial topic (Bernstein et al. 1981, 1983, Vadas et al. 1986), it is clear that devastation of seaweeds occurs only when there is a large increase in the urchin population (Mann 1977, Wharton and Mann 1981). Because of the resistance of *L. longicruris* to wave action and its ability to recolonize quickly when holes are made in the canopy, storms in Nova Scotia do not lead to a reduction in the density of *Laminaria* on the same scale as occurs in stands of *M. pyrifera* in California.

While not so extensively studied, there is also good evidence of strong competitive interactions among kelp species in the higher latitudes of the Pacific rim. Kelp beds in this area are also characterized by dynamic patchiness in their composition, although the structure of these communities differs from their Californian counterparts. Subtidal surveys and experimental evidence have shown that species of *Laminaria* are the competitive dominants in most areas. When sea urchins are removed from barren areas, there is a succession of algae that usually leads to eventual dominance by species of *Laminaria*, but unlike the situation in Nova Scotia, this is attained at the earliest in the 2nd yr of succession when *Laminaria* outcompetes opportunistic annual kelps like *Alaria* spp. and *Nereocystis luetkeana* that dominate initially (Vadas 1968, Paine and Vadas 1969, Dayton 1975b, Estes et al. 1978, Duggins 1980). Patches of *Agarum* spp. in shallow water (Vadas 1968, Dayton 1975b, Estes et al. 1978), and of *Nereocystis* (Vadas 1968, Foreman 1977, Duggins 1980) and *Alaria* (Dayton 1975b) may be maintained by disturbance. However, interactions are not always this straightforward. From our reading of the literature, the following questions appear to be unanswered: (1) Why in some sheltered areas does *Alaria* establish but *Laminaria* species do not (Estes et al. 1978)? (2) Why in some cases does *Laminaria* not displace *Nereocystis* for many years (Foreman 1977, Breen et al. 1982)? (3) What are the competitive interactions among the several species of *Laminaria*? (4) What factors govern the establishment and stability properties of patches of *Macrocystis integrifolia* (Druehl 1978), *Pterygophora californica* (Pace 1981, De Wreede 1984), *Costaria cos-*

*tata*, and others (Neushul 1967, Vadas 1968)? In spite of these deficiencies it is nonetheless clear that strong competitive interactions occur among these macroalgae, that stresses and disturbances can modify the outcome of the interactions, and that in large part it is these factors that cause dynamic patchiness in the composition of the kelp assemblage.

These comparisons highlight several points. First, there are only two broad similarities among the three communities: the potential of sea urchin grazing to destroy fleshy algal beds on a large scale, and the importance of storms as a source of kelp mortality. When these disturbances cease, the subsequent successional processes and variables that dictate stability and structure are vastly different in each community. In Nova Scotia, succession nearly always leads to dominance by *L. longicruris* (although it may share this position with *L. digitata* at some sites), and if a source of spores is available, the kelp dominates at all but the incipient stages (Breen and Mann 1976, C. R. Johnson, *personal observation*). Moreover, dominance is realized over a wide range of exposures and nutrient levels. This differs markedly from the pattern on the Pacific Coast, in which disturbance modifies competitive interactions so that the "endpoint" of succession is different at different sites. In the Pacific, the sequence of succession and the ability of patches to rebound after disturbance is influenced by variation in the timing and scale of disturbance and stress, the dispersal abilities of the different kelps, the season of spore production, and the proximity of spore sources. In Nova Scotia, variation in these factors changes only the rate of succession, and inhibition in succession (*sensu* Connell and Slayter 1977) does not occur. Dominance of *Laminaria* in both the early and late stages of succession in Nova Scotia also contrasts with the pattern in many intertidal communities (e.g., Dayton 1971, Sousa 1979a, 1984, Ayling 1981, Paine and Levin 1981, Dethier 1984) in which disturbance or stress that is patchy in time and space allows the proliferation of poorer competitors in patches, which may in turn inhibit the establishment of competitive dominants (Sousa 1979b).

*Diversity and patterns of adaptation.*—What factors might account for the different dynamics and stability among kelp beds in Nova Scotia and on the west coast of North America? The most striking difference in these communities is in the diversity of kelp species. We suggest that in Nova Scotia low diversity results in low levels of competition that permit *L. longicruris* to grow close to its physiological limits of light and wave stress, and thus to dominate early and late stages of succession in environments of disparate levels of stress and disturbance. If a greater number of competitors were present, e.g., species that formed perennial surface canopies (*Macrocystis*) or rapid colonizers tolerant of wave stress (*Nereocystis*), the even band of *Laminaria* along the coast would be broken into a mosaic of patches whose dynamics and stability properties would parallel closely

the patterns of the West Coast. We predict that the present dynamics of kelp beds in Nova Scotia would change significantly if even a single additional kelp species was introduced into the system and established successfully. Invasion of kelp communities in California by the introduced alga *Sargassum muticum* has influenced the resilience stability of patches in some areas by limiting recruitment of *M. pyrifera* (Ambrose and Nelson 1982).

This argument differs fundamentally from that of Menge and Sutherland (1976), who used a comparison of the dynamics of rocky intertidal communities of the East and West Coasts of North America to support their contention that predation is most important as a structuring agent in trophically complex, high-diversity communities (West Coast), but that in trophically simple communities (East Coast) the reverse holds and competition predominates in determining community structure and dynamics. Our results indicate that in the relatively simple subtidal community in Nova Scotia, levels of competition among macroalgae are low as a result of low diversity of kelps, and that among seaweeds, competition and disturbance (excepting widespread destructive grazing by urchins) are relatively unimportant to community structure. In subtidal communities on the West Coast, competition among seaweeds is high, and both competition and disturbance are pivotal in shaping their dynamics and organization. In these highly diverse communities, disturbance (biological and physical) helps to maintain diversity by preventing competitive exclusion (Vadas 1968, Dayton 1975b, Estes et al. 1978, Duggins 1980, Dayton et al. 1984). Considering the contribution of higher trophic levels to community organization, "predation" by sea urchins is important on both coasts, and predators of urchins can play a critical role on the West Coast (sea otters; see Estes and Palmisano 1974, Estes et al. 1978, Simenstad et al. 1978, Duggins 1980, Breen et al. 1982) and perhaps also in Nova Scotia (cf. Wharton and Mann 1981, Bernstein et al. 1983, Miller 1985b, Keats 1986, Vadas et al. 1986). It seems, then, that the relation of community stability to diversity, competition, predation, and other kinds of disturbance cannot be generalized, and may vary according to the behavioral, life history, and physiological characteristics of component species in communities.

Of course, low levels of competition alone do not bring about dominance. Also important to the success of *L. longicruris* are its multiple patterns of adaptation. It demonstrates a suite of life history and physiological characteristics that confer a generalist nature and increase its ability to establish rapidly and maintain dominance. Enormous reproductive output (Chapman 1984), high capacity of dispersal by drift fragments bearing spores, the ability to store nitrogen (Chapman and Craigie 1977), and high growth rates facilitate rapid recolonizing after disturbances. Having colonized, its perennial nature and relatively large size, antither-

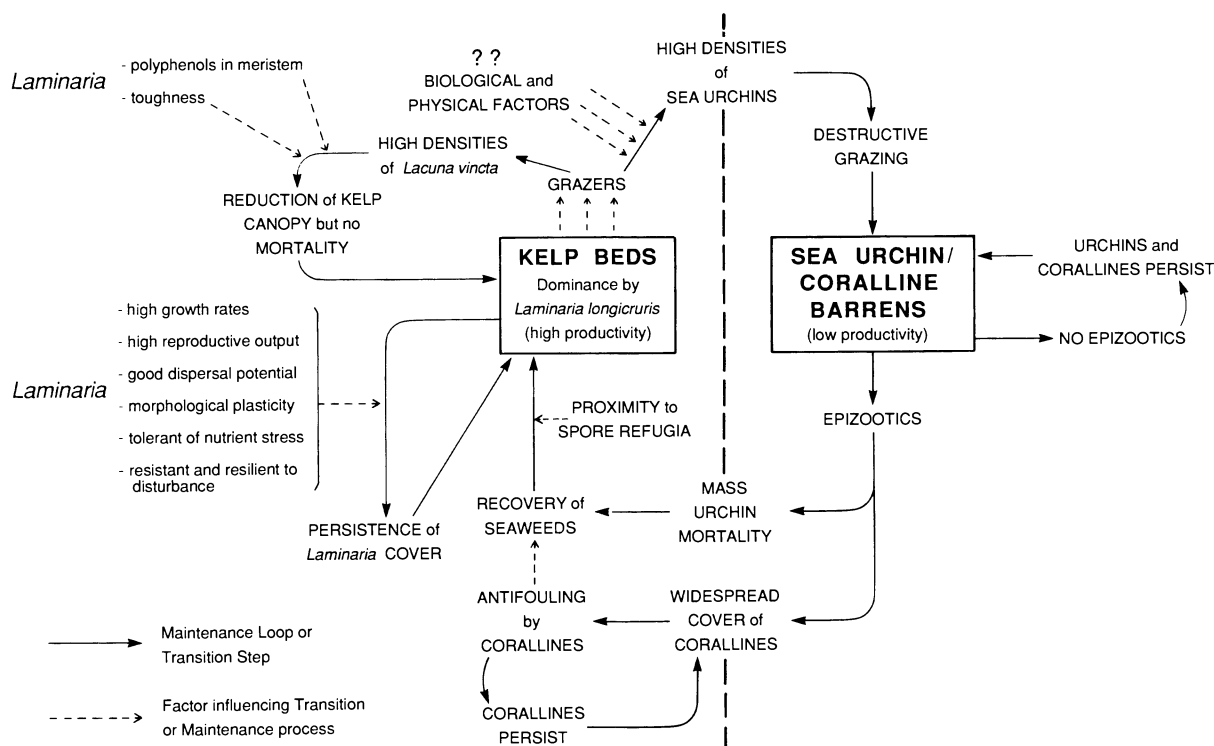


FIG. 10. Qualitative model of the dynamics of community structure of the rocky subtidal in Nova Scotia. Biological interactions define community structure within the two alternate stable configurations of the community (kelp beds and sea urchin/coralline alga community) and mediate transitions from one state to the other. Notice that the principal void in the model concerns the factors that lead to increased densities of sea urchins and their behavioral changes that result in destructive grazing of seaweeds.

bivore properties (Johnson and Mann 1986b), resistance to wave action (Gerard and Mann 1979), and tolerance of nutrient stress, confer flexibility that enables the plant to maintain its dominance in a wide range of habitats.

#### *Summary: alternate stable states and dynamics of structure*

From our results and those of previous studies we constructed a qualitative model that summarizes the gross behavior and dynamics of structure of the rocky subtidal in Nova Scotia (Fig. 10). In this model we consider the highly productive (Mann 1972b) *Laminaria*-dominated seaweed beds, and the poorly productive (Chapman 1981) urchin/coralline community to be two alternate and stable configurations, since either community state can persist for much longer than the lifespan of their dominant species, with the possible exception of coralline algae, whose lifespan is unknown. A biological mechanism causes switching from one state to the other, and biological interactions determine the stability properties and community structure of each configuration. Destructive grazing by the sea urchins (Mann 1977) causes the transition from

kelp beds to the unproductive state, and an amoeboid disease (Jones 1985, Jones and Scheibling 1985, Jones et al. 1985) appears to be the mechanism that destabilizes the urchin populations and facilitates recovery of the kelp beds (Johnson 1984, Miller 1985a, Novaczek and McLachlan 1986, Scheibling 1986).

Biological interactions also define structure within each community state. When sea urchins are abundant they are clearly the single strongly interacting species (*sensu* Paine 1980) that largely determines community structure. In contrast, although *L. longicruris* replaces the urchins as the strongly interacting species in the kelp-dominated phase, it influences community structure in concert with a suite of weakly interacting species. For example, the encrusting coralline algae that cover nearly all of the hard substratum in the subtidal and persist when the seaweed beds recover and overgrow them, limit the abundances of filamentous and foliose understory species (Johnson and Mann 1986a). Local invasions by the gastropod *Lacuna vincta* can affect the kelp beds by significantly reducing canopy cover (Johnson and Mann 1986b). In some shallow (atypical) areas, grazing by limpets and chitons affects algal community composition (R. E. Scheibling, *personal communication*).

The stability and persistence of the urchin/coralline community is ascribed to the physiological and life history traits that enable the urchins to survive and reproduce after macroalgae have been eliminated (Johnson and Mann 1982), and to the adaptations of the coralline crusts for tolerating intense grazing by the urchins (see Littler et al. 1983, Steneck 1983, 1986). We attribute the widespread dominance and high degree of stability of *Laminaria* beds when sea urchins are rare to both (1) the low diversity of the system, and (2) the kelp's multiple patterns of adaptation or generalist nature, i.e., its life history and physiological adaptations that enable it to compete in environments of disparate levels of stress and disturbance.

In summarizing, we suggest that this model may be fruitfully viewed as a set of several deterministic "sub-routines," each describing the outcome of a specific biological interaction. This conceptualization emphasizes that, unlike the other subtidal communities we have discussed, at a first level of organization the structure and dynamics of this community are prescribed wholly by biological and not physical factors. Physical factors assert their influence at a secondary level in that the subroutine or set of subroutines that are foremost at any point in time or space are probably determined by hydrographic events that are largely unpredictable. For example, the occurrence of the epizootics may be dependent on physical factors that cause above average water temperatures (Scheibling and Stephenson 1984), or the arrival of exotic water masses (Scheibling 1986). Similarly, the successful recruitment of high densities of sea urchins or of the gastropod *Lacuna vincta*, and to some extent the rate of recovery of *Laminaria* stands, is probably dependent on some combination of wind patterns, local and coastal current movements, water temperature, amount of coastal runoff, etc., all of which have a large stochastic component. This point of view is supported by the review of Pringle (1986). However, the experiments and observations discussed in this paper indicate that once disease is introduced, or immigration, or disturbance, or a recruitment event occurs, the outcome in terms of community structure is highly predictable.

Of course much remains to be done if this model is to be rigorously tested in its entirety. But of the unanswered questions, one stands apart from all others. What are the biological and/or physical factors that lead to the switch from dense, highly productive kelp beds to the alternate state in which sea urchins destructively graze the kelp, and prevent the regeneration of kelp beds by their continued browsing? In California kelp beds Harrold and Reed (1985) observed that in places where kelp biomass was high the urchins lived in crevices and probably fed on drift algae. In other areas, where kelp was sparse or nonexistent, the urchins lived in exposed situations and browsed on the surfaces of the rocks. The authors observed a situation

in which a marked increase in kelp biomass occurred and the urchins switched from living on the open rock surfaces to living in crevices. The converse change was observed in Nova Scotia (Mann 1985). While kelp biomass remained approximately constant, the biomass of urchins increased dramatically and the urchins switched from being passive, cryptic detritivores to being aggressive herbivores living openly on the rocks. The crucial factor in both situations seems to be the ratio of kelp biomass to urchin biomass. When it is high, the urchins live cryptically as detritivores; when it is low they are unable to obtain sufficient nourishment as passive detritivores and emerge onto the open rock surface. The next question is, when the urchins switch to living on the open rock surface, what factors determine that they will aggregate on individual kelp plants and destroy them, rather than remaining dispersed and doing small amounts of damage to a larger number of plants? Bernstein et al. (1983) presented evidence to indicate that grouping of urchins was a defense response to the presence of predators, but Vadas et al. (1986) found that urchins fled from predators and that aggregations formed only around a food source. However, the results of the two studies are not easily compared, since there were considerable differences in cage design, in the size and densities of urchins used in the experiments, and in the physical environment of the study sites, all of which may influence behavior. The question of the exact mechanism causing aggregation needs further work, but it is still subsidiary to the main question of what caused the marked increase in urchin abundance that led to the decrease in ratio of kelp biomass to urchin biomass, and hence to the change in urchin behavior. The choice is between increases in recruitment success and decreases in urchin mortality patterns as a result of predator removal (or some combination). Further work is needed to resolve this matter.

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## APPENDIX

Noncalcareous seaweeds recorded at Paul Pt. and Mill Cove, May 1982–October 1983, indicating unmanipulated species that were included in the analysis for response to removal of dominant perennial and annual species (peak percentage cover  $\geq 4\%$ ).†

Species	Site	
	Paul Pt.	Mill Cove
<b>Canopy-forming</b>		
<b>Phaeophyta</b>		
<i>Laminaria longicuris</i>	*	*
<i>Laminaria digitata</i>	N	nr
<b>Understory</b>		
<b>Chlorophyta</b>		
<i>Spongomorpha</i> spp.	N	N
<i>Chaetomorpha</i> spp.	N	N
<i>Cladophora</i> spp.	nr	N
<i>Rhizoclonium</i> spp.	nr	N
<b>Phaeophyta</b>		
<b>Ectocarpoids</b>	Y	N
<i>Giffordia granulosa</i>	nr	N
<i>Chordaria flagelliformis</i>	N	N
<i>Acrothrix novae-angliae</i>	N	*
<i>Dictyosiphon foeniculaceus</i>	N	nr
<i>Petalonia fascia</i>	N	N
<i>Scytosiphon lomentaria</i>	nr	N
<i>Desmarestia aculeata</i>	*	*
<i>Desmarestia viridis</i>	Y	Y
<i>Chorda filum</i>	nr	N
<i>Agarum cribrosum</i>	N	N
<i>Saccorhiza dermatodea</i>	Y	N
<i>Haplospora globosa</i>	N	nr
<i>Tilopteris mertensii</i>	N	nr
<i>Sphacelaria furcigera</i>	N	N
<i>Sphacelaria plumosa</i>	N	Y
<i>Halopteris scoparia</i>	N	N
<i>Fucus</i> spp.	N	N
<b>Rhodophyta</b>		
<i>Bonnemaisonia hamifera</i>	Y	Y
<i>Cystoclonium purpureum</i>	N	N
<i>Chondrus crispus</i>	N	N
<i>Antithamnion</i> spp.	*	*
<i>Callithamnion</i> spp.	Y	Y
<i>Ceramium rubrum</i>	*	*
<i>Phycodrys rubens</i>	N	nr
<i>Polysiphonia harveyi</i>	nr	N
<i>Polysiphonia nigrescens</i>	Y	*
<i>Polysiphonia urceolata</i>	*	*
<i>Rhodomela confervoides</i>	Y	Y

† \* = Dominant species that were manipulated (percentage cover at time of manipulation  $\geq 15\%$ ); nr = species not recorded; Y = included in analysis; N = not included in analysis.