

Latitudinal Variation in Intertidal Algal Community Structure: the Influence of Grazing and Vegetative Propagation

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Summary. The hypothesis that sea urchin grazing and interactions with turf-forming red algae prevent large brown algae from forming an extensive canopy in the low intertidal zone of southern California was tested with field experiments at two study sites. Experimental removal of sea urchins resulted in rapid algal recruitment. Crustose coralline algae which typically dominate the substratum in areas with dense urchin populations were quickly overgrown by several species of short-lived green, brown and red algae. The removal of urchins also significantly increased the recruitment of two long-lived species of large brown algae (*Egrecia laevigata* and *Cystoseira osmundacea* at one study site and *E. laevigata* and *Halidrys dioica* at the other). The experimental plots at both sites were eventually dominated by perennial red algae.

A two-factorial experiment demonstrated that sea urchin grazing and preemption of space by red algae in areas where urchins are less abundant are responsible for the rarity of large brown algae in the low intertidal of southern California. The three dominant perennial red algae, *Gigartina canaliculata*, *Lawrencia pacifica* and *Gastroclonium coulteri*, recruit seasonally from settled spores but can rapidly fill open space with vigorous vegetative growth throughout the year. These species encroach laterally into space created by the deaths of large brown algae or by other disturbances. Once extensive turfs of these red algae are established further invasion is inhibited. This interaction of algae which proliferate vegetatively with algae which recruit only from settled spores is analogous to those which occur between solitary and colonial marine invertebrates and between solitary and cloning terrestrial plants.

It is suggested that a north-south gradient in the abundance of vegetatively propagating species, in grazing intensity and in the frequency of space-clearing disturbances, may account for latitudinal variation in intertidal algal community structure along the Pacific coast of North America.

Introduction

Causes of geographical variation in community structure, particularly at different latitudes, have long been a subject of discussion and debate in ecology (Dobzhansky 1950; Connell and Orias 1964; MacArthur 1965, 1972; Paine 1966; Pianka 1966). Most studies of geographical differences in community structure, especially those of terrestrial systems, tend to be observational and non-experimental. Such studies (e.g. Pianka 1975; Inger

and Colwell 1977) compare measures of the structure of particular communities (e.g. mean niche width, mean niche breadth, percentage of the assemblage which is predatory, microhabitat diversity, tightness of guilds, etc.). Possible causes of observed differences in community composition or structure are inferred from any detectable differences in these measures. This inference is usually guided by the predictions of mathematical theory.

Geographical variation in the structures of marine invertebrate intertidal communities has more often been studied with field experiments. Connell (1975) and Menge and Sutherland (1976) have compared the results of experimental manipulations of assemblages of intertidal invertebrates on Pacific and Atlantic intertidal shores, and Paine (1966, 1971, 1974) has compared the effects of removing the top predator, a starfish, from two similar communities, one in Washington State in the northwestern U.S. and the other near Auckland, New Zealand.

With the exception of the ongoing work of J. Lubchenco and B. Menge (pers. comm.), there seems to be no experimental evidence regarding the causes of latitudinal variation in intertidal algal community structure. Such variation can be striking, and has generally been attributed to changes in the physical environment with latitude. A general trend is for large brown algae (e.g. Laminariales or Fucales) to predominate at higher latitudes while turf-forming red algae dominate the shores at lower latitudes (see appendix in Garbary 1976). This trend is well documented along the Pacific coast of North America (Stephenson and Stephenson 1972). In the Pacific Northwest the low intertidal algal assemblage is dominated by large brown algae, the dominant species changing with the degree of exposure to wave action (Widdowson 1965; Dayton 1975). *Hedophyllum sessile* dominates in protected areas, *Laminaria* spp. in areas of intermediate exposure, and *Lessoniopsis littoralis* in exposed areas. Low intertidal algal assemblages south of Point Conception, California (34°28' N 120°27' S) differ considerably from those in the north (Thom 1980). They are usually strongly dominated in unpolluted areas by a perennial turf of calcareous or noncalcareous red algae with only a sparse cover of large brown algae (Emerson and Zedler 1978; Murray and Littler 1978; Sousa 1979) these being *Egrecia laevigata*, *Cystoseira osmundacea* and *Halidrys dioica*. In the shallow subtidal these three species are more common.

Sea water temperature is most often invoked as the factor explaining the geographical distributions of marine algae (Chapman 1943; Stephenson 1943; Lewis 1964; van den Hoek 1975; but see Lubchenco 1980). Abbott and North (1972) have attributed patterns of floral composition along the coast of California to a north-south gradient in water temperature. In addition to

temperature influences on the southern California flora, Thom (1980) has suggested that the predominance of fleshy and bladed species to the north and of turf algae and articulated coralline algae in the south is caused by differences in the frequency of upwelling, sand movement, human disturbance, and wave action.

Gradients in the physical environment may sometimes cause geographical differences in the species compositions of communities of intertidal algae; however, differences in the structures of these communities (e.g. the presence or absence of a canopy dominated by large brown algae) may result from variation in the kinds and intensities of interspecific biological interactions occurring in different locations. The studies reported here were initiated independently with the common intent of gathering experimental evidence on the roles of biological interactions in generating the north-south gradient in low intertidal algal community structure along the Pacific coast of North America. More specifically, by manipulating both the patterns of algal succession on experimentally cleared rock surfaces and the density of a common herbivore, the sea urchin, *Strongylocentrotus purpuratus*, we hoped to determine if algal interactions, and grazing played significant roles in generating the latitudinal pattern. Our experiments were designed after those of previous investigations of similar phenomena in the Pacific Northwest (Paine and Vadas 1969; Dayton 1975; Paine 1977). The aim was to generate data complementary to those already available from northern areas thereby allowing a direct comparison of successional dynamics at different latitudes.

Observations on sea urchin grazing and on interactions of red and brown algae made prior to our experimental studies suggested that these biological interactions might be responsible for differences in algal community structure with latitude. In boulder fields, a common intertidal habitat of southern California, winter storms often overturn boulders thereby making space available for colonization (Sousa 1979 and 1979a). In the absence of such disturbances, space on the upper surfaces of boulders is dominated by one or two species of turf-forming red algae. When such disturbances make space available, however, several species of brown algae including *Macrocystis pyrifera*, *Egregia laevigata*, *Cystoseira osmundacea*, and *Desmarestia ligulata* were observed to colonize the tops and sides of boulders (also see Murray and Littler 1978, p. 511). At some sites, sea urchins occur in locally dense beds around the bases of boulders. Occasionally, urchins in portions of these beds are crushed by moving boulders or killed by freshwater runoff following large storms. Brown algae rapidly colonize the hard substrata in these areas and persist until removed by wave action or by reinvading urchins. These observations suggested the hypothesis that large brown algae are relatively rare in the low intertidal zone of southern California because of: 1) intensive grazing by sea urchins and; 2) interactions with turf-forming red algae which prevent the establishment and persistence of a dense brown algal canopy in areas where urchins are rare.

Study Sites

Ellwood Beach

One study by the first two authors (W.P.S. and S.C.S.) was conducted in several adjacent low intertidal boulder fields at Ellwood Beach, California (34°25' N, 119°41' W) approximately 9 km west of the University of California, Santa Barbara campus (Fig. 1). Sandstone boulders up to 1 m² top surface area overlie a gently sloping shale platform which extends into the low intertidal zone (from -0.30 m

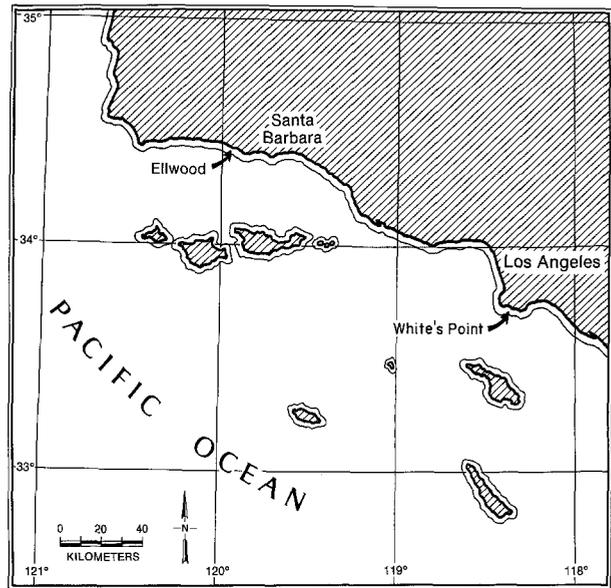


Fig. 1. Map of the south coast of California from Point Conception to Los Angeles showing the locations of the study sites at Ellwood Beach and White's Point. The Santa Barbara Channel Islands are also indicated

to +0.30 m above mean lower low water, hereafter MLLW). All of the work described from this site was done between these tidal levels, the majority at approximately MLLW.

The top surfaces of stable boulders positioned between +0.30 m and 0.0 m are dominated by the red alga, *Gigartina canaliculata* (Sousa 1979). At or below 0.0 m MLLW, this assemblage grades into one dominated by the red algae, *Laurencia pacifica* and *Gastroclonium coulteri*. At 0.0 m MLLW these three species form a mixed mosaic on boulder surfaces with *G. canaliculata* predominating on surfaces with a southern exposure and the latter two species dominating surfaces receiving less direct insolation. The lower edge of the boulder habitat occurs at approximately -0.45 m MLLW where a bench of soft shale sparsely covered with coralline algae and the surf grass *Phyllospadix torreyi* extends into the subtidal.

At 0.0 m MLLW, dense populations of the purple sea urchin, *Strongylocentrotus purpuratus* (range of 205-775/m², n=13), occupy the interstices between boulders. Urchins do not graze the top surfaces of boulders. Presumably, either increased wave shock, desiccation stress, and/or bird predation prevent them from doing so. Large numbers of sea gulls were observed feeding on urchins during daytime low tides. Urchins do, however, graze intensively on the algae occupying the sides of boulders as described later. A number of other grazers occur in the habitat including limpets, chitons, coiled snails, sea hares, hermit crabs, grapsid crabs, and fish. Their roles in structuring the algal community are documented in an earlier paper (Sousa 1979).

A dense canopy of the large brown algae *Egregia laevigata* and *Cystoseira osmundacea* occurs in the shallow subtidal just shoreward of dense beds of the giant kelp *Macrocystis pyrifera* but only sparse populations of *E. laevigata* and *C. osmundacea* occur in the intertidal. Rare individuals of *Macrocystis pyrifera* and *Desmarestia ligulata* can also be found.

White's Point State Beach

A second, independent study of sea urchin grazing on algal colonization and succession was conducted by the third author (S.D.G.) at White's Point State Beach (Fig. 1) in Palos Verdes, California (33°46' N, 118°14' W). Field experiments were carried out on a large flat intertidal bench composed of dense shale. The surface of the bench is dominated by *Gigartina canaliculata* in the mid-intertidal (0.0 to +0.6 m above MLLW) and by a mixture of ephemeral species including diatoms, blue-green algae, the green alga, *Ulva californica*, and members of

the Ectocarpaceae on the lower shore (-0.3 to 0.0 m MLLW). A dense population of *Strongylocentrotus purpuratus* occupies this lower zone (range of 14 to 84/m², $N=20$). As at Ellwood, other herbivores commonly include sea hares, crabs, and limpets. Sparse populations of the large brown algae *Egregia laevigata* and *Haliidrys dioica* occur in the low intertidal but form dense beds on hard substrata just offshore.

Data gathered in the White's Point study lend additional strength to the latitudinal comparison aside from the obvious merits of replication. The studies of intertidal urchin grazing along the outer coast of Washington State (cited in the introduction) were conducted in areas of continuous rocky intertidal habitat rather than in boulder fields such as at Ellwood Beach. The rocky benches at White's Point are more similar to the habitat at these northern sites.

Methods

Ellwood Beach Study

Laboratory Food Preference Experiment

To determine if *Strongylocentrotus purpuratus* grazed selectively on algae in the low intertidal zone at Ellwood Beach a laboratory food preference experiment was run. Preference was measured by simultaneously offering each animal 5 g blotted damp weight of 9 species of macroalgae. All algal species tested were available to sea urchins in the low intertidal at Ellwood Beach as attached plants and/or as plants which drifted ashore from nearby kelp beds (i.e. the brown algae *Macrocystis pyrifera*, *Egregia laevigata* and *Cystoseira osmundacea*). Only mature plants free of epiphytes were used. Selectivity was determined by comparing statistically the mean blotted weight consumed of each alga. Group means were compared by testing at the $p \leq 0.01$ level using multiple Welch-Aspin test (Snedecor and Cochran 1967; p. 115). This method of testing takes account of heterogeneity in the group variances which violates assumptions of the one-way analysis of variance model. Ten different urchins were tested in this manner.

Individual sea urchins (average test diameter=42.8 mm, SD=3.2) were enclosed in 3 cm x 30 cm x 36 cm plastic freezer boxes through which unfiltered aerated sea water flowed (16.1 to 17.5° C). The experiment was run for 43 h until it was clear that animals in all replicates had been feeding on the enclosed plants. To correct for algal weight losses due to respiration rather than feeding, two complete sets of algae (i.e. 5 g each) were run for the same length of time without urchins. Average weights lost by these plants were assumed to have been respired away and were subtracted from weight losses of plants enclosed with urchins to get true estimates of the weights of algae consumed. The experiment was conducted in July of 1976. Seasonal differences in preference (Himmelman and Carefoot 1975) were not examined.

This method of testing grazer food preferences does not distinguish between the edibility and the attractiveness of the algae being offered (Vadas 1977; Nicotri 1980). Both characteristics influence the weight of each alga consumed. While important insights concerning the evolution of food preferences may come from tests which distinguish between these characteristics (Nicotri 1980), Vadas (1977) suggests that the method employed in this study provides the best single measure of preference.

Field Experiments

Two types of manipulative experiments were conducted to examine the effects of sea urchin grazing and the preemption of space by perennial red algae on brown algal recruitment and survival. The first set of experiments tested for the effects of urchin grazing alone. All urchins were removed from several permanently marked 1 m² quadrats. The densities of brown algae were periodically monitored in these plots and compared with similar data collected from adjacent 1 m² control plots where urchins were temporarily removed, counted, and replaced. This experiment was conducted twice. It was first performed on June 13, 1975. Four treatment and three control plots were monitored at varying intervals until May 6, 1977. The fourth removal quadrat was not sampled after August 9, 1976. While a dense popula-

tion of urchins surrounded the removal plots, they were slow to invade them. Occasional monitoring was sufficient to maintain very low densities of urchins within the treatment plots.

Several species of green, red and brown algae rapidly colonized the sides of boulders following the removal of sea urchins. To document the patterns of this algal succession, six 100 cm² permanent quadrats were established on the sides of boulders in both the removal and control plots. The percentage cover of algae in these quadrats was estimated periodically until August 1976. Field estimates of cover were made with the aid of a 100 cm² plexiglass sheet on which a uniform array of 100 dots was marked.

A second urchin removal experiment lacking the small successional quadrats described above, was conducted on September 7, 1975. Urchins were removed from three 1 m² plots and left undisturbed in three control plots. The six plots were sampled at varying intervals until March 6, 1977. Unlike the first experiment, urchins were allowed to re-invade the removal plots following the initial removal. Their average density at the end of the experiment was roughly half that at the beginning.

A 2 x 2 factorial design experiment tested both the effects of sea urchins and of competitive interactions with perennial red algae on the recruitment of brown algae. Several boulders were overturned in an area from which sea urchins were removed and in adjacent areas where urchins were present. The tops and sides of these overturned boulders were bare. Urchins were also removed from areas surrounding half of a set of undisturbed boulders, the tops and sides of which were over 90% covered with a mixture of perennial red algae including *Gigartina canaliculata*, *Laurencia pacifica*, and *Gastroclonium coulteri*. By monitoring the recruitment of brown algae to these 4 sets of boulders (all approximately equal in size) it was possible to evaluate the relative effects of the four combinations of sea urchin grazing and red algal cover. Two trials of the experiment were performed, the first starting on August 9, 1976, the second on February 5, 1977. Both ended on May 6, 1977 when the brown algae on all boulders were counted. No brown algae were present on any of the boulders at the start of either trial. Initially there were 4 replicates of each cell in the design; however, winter storm waves disturbed several of the boulders, reducing the number of replicates to two in each cell. Before being analyzed statistically, all experimental data (numbers of plants) were normalized with a log (x + 1) transformation.

White's Point Study

Field Experiments

Sea urchin removal experiments were also performed in the low intertidal (0.0 m MLLW) at White's Point. The design at this site included a removal treatment and three types of controls. Urchins were excluded from a 70 cm x 90 cm plot with a 0.4 m tall stainless steel mesh fence (1.27 cm mesh, No. 16 gauge wire). The fence proved to be an effective barrier to urchins since only one individual entered a removal quadrat during the nine months of this study. All other herbivores had access to the plot; limpets crawled through the mesh fence and sea hares and crabs climbed over it. The three controls run on adjacent plots of the same size included 1) an urchin enclosure in which the original urchins on the plot (initial mean density=22) were surrounded with a similar mesh fence to control for the possibility that the foraging of herbivores other than urchins might be reduced by the fence barrier, 2) a plot with urchins (initial mean density=18.4) half-surrounded by a fence to control for any effects of the stainless steel mesh or mounting hardware and 3) a plot without a fence and with natural densities of sea urchins (initial mean density=22.3).

To initiate each experiment the treatment and control quadrats were scraped clean of all organisms then burned with a propane torch so that each quadrat would be as similar as possible to begin with. The original urchins in the control plots were replaced after this procedure was completed. It became apparent that the burning did not kill all the crustose coralline algae. However, the quadrats were fairly similar with respect to their initial cover of coralline algae and there was little evidence of any substantial change in this cover during the fairly short duration of the study. The plots were photographed at

approximately 2 month intervals and cover estimates made in the lab with a uniform array of 100 dots superimposed on the projected image. These estimates were in close agreement with those made visually in the field. All percent cover values were normalized with an arcsine transformation before statistical analysis.

To detect the effect of seasonality in algal recruitment on the pattern of succession the experiment was initiated twice, first in August 1976 and again in December 1976. Each time there were four replicates of the removal treatment and of each control. The study site was located in an area approximately 1 km north of the access road to White's Point to reduce the likelihood of human disturbance. Unfortunately this was a poor assumption as the experiments were vandalized in late March 1977 and terminated at that time.

Results

Ellwood Beach Study

Laboratory Food Preference Experiment

As expected from previous studies (see Lawrence 1975 for a review), *Strongylocentrotus purpuratus* showed a strong preference for some species of brown algae (Table 1). Urchins consumed significantly more of *Macrocystis pyrifera* than of any other alga with the exception of *Egregia laevigata*. Urchins consumed over four times as much *E. laevigata* as they did of the four red and green algal species whose weight losses ranked immediately below it. This latter difference, however, was not statistically significant due to large variation among the replicates which is not uncommon in such experiments (Littler and Littler 1980). In contrast, the brown alga, *Cystoseira osmundacea*, was hardly fed upon at all, ranking next to last in the amount consumed.

Intertidal urchins feed predominately on drift *M. pyrifera* plants which are torn loose in offshore beds during storms and then float ashore. Many of the *E. laevigata* plants available to urchins have also drifted ashore though this species more frequently grows to adult size in the low intertidal than does *M. pyrifera*. The ecological and evolutionary significance of drift algae in the diets of sea urchins has been discussed by Himmelman and Carefoot (1975) and Vadas (1977).

Field Experiments

The experimental removal of sea urchins resulted in rapid colonization by algae of the permanent quadrats on the sides of boulders (Fig. 2). Encrusting coralline algae, mostly *Lithothamnium* spp., characteristic of control areas with dense urchin populations were quickly overgrown by a mixture of *Ulva* spp. and a filamentous red algal turf dominated by *Spermothamion* sp. and *Pterosiphonia* sp. This turf was in turn replaced and the plots dominated by the perennial red algae, *Gigartina canaliculata*

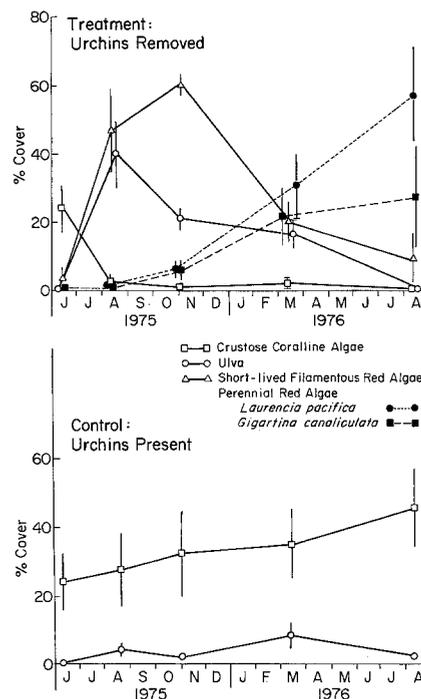


Fig. 2. Patterns of succession on the sides of boulders in the removal and control plots during the first sea urchin removal experiment at Ellwood. The mean percent covers (\pm one standard error of the mean) of algae which colonized the 100 cm² plots are indicated. Removal of urchins began in June 1975 and was continued until the experiment was terminated in May 1977

and *Laurencia pacifica*. The dominance of these species at the end of the experiment was strong, more so than indicated by the average values plotted in Fig. 2. *G. canaliculata* held greater than 75% of the cover on two south-facing replicates while *L. pacifica* held more than 80% of the cover on the remaining four north-facing replicates. The only *Egregia laevigata* to recruit to the small plots was a single plant in one of the urchin removal quadrats. There was little change in the algal cover on the sides of boulders subject to grazing by urchins. The cover of encrusting coralline algae increased slightly over the experimental period while a sparse of *Ulva* spp. persisted throughout.

Urchin grazing also reduces the abundance of large brown algae in the low intertidal as evidenced by the number of plants recruited to the larger 1 m² plots (Fig. 3 and 4). In the June experiments, *Cystoseira osmundacea* recruited more heavily to the urchin removal plots in the fall of 1975 and again in the fall of 1976 and survived better than in the control plots with urchins (Table 2). The same was true for the recruitment of

Table 1. Results of laboratory sea urchin food preference experiment. Entries are the mean weights of each species of algae consumed corrected for weight loss due to respiration. Underlines indicate means which are not significantly different at the $p \leq 0.01$ level using multiple Welch-Aspin tests. Species of algae tested were *Cystoseira osmundacea* (C.o.), *Egregia laevigata* (E.l.), *Gelidium coulteri* (Ge.c.), *Gigartina canaliculata* (G.c.), *Gigartina leptorhynchos* (G.l.), *Laurencia pacifica* (L.p.), *Macrocystis pyrifera* (M.p.), *Rhodoglossum affine* (R.a.) and *Ulva* sp. (U.)

Weight of each alga offered (g)	Length of time offered (h)	Number of replicates	Mean weights consumed										
			Ge.c.	C.o.	R.a.	L.p.	U.	G.c.	G.l.	E.l.	M.p.		
5.0	43	10	0	0.01	0.02	0.12	0.14	0.16	0.21	0.97	1.64		

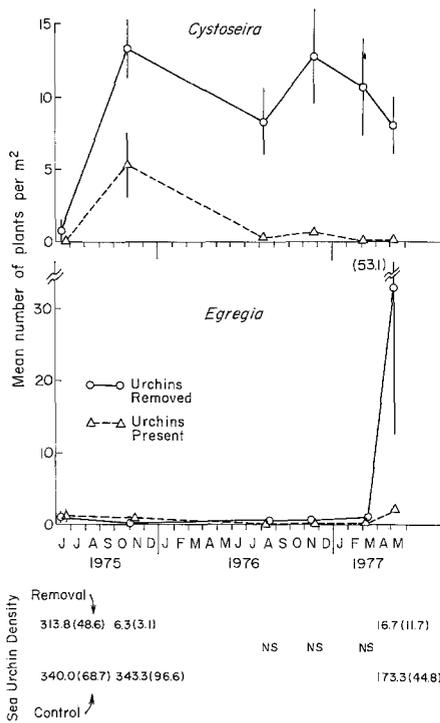


Fig. 3. Mean numbers (\pm one standard error of the mean) of *Egregia laevigata*, *Cystoseira osmundacea* and sea urchins in the 1 m² removal and control plots during the first urchin removal experiment at Ellwood. Removal of urchins began in June 1975 and was continued until the experiment was terminated in May 1977. The mean densities (SE enclosed in parentheses) of sea urchins in the removal and control plots appear below their respective sampling dates indicated in the figure. Initial values are densities prior to manipulation. NS indicates that sea urchin densities were not sampled on a particular date

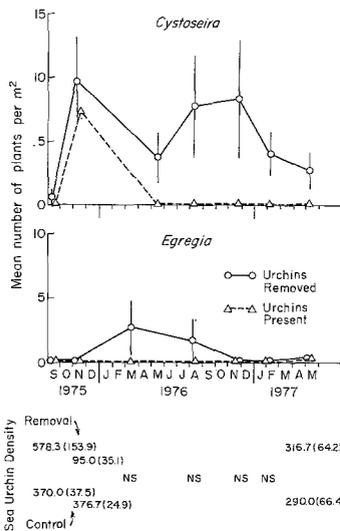


Fig. 4. Mean numbers (\pm one standard error of the mean) of *Egregia laevigata*, *Cystoseira osmundacea* and sea urchins in the 1 m² removal and control plots during the second urchin removal experiment at Ellwood. Urchins were removed once on September 1975 then allowed to reinvade. The mean densities (SE enclosed in parentheses) of sea urchins in the removal and control plots appear below their respective sampling dates indicated in the figure. Initial values are densities prior to manipulation. NS indicates that sea urchin densities were not sampled on a particular date

Table 2. Two-way analyses of variance testing for the effects of sea urchin grazing and time of sampling on the density of *Cystoseira osmundacea* and *Egregia laevigata*. Data are from the first urchin removal at Ellwood Beach initiated on June 13, 1975

Source of variation	Sum of squares	df	Mean square	F	Significance level
<i>Cystoseira</i>					
Main effects	0.050	6	0.008	8.19	0.001
Urchin	0.031	1	0.031	30.56	0.001
Time	0.019	5	0.004	3.67	0.012
Two-way interactions					
Urchin-time	0.010	5	0.002	1.97	0.115
Explained	0.062	11	0.006	5.56	0.001
Residual	0.027	27	0.001		
Total	0.090	38	0.002		
<i>Egregia</i>					
Main effects	0.667	6	0.111	4.50	0.003
Urchin	0.119	1	0.119	4.80	0.037
Time	0.563	5	0.113	4.56	0.004
Two-way interactions					
Urchin-time	0.563	5	0.113	4.56	0.004
Explained	1.231	11	0.112	4.53	0.001
Residual	0.667	27	0.025		
Total	1.897	38	0.050		

Egregia laevigata in the spring of 1977. The plots were not sampled in the spring of 1976 so it is not known if this latter difference also existed following the first recruitment season.

Similar results were obtained in the September removal. *Cystoseira osmundacea* recruited more heavily in the fall of 1975 and 1976 to plots from which urchins were removed (Table 3). The same pattern, though statistically non-significant, held for *Egregia laevigata* in the spring of 1976. However, by the spring of 1977, the density of urchins which had reinvaded the removal plots was sufficiently great to prevent any appreciable recruitment of *E. laevigata* (Fig. 4). At the same time, recruitment was very high in nearby June removal plots in which urchin densities were kept low (Fig. 3). Surviving plants of both species became reproductively mature in the experimental plots.

The attrition of newly-recruited intertidal plants was partly caused by urchin grazing as indicated by the greater rate of loss of *Cystoseira osmundacea* in the control plots than in the removals. Other possible sources of mortality included wave impact during winter storms, overgrowth of *C. osmundacea* by epiphytes including encrusting bryozoans (Tarp 1979; W.P. Sousa and S.C. Schroeter, personal observation), and grazing by the limpet *Notoacmaea insessa* on *Egregia laevigata* (Black 1974 and 1976).

The two factorial experiment simultaneously altering urchin density and the cover of perennial red algae showed that both were responsible for the low density of brown algae in the lower intertidal zone. While the recruitment of brown algae to the February trial was slightly increased by either the removal of the urchins or the removal of red algae alone, it was dramatically increased by the removal of both as compared to controls (Tables 4 and 5). However, this effect was very dependent on the exact time that the treatment was initiated. There was no significant effect of removing urchins and red algal cover when the

Table 3. Two-way analyses of variance testing for the effects of sea urchin grazing and time of sampling in the density of *Cystoseira osmundacea* and *Egrecia laevigata*. Data from the second urchin removal experiment at Ellwood Beach initiated on September 7, 1975

Source of variation	Sum of squares	df	Mean square	F	Significance level
<i>Cystoseira</i>					
Main effects	5.293	7	0.756	9.26	0.001
Urchin	2.575	1	2.575	31.53	0.001
Time	2.718	6	0.453	5.55	0.001
Two-way interactions					
Urchin-time	0.825	6	0.137	1.68	0.162
Explained	6.118	13	0.471	5.76	0.001
Residual	2.287	28	0.082		
Total	8.405	41	0.205		
<i>Egrecia</i>					
Main effects	0.341	7	0.049	1.41	0.240
Urchin	0.095	1	0.095	2.76	0.108
Time	0.246	6	0.041	1.89	0.342
Two-way interactions					
Urchin-time	0.251	6	0.042	1.21	0.329
Explained	0.592	13	0.046	1.32	0.260
Residual	0.967	28	0.035		
Total	1.559	41	0.038		

experiment was initiated in August. By the time recruitment of *Egrecia laevigata* began, presumably in early spring (March-April) as in the earlier urchin removal experiments, the tops and sides of the August experimental boulders were 68.3% (SE=11.3) covered with a mixture of *Ulva* spp., filamentous red algal turf, *Laurencia pacifica*, and *Gigartina canaliculata*. This assemblage was similar to that on the small successional plots in the spring of 1976 (Fig. 2). Apparently this cover inhibited the recruitment of *E. laevigata*. The surfaces of the February experimental boulders which received a heavy recruitment of *E. laevigata* had more open space with only 30.1% (SE=6.8) cover of *Ulva* spp. The experiment was not run at the appropriate time to detect the influence of the red algal cover on the recruitment of *Cystoseira osmundacea* which occurs in late fall (Figs. 3 and 4).

White's Point Study

Field Experiments

Despite the short duration of the experiments at this site, a strong effect of urchin grazing on algal community structure similar to that at Ellwood Beach was demonstrated (Fig. 5, Tables 6 and 7). In both the removal and control plots of the August experiments there was a bloom of ephemeral algae including diatoms, blue-green algae, and species of Ectocarpaceae. There was no significant difference in algal composition or abundance between the various types of controls (Table 7). While the ephemerals persisted at fairly high levels in the control plots with urchins, their cover declined in the removal plots being replaced by a mixtures of short-lived green, brown and red algae including *Ulva californica*, *Dictyota flabellata*, and *Gelidium pusillum*. These were in turn replaced by the longer-lived perennial

Table 4. Results of two-factorial experiment in which both sea urchin density and red algal cover were manipulated at Ellwood Beach. Two trials of the experiment, one starting in August, the other in February were run as described in the text. The numbers of brown algae which had recruited to the boulders were counted in May 1977. Brown algae included *Egrecia laevigata* (E), *Macrocystis pyrifera* (M), *Cystoseira osmundacea* (C), and *Desmarestia ligulata* (D)

Start of experiment	Replicate	Urchins absent		Urchin present	
		Red algae present	absent	Red algae present	absent
August 1976	1	0	2E	0	0
	2	1M, 1C	1E, 1M, 1C	0	0
February 1977	1	0	64E, 2M	0	0
	2	1M, 1C	90E, 7D	0	6E

Table 5. Three-way analysis of variance testing for the effects of sea urchin grazing, a cover of red algae and time of manipulation on the recruitment of brown algae to experimental boulders at Ellwood Beach. Raw data are presented in Table 4

Source of variation	Sum of squares	df	Mean square	F	Significance level
Main effects	3.619	3	1.206	19.58	0.001
Urchin	1.271	1	1.271	20.63	0.002
Red algae	1.736	1	1.736	28.17	0.001
Time	0.612	1	0.612	9.94	0.014
Two-way interactions	1.960	3	0.653	10.60	0.004
Urchin-red algae	0.797	1	0.797	12.93	0.007
Urchin-time	0.128	1	0.128	2.07	0.188
Red algae-time	1.035	1	1.035	16.80	0.003
Three-way interactions					
Urchin-red algae-time	0.351	1	0.351	5.70	0.044
Explained	5.930	7	0.847	13.75	0.001
Residual	0.493	8	0.062		
Total	6.423	15	0.428		

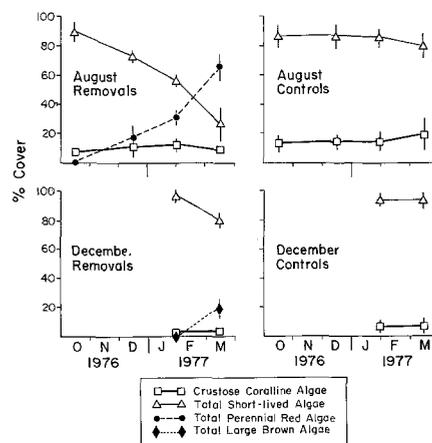


Fig. 5. Patterns of algal succession in the removal and control plots during the sea urchin removal experiments at White's Point. Data from both the August and December 1976 experiments are presented. The mean percent covers of various categories of algae (\pm one standard error of the mean) are indicated. The first data points in each graph are for the first sampling date following the initial clearing and burning of the quadrats

Table 6. Results of urchin manipulations at White's Point. Experiments were initiated in August and December of 1976. March 1977 percent cover values (SE) are listed for the principal algal taxa. Data from the three control treatments are combined due to their similarity (Table 7). Blanks in the mean percent cover data indicate that taxon was absent

Taxa	Urchin removals (N=4)		Controls (N=12)	
	August initiation	December initiation	August initiation	December initiation
Ectocarpaceae/diatoms	9.0 (4.8)	22.9 (5.6)	24.6 (8.8)	19.3 (7.5)
Blue-green algae	14.7 (3.8)	4.0 (4.3)	40.8 (8.9)	29.7 (10.8)
<i>Colpomenia sinuosa</i>	1.4 (1.7)		0.4 (0.7)	
<i>Ulva californica</i>	0.2 (0.5)	48.4 (9.2)	5.7 (5.7)	36.1 (6.2)
<i>Dictyota flabellata</i>	0.4 (0.7)			
<i>Gelidium pusillum</i>		4.8 (3.6)	7.8 (7.5)	8.4 (8.7)
Total short-lived algae	25.7	80.1	79.3	93.5
Crustose coralline algae	9.0 (1.6)	1.2 (2.5)	18.7 (11.0)	5.8 (4.9)
<i>Gigartina canaliculata</i>	45.3 (10.9)		0.5 (0.9)	
<i>Gelidium coulteri</i>	11.3 (7.8)			
<i>Gigartina leptorhynchos</i>	8.7 (1.9)			
Total perennial red algal turf species	65.3	0.0	0.5	0.0
<i>Halidrys dioica</i>	0.1 (0.1)	4.7 (3.0)		
<i>Egrecia laevigata</i>		13.5 (3.9)		
Total large brown algae	0.1	18.2	0.0	0.0

red algae *Gigartina canaliculata*, *Gelidium coulteri*, and *Gigartina leptorhynchos*. *G. canaliculata* had begun to strongly dominate the removal plots by the end of the experiment in March 1977. The brown alga, *Halidrys dioica*, colonized only the removal plots but in very low numbers. While members of the middle successional group including *U. californica* and *G. pusillum* became established on the control plots, they never became very abundant. Of the perennials, only *G. canaliculata* colonized the control plots but attained an average of only 0.5% cover.

The effects of removing urchins in December were significantly different from the effects of removing them in August (Table 7). As in the August experiment, there was an initial bloom of ephemeral diatoms, blue-green algae, and Ectocarpaceae on both the removal and control plots. This assemblage began to be replaced by *Ulva californica* and *Gelidium pusillum* by March 1977 on both. However, in contrast to the August removals, none of the long-lived perennials became established in the December removals (Table 6). All three perennial species have highly seasonal recruitment occurring only between the months of September and December (Sousa 1979). Apparently, the December plots were experimentally cleared after liberation of spores by these species had ceased. In a pattern very similar to that in the two-factorial experiment at Ellwood Beach, significantly greater covers of *Egrecia laevigata* and *Halidrys dioica* occurred in the December removal plots. The cover of long-lived red algae which had developed on the August removal plots by the spring of 1977 appears to have inhibited their recruitment.

Table 7. Summary of results from one-way analyses of variance and Student-Newman-Keuls multiple comparison tests for treatment effects on several groups of algal taxa at White's Point. Treatments include: urchin removals (Rem), unmanipulated controls (Co1), partial fence controls (Co2), and fenced urchin enclosures (Co3). Data analyzed are from the March 1977 monitoring

A. August initiated experiments			
	F	P	Conclusions from Student-Newman-Keuls ($p < 0.05$)
Short-lived algae	21.80	< 0.001	Rem \ll Co1 = Co2 = Co3
Crustose coralline algae	1.32	> 0.25	Rem = Co1 = Co2 = Co3
Perennial red algal turf species	158.53	< 0.001	Rem \gg Co1 = Co2 = Co3
Large brown algae	0.0		Rem = Co1 = Co2 = Co3
B. December initiated experiments			
	F	P	Conclusions from Student-Newman-Keuls ($p < 0.05$)
Short-lived algae	6.77	< 0.01	Rem < Co1 = Co2 = Co3
Crustose coralline algae	2.47	> 0.10	Rem = Co1 = Co2 = Co3
Perennial red algal turf species	0.0		Rem = Co1 = Co2 = Co3
Large brown algae	34.43	< 0.001	Rem \gg Co1 = Co2 = Co3
C. August removal experiments versus December removal experiments			
	F	P	
Perennial red algal turf species	163.10	< 0.001	
Large brown algae	34.02	< 0.005	
D. August controls versus December controls			
	F	P	
Perennial red algal turf species	3.04	> 0.10	
Large brown algae	0.0		

Discussion

The results of our investigations clearly indicate that biological interactions play a significant role in generating and maintaining latitudinal differences in the structures of temperate intertidal communities. While the responses of southern algal assemblages to intensive grazing by sea urchins were similar to those of northern assemblages, unique patterns of interaction among algae in the south resulted in quite different patterns of succession and community structure in the absence of urchin grazing.

In both the Pacific Northwest (Paine and Vadas 1969; Dayton 1975; Paine 1977) and in southern California (Ebert 1977; this study) dense populations of sea urchins can dramatically alter the standing crop, species composition and structure of an intertidal algal community. In both areas, intensive grazing by urchins produces either an assemblage dominated by crustose

coralline algae or a more mixed assemblage of diatoms and small ephemeral blue-green, green, red and brown algal species. The species of the former assemblage appear to be well defended against grazing by their calcareous encrusting morphology. The species of the latter assemblage persist under intense grazing pressure by virtue of some combination of wide dispersal, reduced reproductive seasonality, and rapid growth (Littler and Littler 1980). Grazing by sea urchins clearly reduces the abundance of large brown algae in both the north and the south.

A comment is warranted concerning our study of sea urchin food preferences. In laboratory trials urchins ate very little of the perennial red algae or of the brown alga *Cystosiera osmundacea*; however, these algal species showed large increases in abundance when urchin densities were experimentally reduced in the field. There are at least two explanations of this discrepancy. It is possible that spine abrasion alone, especially when sea urchin populations are dense, causes a reduction in the cover of even those species which are not readily fed upon. A more likely explanation is that urchins feed on *C. osmundacea* and red algal sporelings but not on invulnerable adult plants used in the preference experiment. Preferences of grazers for juveniles stages may differ from those for adult plants and are indeed more relevant to questions concerning the effects of grazers on algal recruitment. The results obtained in our study caution against predictions concerning the effects of grazers on plant populations based exclusively on the laboratory techniques used without experimental field corroboration.

It is the patterns of succession following the appearance of newly cleared space which differ markedly in the south from those reported from northern studies. The experimental removal of urchins or their displacement by predatory starfish from tide-pools on the outer coast of Washington State results in rapid colonization by a rich flora, large fleshy brown algae forming the canopy and a mixture of red and green algae occupying the understory. In about 20 months following the removal of urchins, the canopy layer of shallow exposed outer coast pools is strongly dominated by the brown alga *Hedophyllum sessile* (Paine and Vadas 1969; Paine 1977). In deeper pools more protected from wave action, the diversity of the brown algal canopy remains high for at least 5 years during which time weak dominance by *Egregia menziesii* and *Laminaria setchellii* develops (Dayton 1975). Succession on cleared emergent substrata where urchins are naturally absent also results in dominance of the canopy by brown algae, the dominant species changing with the degree of exposure to wave action as mentioned earlier (Dayton 1975; Paine 1977).

Successional patterns following the removal of sea urchins in southern California are very different from those just described. In both the Ellwood Beach and White's Point studies, urchin removal plots were initially colonized by a diverse assemblage of algae including large brown algae but were eventually dominated by a turf of perennial red algae. Large brown algae are commonest in the middle of the successional sequence, disappearing locally as red algae dominate the space. Similar patterns have been observed in studies of intertidal algal succession on the Santa Barbara Channel Islands (Murray and Littler 1978; Littler and Littler 1980).

The results of the two-factorial experiment at Ellwood Beach and of the urchin removal of White's Point suggest that large brown algae do not form a persistent canopy in the low intertidal zone of southern California in the absence of urchin grazing because of interactions with the red algal turf. The experimental removal of urchins enhanced the recruitment of brown algae, especially of *Egregia laevigata*, but this effect was highly depen-

dent on the timing of the manipulation. If the removal occurs just prior to the recruitment season of the brown algae and after the settlement period for red algae, a dense cover of brown algae results. However, if urchins are removed well before the season of brown algal settlement there is sufficient time for perennial red algae to preempt the space. The experimental removal of the cover of red algae demonstrated that it inhibits the recruitment of brown algae, eliminating or very much reducing any difference in brown algal density in areas with and without urchins. Murray and Littler (1978) also observed much greater recruitment of *E. laevigata* to experimental clearings in the red algal turf than to control plots with red algae on San Clemente Island off southern California. The surf grass, *Phyllospadix torreyi*, which forms extensive beds by rhizomatous growth in sandier areas of the Ellwood Beach site has also been shown to inhibit the recruitment of *E. laevigata* (Black 1974). The mechanism by which the red algal turf interferes with the recruitment of brown algae is not known. It may be that low light levels below the turf prevent the germination of brown algal spores or that little space is available for spore attachment. The turf often accumulates a layer of anoxic sediment (W.P. Sousa and S.D. Gaines, personal observations) which may preclude the invasion and growth of other algal species.

Storms and seasonal defoliation of perennial red algae create space for colonization in the low intertidal zone of southern California in the winter and spring months (Sousa 1979). This is also the period when large brown algae recruit (Black 1974, this study) so it seems rather paradoxical that they are not more abundant. This apparent paradox is resolved with some knowledge of the mechanisms by which the dominant species of the red algal turf secure available space. While their recruitment from spores is highly seasonal, continuous vegetative encroachment of adult plants into cleared space is characteristic of all three low intertidal species common at our study sites: *Gigartina canaliculata*, *Laurencia pacifica*, and *Gastroclonium coulteri* (Sousa 1979 and personal observation). Prostrate axes grow out across the rock surface attaching at their distal ends. New plants grow up at these points of attachment filling open space. Vegetative propagation is common in many Rhodophyta (Dixon 1965; Neushul and Dahl 1967; Stewart 1968) though its ecological significance has barely been examined (Foster 1972; Hay 1978, 1980; Sousa 1979; Brawley and Adey 1980; Lubchenco 1980).

Cleared space is gradually filled by lateral encroachment of the surrounding red algal turf which, once established, inhibits the recruitment of all other species. Experimental 100 cm² clearings in beds of *Gigartina canaliculata* were completely closed almost exclusively by the vegetative growth of surrounding plants in two years' time (Sousa 1979). This ability of the red algal turf to continuously secure open space relegates large brown algae which do not proliferate vegetatively but only recruit from the highly seasonal germination of spores, to the status of fugitive species (Hutchinson 1951). The rate at which space is preempted by red algae combined with the fact that individual *Egregia laevigata* plants only live from 8 to 15 months (Black 1974) prevents the development of a dense persistent canopy of brown algae. Brown algae in the low intertidal of southern California colonize and grow to maturity in disturbance-generated openings in the red algal turf but adult plants are usually unable to replace themselves locally apparently because disturbances are neither frequent enough nor intense enough to generate the space required to ensure the persistence of local populations. The red algal turf is very resistant to and recovers rapidly from damage caused by abrasion, sand burial or urchin grazing (Sousa 1980). In fact, Thom and Widdowson (1978) have suggested that in-

creased disturbance in recent years along the coast of southern California has actually enhanced the development of the intertidal red algal turf community. Probably only rarely and unpredictably do large amounts of space become available for brown algal recruitment.

This pattern of interaction between species which fill space vegetatively and those which do not, is often important to the structure of intertidal algal communities. The annual brown alga, *Postelsia palmaeformis*, occurs in dense stands within patches in mussel beds on the exposed outer coast from central California to British Columbia (Dayton 1973; Abbott and Hollenberg 1976). In the absence of an appropriate regime of space-clearing disturbance, populations of *P. palmaeformis* within these patches often go extinct. Their disappearance is caused by the continuous encroachment of articulated coralline algae and of adult mussels from surrounding beds which preempt space, preventing local recruitment (Paine 1979). Lubchenco (1980) found that the vegetative encroachment of crusts of the red alga *Chondrus crispus* into open areas beneath an established canopy of *Fucus* spp. prevents local recruitment of new plants. In $2^{1/2}$ –3 years after individual plants of the *Fucus* canopy have been removed by wave action and erect blades have perennated from the crusts, a dense stand of *C. crispus* monopolizes most of the space. Sousa (1979) has shown that *Gigartina canaliculata* vegetatively preempts space created by the loss of early and middle successional species of green and red algae to grazing, desiccation, epiphytic overgrowth and strong wave action. The cover of *G. canaliculata* then inhibits their reestablishment.

Interactions of algae which proliferate vegetatively with those which have a discrete holdfast and secure space only by the dispersal of spores are quite similar to interactions which occur between colonial and solitary marine invertebrates (Jackson 1977; Woodin and Jackson 1979). In the latter, colonial organisms often dominate particularly in subtidal tropical habitats. They do so either directly by overgrowing solitary species (e.g. encrusting bryozoans overgrow barnacles and spirorbid polychaetes, Stebbing 1973; Osman 1977; Sutherland and Karlson 1977; Bernstein and Jung 1979) or indirectly, as in the algal interactions described above, by preempting space made vacant by the deaths of individuals of the solitary species from causes extraneous to the interaction (e.g. attacks by natural enemies, removal by physical disturbances, etc.). This latter pattern is exemplified by the colonial hydroid *Hydractinia echinata* which vegetatively secures space cleared of solitary species by foraging urchins (Karlson 1978). In this invertebrate example as in the algal examples above, adult-adult competitive interactions appeared to be relatively unimportant to the development of dominance by the asexually proliferating species.

If a colonial invertebrate dominates the space whether by direct interaction or indirectly by preempting it, the colony often prevents the recruitment of solitary species by inhibiting the settlement of their larvae (Sutherland 1974 and 1978; Sutherland and Karlson 1977). This adult-larval interaction (Woodin 1976) has the same effect as adult-spore interactions in marine algal communities (Sousa 1979; Lubchenco 1980). Dominance by a colonial or vegetatively reproducing species will last only as long as that species effectively inhibits invasion. In some cases, inhibition is temporary and the period of dominance is brief. Colonies of the encrusting bryozoan, *Schizoporella errata*, can prevent the recruitment of larvae of a number of invertebrates including those of the solitary tunicate, *Styela plicata*, for only a maximum of 2 years after which they are invaded and cease to dominate (Sutherland 1978). In contrast, clones of intertidal red algae in southern California are very resistant to both damage

and invasion (Sousa 1979 and 1980) and their dominance of the low intertidal zone appears to be very persistent (Thom and Widdowson 1978).

The importance of vegetative or asexual proliferation in structuring communities is not a peculiarity of marine systems. Many forms of clonal growth are exhibited by terrestrial plants (Salisbury 1942; Harper 1977). In an interaction analogous to those just described in marine systems, clones of pastureland shrubs preempt space made available by disturbances. These shrub thickets then inhibit the reoccupation of the site by trees for many years (Niering and Egler 1955; Niering and Goodwin 1974).

There are undoubtedly numerous reasons for the predominance of large brown algae in the low intertidal at north temperate latitudes and of red algae in the south. While differences in the physical environment may ultimately determine the species composition of the flora in different geographical regions of the temperate Pacific coast of North America, current evidence is largely correlative (Abbott and North 1972; Thom 1980) though sometimes supplemented with laboratory experiments (Young 1971). A definitive field demonstration with a transplant experiment would be welcome but satisfactory controls would be difficult to establish (Connell 1974). The results of this study and of experimental investigations in the Pacific Northwest clearly show, however, that the proximate mechanisms generating differences in low intertidal algal community structure with latitude involve biological interactions among species which differ in their life histories. The ability to grow vegetatively into cleared areas, exhibited by the three species of perennial red algae which dominated our experimental plots has not been reported for any of the long-lived red algae common in Dayton's (1975) northern study areas. A common northern species, *Gigartina papillata*, can perennate rapidly from surviving portions of its holdfast if defoliated; however, it does not undergo the rhizoid-like spreading of its southern congener, *Gigartina canaliculata* (Dayton 1975; W.P. Sousa, personal observation). Undoubtedly, some red algal species common in northern areas are capable of this type of growth (e.g. *Hymenena multiloba* forms vegetatively spreading turfs in local areas on the exposed coast of northern California (Abbott and Hollenberg 1976; W.P. Sousa, personal observation)); however, it does not seem as common a growth pattern as in southern California. At present, there is too little published information on the patterns of algal growth in the field to definitively demonstrate a latitudinal trend in the frequency of species which propagate vegetatively as Jackson (1977) has suggested for colonial invertebrates. The predominance of red algal turf assemblages in many shallow water tropical habitats (Dahl 1972; Connor and Adey 1977), particularly where urchin grazing is reduced by wave surge, certainly suggests that the trend is real. Many species in tropical turf communities have a stoloniferous growth habit which serves both as a means of rapidly occupying space without sexual reproduction and as a means of persisting under intense grazing pressure by fishes and small crustaceans (Foster 1972; John and Pople 1973; Hay 1978, 1980; Brawley and Adey 1980). Algae with a vegetatively spreading crustose morphology are also relatively more abundant in tropical shallow water habitats than on temperate rocky shores (J. Lubchenco, S.D. Gaines and B. Menge, personal communication).

More speculative is the possibility that the differences in the structures of northern and southern algal communities result from different regimes of disturbance in the two areas. If biological and/or physical disturbances which reduce grazing pressure on populations of brown algae or which clear space for their

recruitment are more frequent in the north, an extensive canopy of brown algae could be maintained. As discussed above, the development of the canopy would be relatively unimpeded by vegetatively proliferating red algae. Evidence supporting this idea is circumstantial but suggestive. Predators on sea urchins particularly the starfish, *Pycnopodia helianthoides* (Ricketts and Calvin 1968), and the sea anemone, *Anthopleura xanthogrammica* (Sebens 1977; Francis 1979), are more common in the Pacific Northwest than in our southern study areas. On the outer coast of Washington State, the synergistic effect of *Pycnopodia* and *Anthopleura* predation clears areas of urchins and initiates algal succession (Dayton 1973a, 1975). The reoccupation of these cleared patches by urchins may be relatively slower in the north than in the south because recruitment of *Strongylocentrotus purpuratus* from the plankton is more irregular in the north (Gonor 1973; T. Ebert, pers. comm.). Some forms of physical disturbance (e.g. battering by drifting logs, Dayton 1971) which clear space for colonization in the intertidal of the Pacific Northwest do not occur in the south. Lubchenco (1980) has suggested that a similar latitudinal gradient in the frequency with which space is cleared by ice scouring and limpet grazing along temperate Atlantic shores accounts for the predominance of furoid algae in the low intertidal of Canada and Scotland and of the red alga, *Chondrus crispus*, at the same tidal height in New England.

Finally, our study has some bearing on the question of the causes of intertidal zonation. Our results are somewhat at odds with the generalization that the upper distributional limits of organisms on the seashore are set by physical factors (Connell 1972; Schonbeck and Norton 1978; Lubchenco 1980). While the ultimate upper limit to the distribution of brown algae in the intertidal of southern California may be set by physical factors such as desiccation, the proximate limit is attributable to biological interactions including sea urchin grazing and interactions with red algae. The density of reproductively competent brown algae at the upper limit of their vertical distribution was greatly increased when urchin density and red algal cover were reduced. At Ellwood Beach, *Egregia laevigata* is common on shale reefs at the same tidal height as the boulder fields in which this study was conducted. On this substratum, where urchins are absent and the cover of sessile species low, neither interfere with brown algal recruitment (Black 1974; W.P. Sousa and S.C. Schroeter, personal observation).

The influence of vegetatively propagating species on the successional dynamics and zonation of southern California algal communities is clearly demonstrated by our study. Further investigation of the ecological roles of vegetatively reproducing marine plants in different geographical locations will test our speculations concerning the importance of this form of growth to latitudinal gradients in intertidal algal community structure.

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