Expansion of a Central California Kelp Forest Following the Mass Mortality of Sea Urchins

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Abstract

The mass mortality by disease of a localized population of sea urchins, *Strongylocentrotus franciscanus*, on the seaward side of a kelp forest was followed by the rapid seaward expansion of 4 species of brown algae, *Macrocystis pyrifera*, *Laminaria dentigera*, *Pterygophora californica*, and to a lesser extent, *Nereocystis leutkeana*. One other brown alga, *Cystoseira osmundacea*, failed to become established in the newly available area. Competition among *M. pyrifera*, *L. dentigera*, *P. californica*, and *N. leutkeana* apparently was severe, and within 1 year after the demise of the sea urchins, *M. pyrifera* formed a dense, nearly monospecific stand. Experimental removal of *M. pyrifera* demonstrated that the canopy of these plants limited light penetration to levels below that necessary for the growth and survival of other brown and red algae.

Introduction

The influence of grazing sea urchins on the distribution and diversity of marine algae has been well studied (see excellent review by Lawrence, 1975). Sea urchins can alter nearshore community structure profoundly by limiting the abundance of algal species they prefer for food (e.g., Kitching and Ebling, 1961; Leighton, 1966; Paine and Vadas, 1969; Vadas, 1977) or, under some conditions, by grazing nearly all algae suitable as food (e.g., Leighton, 1971; Breen and Mann, 1976a, b). Along the subtidal coast of California, high densities of sea urchins of the genus *Strongylocentrotus* have been associated with low or declining crops of algae, especially of the giant kelp *Macrocystis pyrifera* (Leighton *et al.*, 1966; Pearse *et al.*, 1970; North, 1971, 1974; Mattison *et al.*, 1977). Treatment of such areas in southern California with quicklime (CaO) destroys most of the sea urchins and is often followed by the development of dense stands of giant kelp (reviewed by North, 1974).

In 1976 a dense population of red sea urchins, *Strongylocentrotus franciscanus*, on the seaward edge of a giant kelp forest off Santa Cruz, California, was decimated by disease (Pearse *et al.*, 1977). We had been quantitatively following population changes of the major algae and invertebrate animals in the forest for the previous 2 years, and we therefore had the opportunity to document the changes that followed the rapid demise of the sea urchins. These changes provide insights into the interactions of several major algal species in the kelp forest, the role of biological factors limiting their distribution and abundance, and the process of succession of the algae.

Materials and Methods

The study area, situated on the eastern side of Point Santa Cruz in northern Monterey Bay, California ($36°57"N$; $122°03"W$), was described by Mattison *et al.* (1977). Before 1976, the kelp forest extended nearly parallel to the shoreline (see Fig. 3), with a depth range between about 3 and 7 m. It consisted mainly of canopy-forming giant kelp plants, *Macrocystis pyrifera* (Linnaeus) C.A. Agardh; two species of understory kelps, *Laminaria dentigera* Kjellman and *Pterygophora californica* Ruprecht; and a luxuriant ground cover of foliose red algae. Along the seaward border of the forest was a band of the understory brown alga *Cystoseira osmundacea* (Menzies) C.A. Agardh and a small stand of the canopy-forming bull kelp *Nereocystis leutkeana* (Mertens) Pas-

tels and Ruprecht. A large population of red sea urchins, *Strongylocentrotus franciscanus* (Agassiz), was along the border of the forest and extended to over 100 m seaward; few algae grew seaward of the forest and the appearance of the gently sloping soft shale bottom was generally barren with a low cover of encrusting coralline algae, small filamentous red algae, bryozoans, ascidians, hydroids, and scattered clumps of the brown alga *Desmarestia ligulata* var. *ligulata* (Lightfoot) Lamouroux.

Qualitative and quantitative SCUBA surveys of the area in the summers of 1971-1974 provided the general description given above, and little change was noted during that time. Aerial photographs in 1972-1974 showed a general constancy of the extent of the kelp canopy, especially with respect to its seaward border (see Fig. 3). Four permanently marked study stations, each 625 m^2 in area, were established in June, 1974. The center of Station 1 was 50 m within the seaward border of the forest at a depth of 4 m, that of Station 2 was at the border at a depth of 6 m, and those of Stations 3 and 4 were 50 and 100 m seaward of the border and at depths of 8 and 9 m, respectively (see Fig. 3).

The densities of the large brown algae and invertebrates within each station were estimated from counts in 10 to 12 randomly located 10 m^2 circular plots. Fronds of giant kelp plants extending more than 1 m above the bottom were counted for each plant in each plot. From 1974 through 1977, density estimates were made at most stations twice each year, in June after the winter storms and in September after the summer period favoring canopy development. Stormy weather interfered with effective work in the winter; however, estimates were made at some stations in December or January of 1975, 1976 and 1977.

Estimates of the biomass of the ground-cover algae, mainly foliose red algae and juvenile brown algae, were made in 1976 and 1977 by plucking all plants from within 0.25 m^2 quadrats placed at the center of each 10 m^2 circular plot. The algae were sorted and weighed wet in the laboratory.

A 10 x 20 m portion of Station 3 was cleared of all giant kelp sporophytes in June, 1977, by prying loose the plants within the delineated area. The dislodged plants floated to the surface and drifted out of the forest, leaving a conspicuous opening in the canopy which was not covered by fronds from adjacent giant kelp plants. An adjacent 10 x 20 m uncleared portion in Station 3 served for comparison with the cleared portion.

Results

Few *Strongylocentrotus franciscanus* were ever found at Station 1 inside the kelp forest (Fig. 1). High mean densities of sea urchins (50 to 60 per 10 m^2) occurred along the seaward border of the forest at Station 2 in 1974 and 1975. The population extended seaward of the kelp forest, with mean densities of 20 to 30 sea urchins per 10 m^2 at Stations 3 and 4. After the mass mortality of the sea urchins in early 1976, there were almost no sea urchins at Stations 3 and 4, and their numbers within Station 2 were reduced by about half. The sea urchins were nearly absent from Station 2 in 1977, and the decrease between 1976 and 1977 apparently resulted from predation by sea otters. Few sea otters were seen in 1974, 1975, and 1976, and those few were usually seen during the winter and spring. In the spring of 1977, when the northern edge of the expanding range of sea otters reached within 5 km of Point Santa Cruz (personal observation), as many as 11 "advance" sea otters were seen in the study area. Many of the sea otters at Point Santa Cruz in the spring of 1977 were feeding on sea urchins within or near Station 2, and broken sea urchin tests littered the bottom there during the June, 1977, study period.

The mass mortality of sea urchins did not seem to affect the asteroids *Patiria miniata* (Brandt), *Pisaster brevispinus* (Stimpson), *P. giganteus* (Stimpson) and *P. ochraceus* (Brandt). Their densities and distributions remained more or less constant at the 4 stations during the 4 years of the study, showing erratic fluctuations with no apparent pattern.

Densities and sizes of the giant kelp plants at Station 1 remained relatively constant throughout the 4-year study period (Fig. 2). During 1974 and 1975 kelp plant densities at Station 2 were similar to those at Station 1. However, there were about half as many fronds per plant at Station 2, so that the mean number of fronds per unit area was much lower at Station 2 than 1. Almost no giant kelp plants were found at Stations 3 and 4 during 1974 and 1975. After the mass mortality of sea urchins in early 1976, the number of giant kelp plants at Station 2, and especially Stations 3 and 4, increased dramatically to reach peak values in September, 1976. The new plants increased in frond number during the following year, and plant density decreased with the loss of many juvenile plants. By September, 1977, plant density and size, and the number of fronds per unit area were similar at all 4 stations.
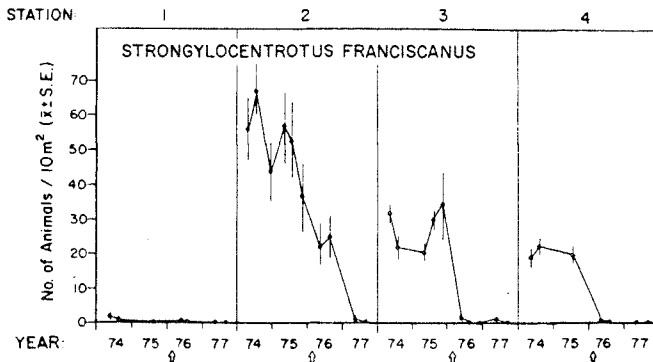
Fig. 1. *Strongylocentrotus franciscanus*. Changes in densities of sea urchins between 1974 and 1977 within the four stations (each 625 m^2) off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins
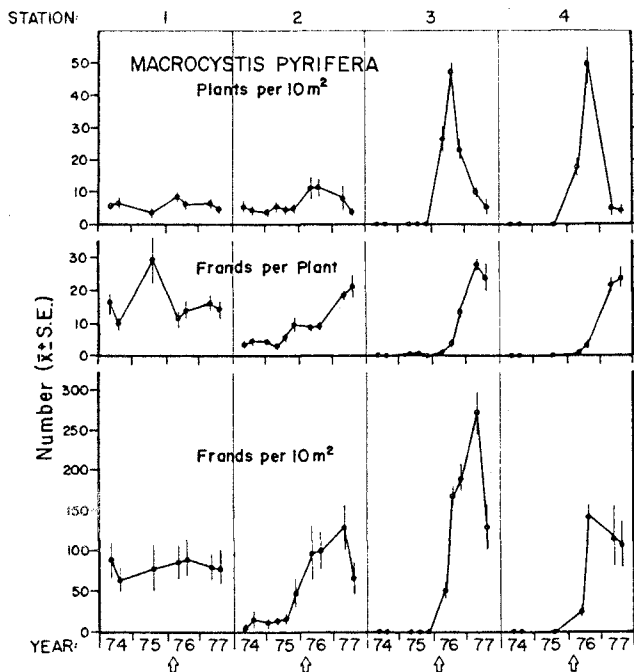

Fig. 2. *Macrocystis pyrifera*. Changes in plant densities, plant sizes, and frond densities of giant kelp between 1974 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

The expansion of the kelp forest following the mass mortality of the sea urchins also can be seen from aerial photographs of the canopy (Fig. 3). These show that the seaward (eastern) border of the canopy was relatively constant from August 1972 to May 1976, and Station 2 was located on this border. Although no "new" canopy had appeared in May, 1976, immediately following the sea

urchin mass mortality, many new giant kelp plants had grown to within a few meters of the surface at Stations 3 and 4. By September, 1976, some of the newly recruited kelp plants had reached the surface to form a canopy immediately south of Stations 3 and 4 and, by June, 1977, both Stations 3 and 4 were completely within the canopy. The "new" canopy in 1977 extended nearly 500 m south of Station 4 and covered an area of over 10 hectares.

Two species of understory kelp plants, *Laminaria dentigera* and *Pterygophora californica*, responded rapidly to the decreased grazing pressure following the mass mortality of the sea urchins (Fig. 4). The understory laminarians fluctuated erratically but at relatively high densities at Stations 1 and 2 throughout the 4-year study period, while they were nearly absent within Stations 3 and 4 during 1974 and 1975. Following the demise of the sea urchins in 1976, there was a large recruitment of these two species at Stations 3 and 4, resulting in mean densities of over 100 plants per 10 m^2 by September, 1976. However, in 1977 numerous dead and bladeless stipes of *L. dentigera* and *P. californica* were conspicuous at Stations 3 and 4, and nearly no live plants were found.

The population of *Nereocystis leutkeana*, an annual species, fluctuated annually in 1974, 1975 and 1976 at Station 2, and to a lesser extent at Station 1 (Fig. 5). Low recruitment was also recorded within Station 3 in 1976 following the die-off of sea urchins. However, almost no recruitment was found within any station in 1977.

The perennial brown alga *Cystoseira osmundacea* did not show an expanded distribution in response to the decimation of the sea urchin population (Fig. 5). Before the mass mortality of the sea urchins, the population of this species formed a band along the seaward border of the kelp forest. After 1976, when the border of the forest extended seaward, the band of *C. osmundacea* was nearly in the middle of the forest, and this plant remained scarce or absent from Stations 3 and 4.

Biomass of the ground-cover red algae was measured only in 1976 and 1977, after the mass mortality of the sea urchins (Fig. 6). The main species of foliose and filamentous red algae in these samples included: *Prionitis lanceolata* (Harv.) Harv., *Callophyllis pinnata* Setch. and Swezy, *Rhodymenia pacifica* Kyl., *Phycodrys setchellii* Skottsb., *Polyneura latissima* (Harv.) Kyl., *Hymenena setchellii* Gardn., *Botryoglossum farlowianum* (J. Ag.) DeToni, and *Polysiphonia pacifica* Hollenb. Between
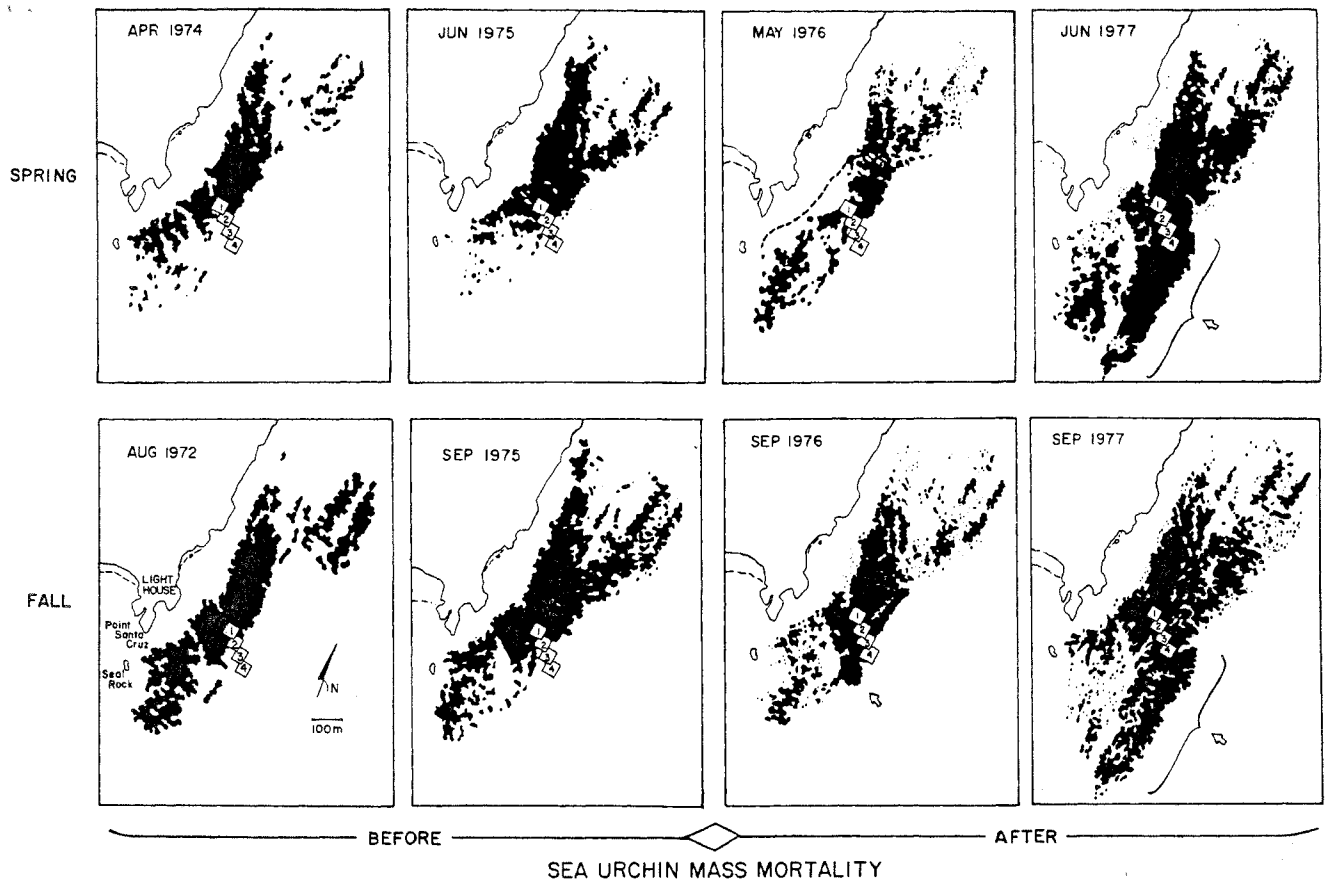
Fig. 3. Changes in extent of canopy of giant kelp plants between August, 1972, and September, 1977, off Point Santa Cruz, California, before and after mass mortality of sea urchins; traced from aerial infrared photographs. Numbers in the boxes indicate positions and sizes of the four 625 m^2 stations established in June, 1974. Arrows indicate major portion of the expanded kelp forest following mass mortality of sea urchins in spring of 1976
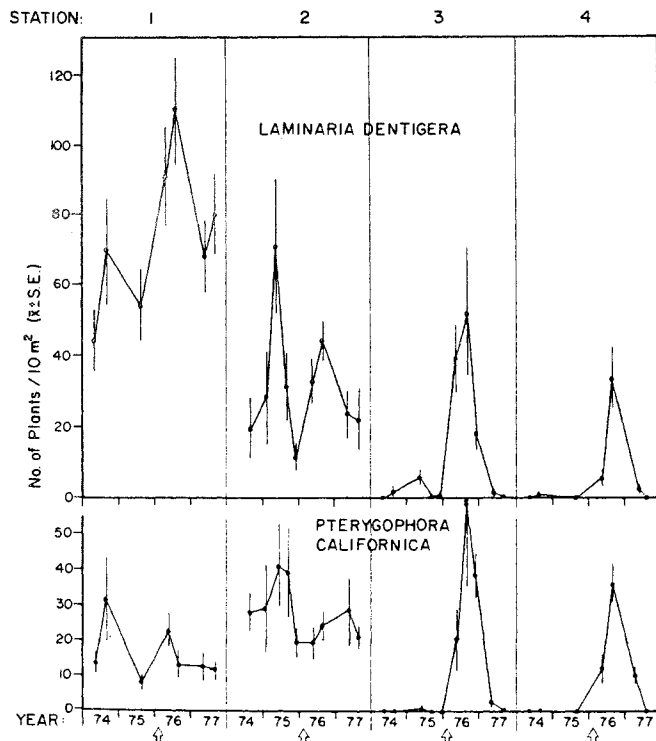

Fig. 4. *Laminaria dentigera* and *Pterygophora californica*. Changes in densities of understory laminarians between 1974 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins
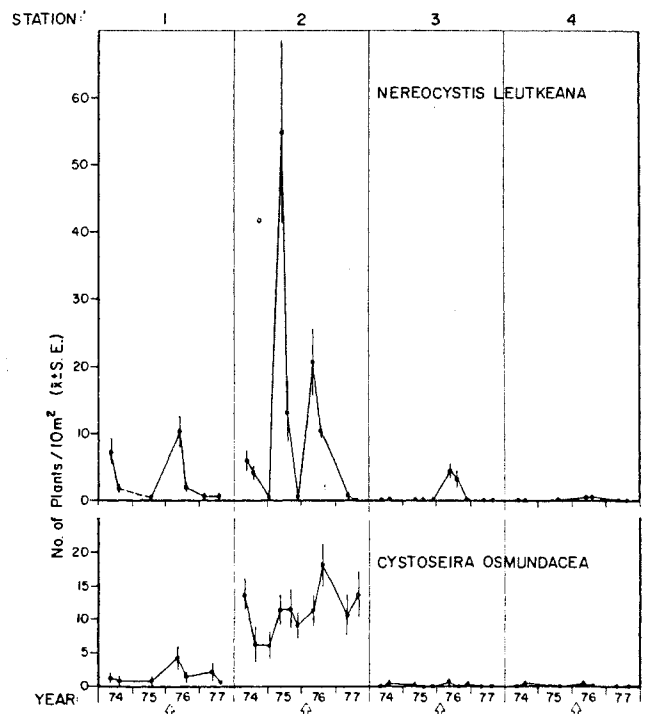

Fig. 5. *Nereocystis leutkeana* and *Cystoseira osmundacea*. Changes in densities between 1974 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins
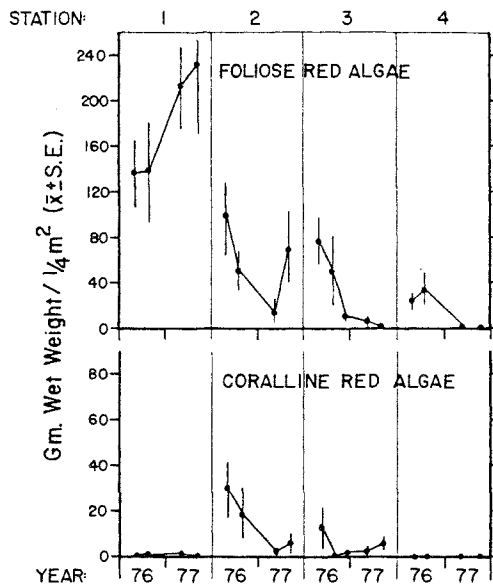
Fig. 6. Changes in biomass of foliose red algae and coralline red algae between 1976 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Mass mortality of sea urchins occurred before sampling began

June, 1976, and June, 1977, the biomass of foliose red algae decreased significantly at Stations 2, 3 and 4 (ANOVA, P <0.05 for Station 2, and P <0.005 at Stations 3 and 4). However, by September, 1977, at Station 2 the foliose red algae increased significantly above the June, 1977, level to a biomass not different from the 1976 levels. The biomass of foliose red algae at Station 1 in 1976 and 1977 are not significantly different (ANOVA, P <0.2). The apparent decreases in the mean biomass of upright coralline red algae, mainly *Calliarthron* sp., at Stations 2 and 3 from 1976 to 1977 were not significant (ANOVA, P <0.2).

The decrease of the understory brown algae *Laminaria dentigera* and *Pterygophora californica* and of the ground-cover foliose red algae between 1976 and 1977 at Stations 3 and 4 corresponded to the period of full development of the giant kelp canopy (see Figs. 2 and 3). This correspondence suggests that reduced light penetration of the giant kelp canopy in late 1976 limited the understory and ground-cover algae. The continuously greater biomass of foliose red algae at Station 1 and the increase in biomass of these algae at Station 2 in September, 1977, coincident with the decrease in giant kelp (Fig. 2), would be consistent with greater light penetration at these shallower stations.

To test the hypothesis that insufficient light penetration of the giant

kelp canopy limited the understory and ground-cover algae, we removed all the giant kelp plants from a 10 x 20 m plot within Station 3 on 22 June 1977, leaving a 10 x 20 m adjacent portion of Station 3 uncleared for comparison. Light measurements taken on 7 July 1977 with a LiCor model Ll-185 quantum radiometer/photometer equipped with an underwater sensor gave values of 1700 μE m^{-2} sec^{-1} on the surface at Station 3, 3 μE m^{-2} sec^{-1} on the bottom under the canopy, and 65 μE m^{-2} sec^{-1} on the bottom in the area where the giant kelp plants had been removed. These measurements show that only about 0.2% of the light on the surface reached the bottom under the canopy, while about 3.8% of the surface light reached the bottom in the absence of the canopy; thus, the canopy reduced the amount of light reaching the bottom by about 96%.

At the start of the experiment, the portion of Station 3 which was cleared of giant kelp plants was not significantly different from the adjacent uncleared plot (Table 1). However, on 12-13 September, 1977, nearly 3 months after the giant kelp plants were removed, there were significantly more juvenile individuals with 2 fronds and greater juvenile biomass of *Macrocystis pyrifera* in the cleared plot than in the uncleared plot. Moreover, there were significantly more individuals of *Laminaria dentigera*, *Pterygophora californica*, and unidentified juvenile laminarians (single-bladed sporelings without easily recognizable field characters), as well as significantly larger wet weights of foliose red algae within the cleared plot than within the uncleared plot. The increased densities of *L. dentigera* and *P. californica* resulted from sporelings recruited during the experimental period, not from regeneration of older, bladeless stipes. These experimental data indicate that shading by the giant kelp canopy inhibited the development of both understory and ground-cover algae, and such shading may have accounted for the general decreases of these plants seen at Stations 3 and 4 between 1976 and 1977.

In June, 1977, we surveyed the bottom along the new seaward border of the kelp forest. The bottom along the border northeast of Station 4 was marked by an abrupt transition from shale to sand, and in this region, at least, as well as in sand-filled areas of the forest where the kelp canopy was consistently absent (e.g. ca. 100 m southwest of Stations 2 and 3; see Fig. 3), the borders of the kelp forest were probably determined by the availability of suitable rocky substrates. However, the nearly straight

Table 1. Comparisons of algal density and biomass in two adjacent 200 m² plots at Station 3. Comparisons made before (June 22, 1977) and 3 months after (September 12, 1977) clearing all giant kelp sporophytes from one of the plots. The two plots are compared on each date by Student's t-tests assuming unequal variances. Numbers give mean and 1 standard error of mean; * = P <0.05; ** = P <0.01

Algae	Density (no. 10 m⁻²)				Biomass (g wet weight 0.25 m⁻²)			
	22 June		12 September		22 June		12 September	
	Not cleared (n=6)	Cleared (n=6)	Not cleared (n=12)	Cleared (n=12)	Not cleared (n=6)	Cleared (n=6)	Not cleared (n=12)	Cleared (n=12)
Macrocystis pyrifera								
Plants with >2 fronds	10.3±0.6[a]	9.5±1.1[b]	5.6±1.2[c]	0**	–	–	–	–
Plants with 2 fronds	0.2±0.02	0.2±0.02	0.1±0.01	1.5±1.1**	0	0	0.3±0.3	4.5±1.8*
Unidentified juvenile laminarians	0	0	0	149.7±23.4**	0	0	0	6.1±3.5
Laminaria dentigera	0.7±0.5	0	0.6±0.4	4.3±1.0**	0	0	0	0.7±0.5
Pterygophora californica	1.8±1.1	0.7±0.7	0.7±0.5	4.2±1.5*	0	0	0.3±0.3	1.3±0.7
Cystoseira osmundacea	0	0	0	0.3±0.1	0	0	0	0.2±0.2
Desmarestia ligulata	–	–	–	–	0	0	0	4.4±2.5
Foliose red algae	–	–	–	–	6.0±5.3	0.9±0.8	0.8±0.6	21.9±5.8**
Upright coralline algae	–	–	–	–	3.2±2.3	4.7±4.8	5.1±2.9	0.1±0.04

[a]Mean plant size = 27.6 fronds/plant.
[b]Mean plant size = 27.3 fronds/plant.
[c]Mean plant size = 23.4 fronds/plant.

border southeast of Station 4 consisted of a gently sloping soft shale bottom at about 10 m depth with no obvious discontinuity, and apparently suitable shale substrate between 10 and 12 m depth extended at least 100 m seaward of the newly established border. No sea urchins were seen along or beyond the border, and the main cover included sparse clumps of filamentous and foliose red algae, hydroids, and ascidians.

Discussion

Regulation of algal distributions and densities by grazing sea urchins has been suggested in several studies recently reviewed by Lawrence (1975). Many such studies describe sea urchin-dominated areas that appear barren of algae, and when the grazing sea urchins were removed, large populations of algae often appeared (e.g. Kitching and Ebling, 1961; Kain and Jones, 1966; Jones and Kain, 1967; Paine and Vadas, 1969; Breen and Mann, 1976a, b; Foreman, 1977; Vadas, 1977). Moreover, Jones and Kain (1967) and Dayton (1975) provide evidence that the lower portions of subtidal populations of *Laminaria* spp. are limited by sea urchin grazing off Great Britain and Alaska, respectively. We found that when the grazing pressure of sea urchins (*Strongylocentrotus franciscanus*) was eliminated along the seaward border of a central California kelp forest, at least 4 species of brown algae, *Macrocystis pyrifera*, *Laminaria dentigera*, *Pterygophora californica* and, to a lesser extent, *Nereocystis leutkeana*, rapidly expanded the seaward (lower) portions of their distribu-

tions. The dense populations of sea urchins along the seaward borders of other kelp forests on the Santa Cruz County coast showed little evidence of diseases in 1976 nor of recently extended kelp populations (Yellin *et al.*, 1977), indicating that the expanded kelp forest at Point Santa Cruz was not a function of a broader regional phenomenon.

Before the mass mortality, the sea urchins were most numerous at Station 2 on the border of the kelp forest, where they were about twice as dense as at Stations 3 and 4, 50 and 100 m seaward of the border (see Fig. 1). However, almost no brown algae were found at that time at Stations 3 and 4 while nearly as many were found at Station 2 as at Station 1 in the kelp forest where there were very few sea urchins. Mattison *et al.* (1977) found that the sea urchins along the seaward border of the kelp forest were nearly stationary and fed mainly on pieces of algal litter supplied by the adjacent kelp forest, while those to seaward moved around apparently in search of food. The foraging sea urchins seaward of the forest border probably continually cropped new sporophytes, while such plants along the border could grow among the nearly stationary sea urchins despite the high densities of the latter. This observation indicates that it is not simply the density of the sea urchins which determines whether algae will be severely overgrazed, as suggested by Leighton *et al.* (1966), but that the availability of algal litter for food is also important.

Leighton (1966) showed that *Strongylocentrotus franciscanus* preferred *Macrocystis pyrifera* as food over other algal species

tested, including *Laminaria farlowii*, *Pterygophora californica* and *Cystoseira osmundacea*; these latter species were not eaten until all available *M. pyrifera* was consumed. This finding is consistent with our observations that only *M. pyrifera* was adversely affected by the high sea urchin densities at Station 2, where these plants had fewer fronds than either those at Station 1 or those at Station 2 after the demise of the sea urchins. Sea urchins were not seen climbing up *M. pyrifera*, but probably caught fronds knocked down by surge. *L. dentigera* and *P. californica* were limited by grazing sea urchins only at Stations 3 and 4, where *M. pyrifera* was absent.

Anderson and North (1966) showed that despite the high rates of spore production by *Macrocystis pyrifera*, the dilution of the spores released by single plants is very great and new sporophytes are likely to develop only a few meters from parent plants. However, they found that a dense stand of giant kelp plants in southern California provided enough spores for heavy recruitment of new plants up to 40 m distant. Our observations at Point Santa Cruz show that *Laminaria dentigera* and *Pterygophora californica*, as well as *M. pyrifera*, also are capable of dispersing well over 100 m from the parent populations within only a few months, assuming dormant gametophytes were not present.

As an annual, *Nereocystis leutkeana* might be expected to be a good colonizer, and it did show a small recruitment at Station 3 after the sea urchin mass mortality. However, in 1977, plants of this species were rare or absent, even at Stations 1 and 2 where they had been present during the previous 5 years. Paine and Vadas (1969) showed that *N. leutkeana* can rapidly colonize new areas, but Foreman (1977) found it required a few years to become established after the removal of sea urchins.

The failure of *Cystoseira osmundacea* to establish seaward of the kelp border following the decimation of sea urchins may in part be a result of the timing of its gamete release in summer (personal observations), but it is not clear what is limiting the distribution of this perennial species.

One year after the seaward expansion of the kelp forest, a limited number of *Macrocystis pyrifera* plants remained and apparently shaded out most understory *Laminaria dentigera* and *Pterygophora californica*, as well as most juvenile *M. pyrifera*. Foliose red algae also were nearly absent from under the dense canopy of *M. pyrifera*, and the initial recruitment of *Nereocystis leutkeana* at Station 3 was gone. The substrate under the canopy received less than 1% of the light at the surface in the summer of 1977, and Neushul (1971) showed that minimal light levels necessary to support positive net photosynthesis of marine algae are about 1% of the light on the water surface. Experimental clearing of the *M. pyrifera* canopy in the present study confirmed that reduced light penetration excluded the other species of algae under the canopy. Sea urchins were absent along the "new" seaward edge of the kelp forest in the summer of 1977, where at 10 m depth, insufficient light might be limiting kelp growth.

A year after the mass mortality of sea urchins, the kelp forest could be divided into a seaward portion lacking understory and ground-cover algae and a landward portion with well-developed stands of *Laminaria dentigera*, *Pterygophora californica* and foliose red algae. *Cystoseira osmundacea*, which previously marked the seaward edge of the forest, separated the two portions. By September, 1977, much of the newly established canopy had deteriorated and the subsequent winter storms further thinned the plants. The increased light on the bottom probably will allow the understory to reestablish, resulting in convergence of the forest structure of the seaward portion with that of the landward area.

The species which becomes the "competitive dominant" in any particular kelp forest appears to depend on specific conditions. Thus, Paine and Vadas (1969) found that in Puget Sound, dense stands of the annual, canopy-forming kelp, *Nereocystis leutkeana*, developed within months after sea urchins had been excluded, but within a year these plants were replaced by *Laminaria* spp. However, in a similar study in another area of Puget Sound, Foreman (1977) found that *N. leutkeana* did not become well-established until 4 to 6 years after sea urchin removal. Kain and Jones (1966) showed that the annual laminarian *Saccorhiza polyshides* rapidly colonized space off Great Britain, but was replaced by *Laminaria hyperborea*. Dayton (1975) showed that when several understory species of *Laminaria* were removed off Alaska, the canopy-forming *Alaria fistulosa* rapidly colonized these areas. In the present study, *Macrocystis pyrifera* rapidly became established as the competitive dominant, and appeared to limit *N. leutkeana* as well as understory laminarians.

The specific conditions which result in the dominance of a particular species may be related to the frequency and intensity of environmental disturbances, and repeated disturbance may maintain

species of early successional stages
(Pickett, 1976; Connell and Slatyer,
1977; Connell, 1978). Thus, Yellin *et al.*
(1977) were able to distinguish two
types of kelp forests along the coast of
Santa Cruz County, California, based on
exposure to waves and the predominant
canopy-forming species: (1) those along
leeward portions of the coast with cano-
pies formed mainly by *Macrocystis pyrifera*,
with very low densities of sea urchins
within them but, as at Point Santa Cruz
before 1976, often with dense popula-
tions of sea urchins along their seaward
borders; and (2) those along the most ex-
posed portions of the coast with cano-
pies formed mainly by *Nereocystis leutkeana*
and with large populations of sea ur-
chins both within and seaward of them.
Intense grazing by sea urchins, such as
along the seaward portion of the *M. pyri-
fera* forests, may result in areas of max-
imum disturbance where no kelp species
are able to establish; combinations of
wave exposure and less sea urchin graz-
ing may result in *N. leutkeana* forests;
and those areas of least disturbance and
few sea urchins may result in *M. pyrifera*
forests.

The role of disease in regulating ma-
rine communities has received little at-
tention. Rasmussen (1977) followed the
marked community changes resulting from
the wasting disease of eelgrass, *Zostera
marina*, in Europe. Although disease is
potentially important in regulating popu-
lations of sponges (Smith, 1941), as
well as oysters, lobsters, and clupeoid
fishes (reviewed by Sinderman, 1970),
these studies have dealt mainly with dra-
matic epidemics and their impacts on the
diseased organisms. Because these spe-
cies have important roles as top carni-
vores (lobsters, see Breen and Mann,
1976b), major community structural and
energetic links (sponges and oysters),
or grazers on plankton (clupeoid fishes),
the effects of such diseases may be im-
portant for their respective communities
as well. The sea urchin disease reported
by Pearse *et al.* (1977) led to the rapid
demise of a local population and, as de-
scribed in this paper, had a marked im-
pact not only on the sea urchins, but on
important species of algae in the com-
munity.

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