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## THE EFFECTS OF CANOPY SHADING ON ALGAL RECRUITMENT AND GROWTH IN A GIANT KELP FOREST<sup>1</sup>

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**Abstract.** The subtidal (10–15 m) assemblage in the relatively sheltered giant kelp forest at Stillwater Cove in Carmel Bay, California, consists of perennial species forming three major vertical layers: a *Macrocystis pyrifera* surface canopy, a dense subsurface canopy of another kelp, *Pterygophora californica*, and an understory of articulated and encrusting coralline algae. The kelp canopies alone or in combination can reduce bottom light to <3% (usually <1%) of surface influx. The effects of light reduction by these vegetation layers on algal recruitment and subsequent growth were determined by removing various combinations of canopies over a 2-yr period, and following subsequent changes relative to appropriate controls. Removing both *M. pyrifera* and *P. californica* canopies resulted in moderate recruitment of these species as well as of the annual brown alga *Desmarestia ligulata* var. *ligulata*. None of these algae recruited into control areas where one or both canopies were left intact. Highest brown and red algal recruitment occurred when both kelp canopies plus understory coralline branches were removed. Removal of the latter alone had no significant effect. The time of year when algal canopies were removed had little effect on the composition of subsequent algal colonization, as the recruitment of noncalcareous species occurred primarily during a short period in the spring. These results indicate that the relatively low levels of both physical and biological disturbance in Stillwater Cove allow the establishment of a few perennial algal species that inhibit their own recruitment, as well as invasion of other species, by shading. This contrasts with nearby kelp forests subjected to greater and more frequent disturbance, and characterized by a diverse assemblage of annual algal species.

**Key words:** central California; community structure; competition; coralline algae; disturbance; giant kelp forest; light; *Macrocystis*; *Pterygophora*; recruitment; shading.

### INTRODUCTION

Numerous investigations have shown that competition for light plays an important role in structuring many terrestrial plant communities (for review see Harper 1977). The vertical structure of submarine giant kelp (*Macrocystis* spp.) communities is in many ways comparable to terrestrial forests (Kuhneman 1970, Neushul 1971, Foster 1975a), and correlative studies suggest shading by giant kelp may affect understory algae just as shading by overstory trees affects understory plants on land (Dawson et al. 1960, Neushul 1965, Foster 1975b). Competition for light may be even more dramatic in kelp forests, as light intensity and quality are altered by both the vegetation and the water.

The structure of a community is dependent upon both the interactions between organisms in the community and the physical nature of the environment. Connell (1975) suggests that competition and biological disturbance are two interactions that provide most of the organization in natural communities. The structural significance of competition for light and/or space on algal populations has been shown in a number of marine communities (Dayton 1975a, Hruby 1976, Sousa 1979a, Hodgson 1980, Lubchenco 1980, Foster 1982a). In most cases where competitive interactions

prevail, the algal assemblage is characterized by high abundances of a few competitively superior species that are frequently long lived and inhibit invasion. Grazing disturbance may be equally important to community structure. Grazers, by regulating algal abundance, may indirectly alter competitive interactions (Paine and Vadas 1969, Nicotri 1977, Lubchenco 1978). Natural or artificial reductions in grazer densities have led to increased algal abundance and changes in species composition, and this has altered plant-plant competition (Estes et al. 1978, Lubchenco 1978, Lubchenco and Menge 1978, Pearse and Hines 1979, Duggins 1980). The effects of physical disturbance can be much the same as those of biological disturbance; the disturbance may act directly on plants or indirectly by affecting other organisms which interact with plants. In marine macroalgal assemblages, disturbance is often caused by high water motion that may remove vegetation (Dayton 1971, Rosenthal et al. 1974, Sousa 1979b).

Our knowledge of the importance of competition and disturbance in structuring marine algal assemblages has come primarily from intertidal studies. What little has been done in subtidal algal assemblages suggests that similar mechanisms may regulate community structure in this habitat. Herbivores (primarily sea urchins [Lawrence 1975, Breen and Mann 1976, Foreman 1977, Duggins 1980]), and their predators (Estes and Palmisano 1974, Estes et al. 1978) can strongly influence subtidal algal assemblages. In the absence of herbivores, algal-algal competitive interactions (primarily

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adults inhibiting juveniles) have been shown to be important structuring mechanisms (Dayton 1975a, Pearse and Hines 1979, Duggins 1980). In addition, differences in algal composition have been correlated with spatial and temporal changes in water motion (Barrales and Lobban 1975, Cowen et al. 1982, Foster 1982b).

In terrestrial forests, the often long-lived species which form the highest canopy can monopolize light and thus alter understory vegetation (Harper 1977). In subtidal communities throughout the world, only a few plants occur whose fronds form a surface canopy, and of these, *Macrocystis* spp. is the most abundant and widely distributed. To our knowledge, only one other study conducted in a *M. pyrifera* forest has experimentally examined algal competition for light, and only the effects of the surface *M. pyrifera* canopy on understory species were evaluated (Pearse and Hines 1979).

Our study site, a multilayered *Macrocystis pyrifera* forest in central California, experiences very low levels of the types of biological and physical disturbance discussed above. This suggests that competition may be of primary importance in structuring the algal assemblage at this site. We experimentally examined the effects of shading by overstory plants on understory recruitment and growth, and we present evidence of inhibition by each layer. In addition, we suggest that, contrary to many terrestrial forests, the surface canopy is the shortest lived and that *M. pyrifera* can be out-competed by the longer-lived understory layers.

The experiments in this study were designed to evaluate two basic questions. (1) Is this community structured by competition for light and space among the algae, and if so, what are the relative competitive abilities of the common species? (2) Following a disturbance, what effect do the canopies have on succession? The experimental design also allows us to predict how this vertically complex algal assemblage will respond to various intensities of disturbance.

#### STUDY SITE

Experiments were done in Stillwater Cove within Carmel Bay in central California (36°34'N, 121°56'W). The cove opens to the south, and the *Macrocystis pyrifera* forest is thus protected from large northerly swells associated with winter storms as well as strong northwesterly spring winds. The forest grows on a hard, moderate-relief substratum of sandstone, conglomerate, and lava (Simpson 1972). Low water motion and lack of suspended sediment result in relatively clear water, and *M. pyrifera* plants are found from just below the intertidal zone to depths below 30 m.

The kelp forest algal assemblage is characterized by three layers of perennial algae, a surface *Macrocystis pyrifera* canopy of variable thickness, a subsurface canopy of another kelp, *Pterygophora californica*, and an understory of articulated and encrusting coralline algae. *Pterygophora californica* forms dense stands and has stiff, 1–2 m long stipes that support blades at the

top. These blades produce a subsurface canopy, but rarely touch the bottom. *Macrocystis pyrifera* tends to grow around the perimeter of these stands, but its long fronds often produce a canopy overlying *P. californica*. Seasonal changes are apparent in both kelp canopies, but fluctuation is greatest in that of *M. pyrifera*. Maximum plant density and cover of *M. pyrifera* occur in early summer, with minimums in late winter (Fig. 2; Foster 1982b).

The articulated coralline algae occur as dense mats beneath the *Pterygophora californica* canopy, with branches extending up to 10 cm above the substratum. *Calliarthron tuberosum* is most abundant, with occasional plants of *C. cheilosporoides*, *Bossiella californica* spp. *schmitti*, and *B. orbigniana* spp. *orbigniana*. Encrusting coralline algae occupy space beneath these mats and elsewhere, and very little bare rock is found in the cove. Noncalcareous red algae comprise only a small portion of the understory, and those species that do occur (*Plocamium cartilagineum*, *Laurencia subopposita*, and *Botryoglossum farlowianum* var. *farlowianum*) are most often found as epiphytes on *C. tuberosum*. Sessile invertebrate cover is low except on vertical walls.

#### METHODS AND RESULTS

The effects of the two kelp canopies (under varying conditions of development) on algal recruitment were examined using the experimental design shown in Fig. 1. The term "recruitment" as used here is based on visual observations of macroscopic plants only (> 1 cm tall), not observations of microscopic stages in algal life histories. All underwater work was done using SCUBA, and plants were identified according to Abbott and Hollenberg (1976).

#### *Pterygophora* effects

To determine the effects of the *Pterygophora californica* canopy alone on algal recruitment under conditions of a sparse surface canopy of *Macrocystis pyrifera*, 547 *P. californica* plants were removed in May 1978 from half of the 150-m<sup>2</sup> study area located at 15 m depth (hereafter referred to as site 1). Plants were removed by cutting the stipe just above the holdfast, leaving the substratum undisturbed. The other half of the study area was unaltered and was monitored as a control. At the time of removal, a dense canopy of *P. californica* blades was present in both the removal and control sites, and similar plant densities were recorded (7.3 plants/m<sup>2</sup> in the removal site based on total counts, and  $6.4 \pm 0.6$  plants/m<sup>2</sup> [ $\bar{x} \pm SE$ ] in the control site based on counts in 20 randomly placed 1-m<sup>2</sup> quadrats). These plants were of similar size, 1.5–2 m tall. As a result of unusually large swells during the previous winter, *M. pyrifera* abundance was reduced in the cove, and only a sparse canopy of this species was present over the study area during the time of this first experiment (Fig. 2a–c).

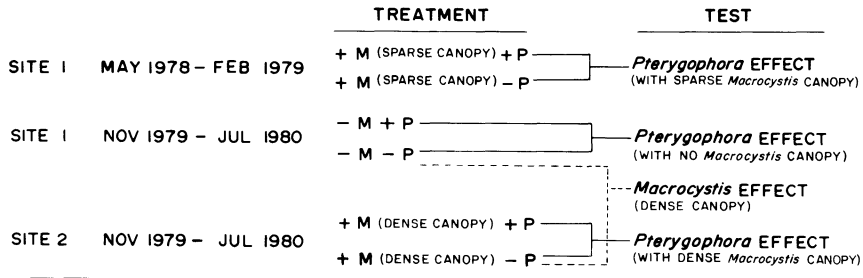


FIG. 1. Diagrammatic representation of experiments designed to evaluate the effects of *Pterygophora* and *Macrocystis* canopies on algal recruitment. M = *Macrocystis*; P = *Pterygophora*; + = present; - = experimentally removed.

The removal of *Pterygophora californica* had a dramatic effect on subsequent algal colonization. Our observations indicated that recruitment of *Macrocystis pyrifera* and *P. californica* occurred almost immediately, as these two species rapidly colonized the *P. californica* removal area. Noticeably lower recruitment by the brown alga *Desmarestia ligulata* var. *ligulata* (hereafter referred to as *D. ligulata*) was also observed. Recruits of other species (primarily fleshy red algae) were much less abundant, and contributed little to the algal understory. Brown algae were counted in 20 hap-

hazardly placed 1-m<sup>2</sup> quadrats in both the removal and control areas in October 1978, and again in February 1979 (Table 1). New recruitment was not obvious between these times, and plant densities for all three species were relatively constant for these two sample periods. No brown algal recruitment was observed in the unmanipulated *P. californica* control area during this experiment (Table 1).

The effects of *Pterygophora californica* alone on algal recruitment in the absence of an overlying *Macrocystis pyrifera* canopy can be evaluated by comparing the

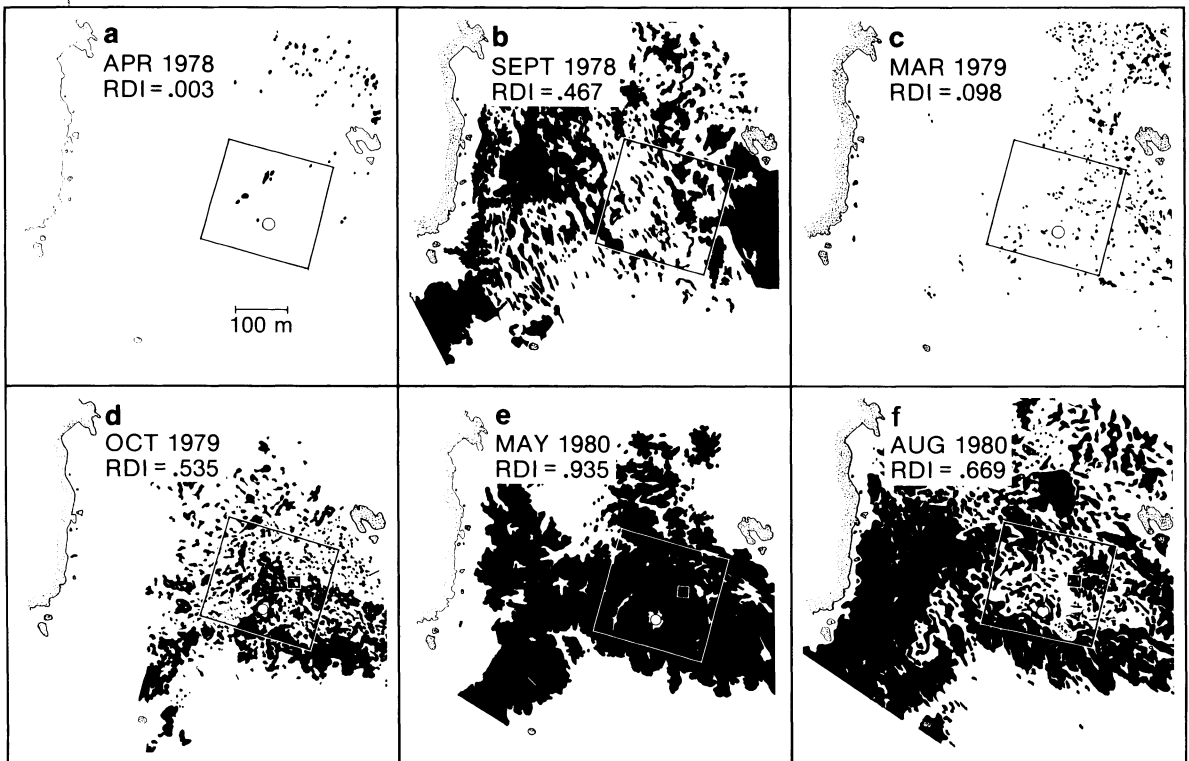


FIG. 2. *Macrocystis pyrifera* canopy cover in the western portion of Stillwater Cove. Canopy traced from aerial infrared photographs. Relative density index (RDI) = area of kelp in large square ÷ area of large square. O indicates location of site 1; □, site 2. Lack of canopy over site 1 in d-f is due to experimental removal.

TABLE 1. Density (plants/m<sup>2</sup>) of all brown algae in the *Pterygophora* removal and control areas at site 1, prior to (May 1978) and after (October 1978, February 1979) *Pterygophora* removal.

Treatment	Date	Algal density (plants/m <sup>2</sup> )				No. 1-m <sup>2</sup> quadrats
		<i>Pterygophora</i> adults	<i>Pterygophora</i> juveniles	<i>Macrocystis pyrifera</i>	<i>Desmarestia ligulata</i>	
		Mean ± 1 SE				
<i>Pterygophora</i> removal	May 78	7.3*	0*	0.02*	0*	...
	Oct 78	0	17.6 ± 3.4	9.6 ± 1.4	1.6 ± 0.4	20
	Feb 79	0	14.1 ± 1.7	7.1 ± 0.7	1.4 ± 0.4	20
<i>Pterygophora</i> control	May 78	6.4 ± 0.6	0	0	0	20
	Oct 78	8.3 ± 1.3	0	0	0	20
	Feb 79	6.7 ± 0.6	0	0	0	20

\* Densities based on total counts in May 1978.

*Pterygophora* removal and control areas in site 1 during the period of November 1979–July 1980 (Fig. 1). As part of other experiments (see coralline understory effects and yearly and seasonal fluctuations), the *M. pyrifera* canopy, which had developed following the *P. californica* clearing in May 1978, was removed over site 1 and from a 20 m wide area surrounding it from November 1979 to July 1980. In addition, all *M. pyrifera* and *P. californica* recruits in the *Pterygophora* removal area were continuously removed during this time. As a result, these two species were absent (except for the stand of *P. californica* in the *Pterygophora* control area) from site 1 in November 1979. By March 1980, the annuals that were present in November had died, and consequently, no brown algae were present in the study area at this time. Following recruitment in May 1980, the density of *Desmarestia ligulata* in 20 permanent 1-m<sup>2</sup> quadrats located in the *Pterygophora* removal area was  $17.1 \pm 5.2$  individuals/m<sup>2</sup> ( $\bar{x} \pm SE$ ). Although counts were not made prior to their removal, our observations indicated that the abundances of newly recruited *M. pyrifera* and *P. californica* in the *Pterygophora* removal site were similar to those found in this area the previous year. The only brown algal recruitment observed during this time in the *Pterygophora* control area were two *P. californica* plants that remained small, and eventually died during their 1st yr.

The effects of a *Pterygophora californica* canopy under a dense cover of *Macrocystis pyrifera* were examined by comparison with a second site (site 2; see □, Fig. 2) located  $\approx 75$  m from site 1 at 10 m depth. The understory at site 2, like that of site 1 (and much of Stillwater Cove [Foster 1982b]), was characterized by a dense *P. californica* canopy, a low-lying coralline mat, and low sessile-invertebrate cover. In November 1979, eight permanent 1-m<sup>2</sup> quadrats, designated with plastic tape anchored by concrete nails, were established within the *P. californica* stand. The same number and size of quadrats were marked outside the *P. californica* canopy. A canopy of *M. pyrifera* was present over the site at this time (Fig. 2d) and, by the time of spring recruitment the following year, was quite dense

(Fig. 2e). This canopy persisted until the end of the experiment (Fig. 2f). Inhibition as a direct result of the *P. californica* canopy was not apparent in this experiment, because by July 1980, no recruitment had occurred in any quadrats or surrounding areas of either treatment. Recruitment, however, did occur at this time in site 1, where both kelp canopies were removed (see above paragraph). This suggests that the effects of *P. californica* on algal recruitment are masked when a dense overlying *M. pyrifera* canopy is present.

#### Macrocystis effects

Comparison of the results from the experiments at sites 1 and 2 conducted at the same time (November 1979 through July 1980; see Fig. 1), suggests that a dense *Macrocystis pyrifera* canopy alone is able to prevent brown algal recruitment. As stated above, no recruitment was observed under a dense *M. pyrifera* canopy in site 2, regardless of whether a *P. californica* canopy was present. In contrast, substantial brown algal recruitment occurred at the same time in site 1, where both kelp canopies had been removed. It appears a sparse *M. pyrifera* canopy is less likely to prevent such algal colonization, as brown algal recruitment was observed under both a sparse surface canopy and no surface canopy (see *Pterygophora* effects section and Table 1). Although the evidence for this is derived from experiments which were done at two different times during two different years, in both cases substantial recruitment of brown algae was observed only in the spring.

#### Kelp canopy effects on light

Light measurements (using a Li-Cor Model LI-185 quantum meter with surface and underwater photosynthetically active radiation quantum sensors) were made within the study areas at maximum (July) and minimum (March) canopy development during two successive years (1979, 1980), in order to determine the amount of light reduction occurring under the various kelp canopies. All measurements were taken during late morning hours under overcast skies.

Although subsurface light varies considerably in

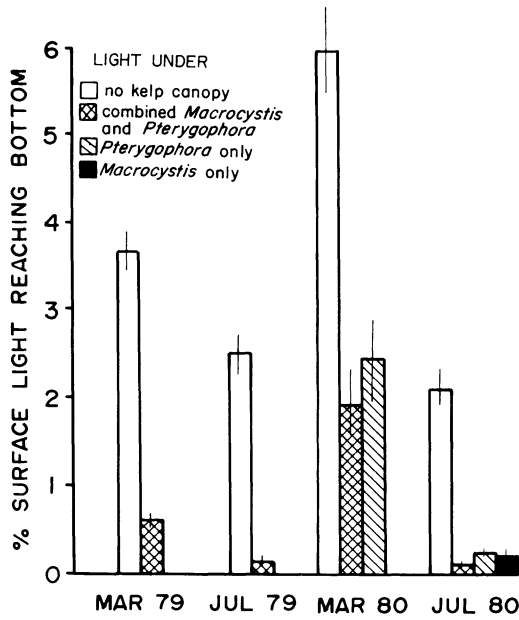


FIG. 3. Subsurface light intensity at minimum (March) and maximum (July) *Macrocystis* canopy development. All measurements were taken at 15 m depth. Variation is  $\pm 1$  SD;  $n = 4$ .

Stillwater Cove, measurements made on four different dates under different conditions of canopy development and type show that either a *Pterygophora californica* or dense *Macrocystis pyrifera* canopy can reduce subsurface light intensity to between  $\frac{1}{3}$  and  $\frac{1}{10}$  of that found at the same depth, but without a canopy (Fig. 3). At these low levels (0.1–2.5% of surface light), the combined effect of both canopies is not much greater than their individual effects. Except for the measurements made in March 1980, the light intensity beneath the kelp canopy or canopies was within or below the range of 0.5–1% of surface illumination. All available information indicates that this range is the lower limit for laminarian growth (Luning 1981), and thus reduction in bottom irradiance caused by the presence of the kelp canopies is capable of inhibiting algal recruitment.

*Coralline understory effects*

In addition to the various overstory canopy manipulations done at site 1 (see above), the area was simultaneously used to examine the effects of the coralline understory on algal recruitment from March to July 1979. To test the hypothesis that branched coralline algae affect the recruitment and growth of other plants, coralline branches were removed within 10 permanent 1-m<sup>2</sup> quadrats located in the kelp canopy removal site. A paint scraper was used to remove the branches from the substratum, leaving only holdfasts and encrusting organisms (mostly corallines). The hy-

pothesis that crustose coralline algae (and holdfasts of articulated species) affect recruitment and growth of other algae was tested by chipping (with an air-driven impact hammer) the coralline crust from a 0.0625-m<sup>2</sup> area located in each of the branch removal quadrats. As a control, 10 permanent 1-m<sup>2</sup> quadrats were established in which the coralline understory was left undisturbed. The 20 1-m<sup>2</sup> quadrats were arranged so each quadrat was adjacent to at least two others. Treatments were randomly assigned within this arrangement. As noted above, *Macrocystis pyrifera* and *Pterygophora californica* readily colonize when kelp canopy shading is reduced. To eliminate additional effects due to these species, *M. pyrifera* and *P. californica* recruits were continually removed, usually when < 5 cm tall.

The effects of coralline manipulations under both a canopy of *Pterygophora californica* and *Macrocystis pyrifera* were examined by establishing, in the kelp canopy control area, treatments and replicates identical to those in the kelp canopy removal area. No recruits were removed in this area, and the surface canopy formed by surrounding *M. pyrifera* plants was not disturbed. This experiment is illustrated in Fig. 4.

Species composition and cover of the algal understory were estimated using a point contact method (Greig-Smith 1964) with modifications for underwater use similar to those described by Foster (1982b). All vegetation layers above (up to 1 m) and below individual points are recorded using this method, so cover can exceed 100%. Twenty points were sampled in each of the coralline branch removal and control quadrats. A 0.0625-m<sup>2</sup> frame, subdivided into 100 squares, was used to estimate cover visually in quadrats chipped to bare rock. Percent cover data were normalized with an arcsine transformation for statistical comparisons (Sokal and Rohlf 1969). Unless otherwise noted, variation about the mean in the text and figures is  $\pm 1$  standard error of untransformed data.

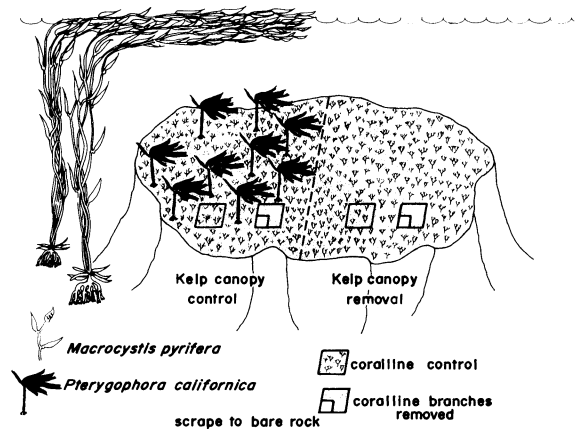


FIG. 4. Schematic representation of the algal assemblage in site 1 and the experimental manipulations which were performed in March 1979. Replicates not shown.

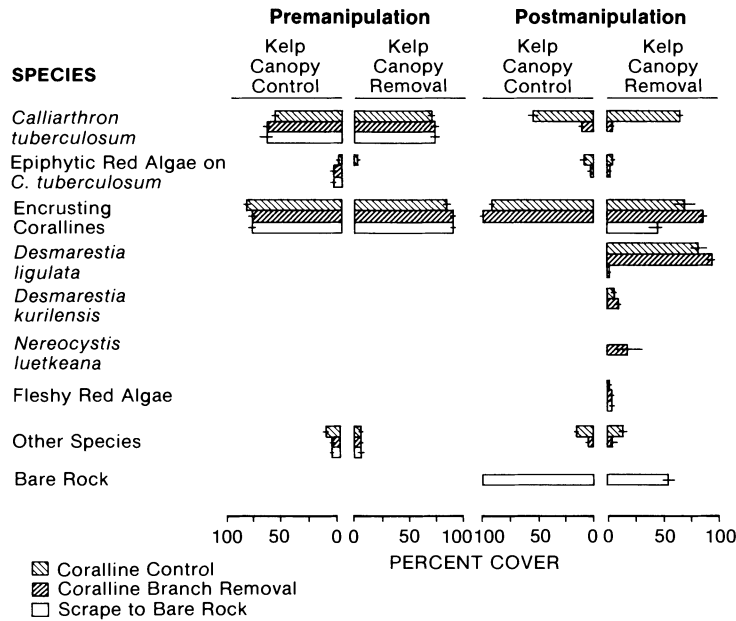


FIG. 5. Mean understory algal percent cover in the kelp canopy removal and control areas in March 1979, prior to initiation of coralline understory treatments, and in July 1979, 130 d after establishment of coralline understory treatments with the removal of *Pterygophora californica* and *Macrocyctis pyrifera* recruits. Epiphytic red algae include *Botryoglossum farlowianum* spp. *farlowianum*, *Laurencia subopposita*, and *Plocamium cartilagineum*. Upright coralline algae other than *Calliarthron tuberculosum* comprise "other species" category;  $n = 10$  quadrats for each treatment. Error bars are  $\pm 1$  SE.

All quadrats were sampled prior to the coralline manipulations in March 1979, and again in July 1979. Brown algae that recruited into the kelp canopy removal area following the *Pterygophora* clearing in May 1978 were removed in February 1979. Consequently, the understory cover in both the kelp canopy removal and control areas was similar in all three of the proposed coralline understory treatments prior to the start of the experiment (Fig. 5). Within 2 wk after manipulations were done, a thick but short-lived diatom film was observed in all three coralline treatments in the kelp canopy removal site. By late April, brown and fleshy red algal recruitment had started in coralline branch removal and control quadrats in this same area. No changes in the understory were recorded in any kelp canopy control quadrats at this time. Recruitment was significantly higher in coralline branch removal quadrats vs. coralline control. Prior to their removal in May 1979, the combined mean density of *Macrocyctis pyrifera* and *Pterygophora californica* recruits (these species were combined, as they are difficult to distinguish when small) was  $324.5 \pm 80.9$  individuals/m<sup>2</sup> in the coralline branch removal quadrats, and  $11.8 \pm 7.3$  individuals/m<sup>2</sup> in coralline control quadrats ( $P < .01$ , two-sample  $t$  test). *Desmarestia ligulata* followed a similar pattern of recruitment ( $112.0 \pm 21.4$  vs.  $24.7 \pm 9.3$  individuals/m<sup>2</sup>,  $P < .01$ , two-sample  $t$  test).

By July 1979, in the absence of young *Macrocyctis*

*pyrifera* and *Pterygophora californica* competitors, *Desmarestia ligulata* attained a high cover in both the coralline branch removal and control quadrats (Fig. 5). Although plant density for this species differed in these two treatments (see above paragraph), percent cover did not ( $P > .05$ , two-sample  $t$  test). *Desmarestia ligulata* can attain lengths up to 8 m (Abbott and Hollenberg 1976) and, as it does not float, can form a dense, low-lying canopy. Consequently, the blades of individual plants from one quadrat frequently overlapped nearby quadrats, biasing the percent cover data for this species.

Six individuals of the surface-canopy-forming kelp *Nereocystis luetkeana* also recruited into the coralline branch removal quadrats, and two eventually reached the surface. *Nereocystis luetkeana* did not occur in any other treatment (Fig. 5). The cover of *Desmarestia kurilensis* and the fleshy red algae *Bonnemaisonia nootkana*, *Callophyllis flabellulata*, *Fauchia laciniata*, *Fryeella gardneri*, *Neoptilota densa*, and *Weeksia reticulata* was slightly higher in the coralline branch removal quadrats (Fig. 5), but overall recruitment of these species was low, and differences were not significant ( $P > .2$ , two-sample  $t$  test).

Recruitment was generally lowest in quadrats scraped to bare rock. By July 1979, coralline crusts comprised the majority of the algal cover in these quadrats (Fig. 5). Most of these were the basal portions of upright corallines, as much of the crust later developed into

TABLE 2. Summary of the effects of the different algal layers on the recruitment of brown algae. M = *Macrocystis pyrifera*; P = *Pterygophora californica*; C = Coralline branches; EC = Encrusting coralline; + = Present; - = Absent or experimentally removed.

Test	Treatment	Brown algal recruitment	Conclusions
<i>Pterygophora</i> effect	+M (sparse canopy) +P+C+EC	None	The <i>Pterygophora</i> canopy prevents successful brown algal recruitment regardless of the condition of the <i>Macrocystis</i> canopy.
	+M (sparse canopy) -P+C+EC	Moderate	
	-M+P+C+EC	Low (two recruits)	
	-M-P+C+EC	Moderate	
	+M (dense canopy) +P+C+EC	None	
<i>Macrocystis</i> effect	+M (dense canopy) -P+C+EC	None	Only a dense <i>Macrocystis</i> canopy is independently able to prevent brown algal recruitment.
	-M-P+C+EC	Moderate	
	+M (dense canopy) -P+C+EC	Moderate	
Coralline branch effect	-M-P+C+EC	None	Inhibition of recruitment by the branched coralline layer is only observed in the absence of kelp canopy shading.
	-M-P-C+EC	Moderate	
	+M (dense canopy) +P+C+EC	High	
	+M (dense canopy) +P-C+EC	None	
Encrusting coralline effect	-M-P-C+EC	None	Recruitment is inhibited on newly exposed rock.
	-M-P-C-EC	High	

*Calliarthron tuberculatum*. Recruitment of *Desmarestia ligulata* and the noncalcareous red alga *Gigartina corymbifera* was also observed in the scraped quadrats, but was low and variable for both species. Fifty-five percent of the surface in these quadrats remained bare rock.

Other than a few epiphytes on regenerated branches in the coralline branch removal quadrats, no recruitment occurred in any of the three coralline understory treatments located in the undisturbed kelp canopy control site during the 130 d following the start of the experiment (Fig. 5). Recruitment was not observed in areas scraped to bare rock until November 1979, 250 d after clearing, when a few coralline crusts appeared. A summary of the effects of the different algal canopies on recruitment is presented in Table 2.

#### Yearly and seasonal fluctuations in recruitment

In order to examine year-to-year differences in algal recruitment, the above coralline manipulations were monitored through an additional growing season, and all quadrats were periodically sampled until July 1980. As before, *Macrocystis pyrifera* and *Pterygophora californica* recruits were continually removed as soon as they were distinguishable. Except for coralline algae and their epiphytes, no plants that recruited in the spring of 1979 persisted through the winter, so that all brown and fleshy red algae recorded in the July 1980 sample recruited in spring 1980.

Based on the two years sampled, year-to-year fluctuations in the composition and cover of the algae that recruited into the site appear to be low (Table 3). *Desmarestia ligulata* cover was relatively high both years, with *D. kurilensis* cover much lower. *Nereocystis luetkeana* did not appear in the July 1980 sampling; how-

ever, it was observed in the spring of that year, but as in 1979 only in upright coralline removal quadrats. It, along with several species of fleshy red algae, began to show signs of deterioration early in the growing season; individuals were gone by late June and consequently were not recorded in the July sampling period.

In both 1979 and 1980, a peak in brown algal recruitment occurred in late April, continued for  $\approx 4$  wk, and then declined. Kimura (1980) found a similar pattern at a nearby site in Carmel Bay. Young *Macrocystis pyrifera* and *Pterygophora californica* sporophytes were rarely observed at other times of the year. Recruitment of fleshy red algae also seemed to occur in the spring, with the exceptions of the perennial species *Gigartina corymbifera* and *Weeksia reticulata*, which first appeared in the fall.

In an attempt to examine seasonal differences in algal recruitment more closely, five additional quadrats of the three coralline understory treatments (coralline control, coralline branch removal, and scraped to bare rock) were established in the kelp removal area in site 1 in November 1979. At this time, the annual *Desmarestia ligulata* was still present in the March (Fig. 4) understory clearings, while the understory in the quadrats cleared in November consisted, before treatments, entirely of coralline algae and their epiphytes (Fig. 6). By February 1980, the cover of *D. ligulata* had dropped significantly in the March clearings (Fig. 6), and by March, this alga had completely disappeared from these quadrats (D. C. Reed and M. S. Foster, personal observation). Regrowth of *Calliarthron tuberculatum* was apparent in coralline branch removal quadrats cleared in November 1979, as was the recruitment of coralline crusts into areas scraped to bare rock (Fig. 6). Our observations indicated that brown



TABLE 3. Percent cover of noncalcified algae in the *Pterygophora* removal site following spring recruitment in 1979 and 1980. In both years, new *Macrocystis pyrifera* and *Pterygophora californica* were continually removed. The same individuals were not sampled in both years, as no plants persisted longer than 10 mo. X signifies presence of a fleshy red algal species.

Species	July 1979 (n = 10)			July 1980 (n = 5)		
	Coralline control	Upright coralline removal	Scrape to bare rock	Coralline control	Upright coralline removal	Scrape to bare rock
	Mean ± 1 standard error					
<i>Desmarestia ligulata</i>	82.2 ± 9.2	94.0 ± 2.9	1.1 ± 0.9	96.0 ± 3.9	94.0 ± 4.8	36.0 ± 16.0
<i>Desmarestia kurilensis</i>	8.3 ± 4.6	10.5 ± 3.5	1.1 ± 0.9	12.0 ± 3.5	12.0 ± 3.5	80.0 ± 5.8
<i>Nereocystis luetkeana</i>		20.0 ± 13.5				
Fleshy red algae (all species combined)	1.22 ± 0.5	3.0 ± 2.0	3.0 ± 2.1	1.0 ± 1.0	3.0 ± 1.0	4.0 ± 3.9
<i>Bonnemaisonia nootkana</i>	X	X		X	X	
<i>Callophyllis flabellulata</i>	X	X			X	
<i>Faucia laciniata</i>	X	X		X	X	
<i>Fryeella gardneri</i>		X		X	X	
<i>Gigartina corymbifera</i>			X			X
<i>Neoptilota densa</i>		X				
<i>Pikea robusta</i>					X	
<i>Weeksia reticulata</i>		X			X	X

algae did not recruit into any quadrats until late April 1980. In July, the algal composition of quadrats cleared at the two different times were quite similar (Fig. 6), although percent cover of *Desmarestia* spp. was significantly lower in all three of the coralline understory treatments in quadrats cleared in November, compared to those cleared in March ( $P < .05$  for each understory treatment, two-sample  $t$  test). These results indicate that the time of year manipulations were done had little effect on the timing of algal recruitment or subsequent composition.

The settlement and subsequent growth of *Calliarthron tuberculosum* were followed from March 1979 to July 1980. There was a slow but steady increase in growth (cover) of this species independent of branch

removal time (Fig. 7b). This increase was probably the result of regrowth from basal crusts. Recruitment of *C. tuberculosum* was evident throughout the year in quadrats scraped to bare rock, although there appeared to be a lag period, as colonization was not immediate after scraping (Fig. 7c). This lag period may be an artifact of difficulties in distinguishing young coralline species. In the unmanipulated coralline control quadrats, *C. tuberculosum* cover remained relatively constant throughout the study (Fig. 7a).

DISCUSSION

The results of these experiments show strong competitive interactions among the various perennial species of algae that are of major importance in struc-

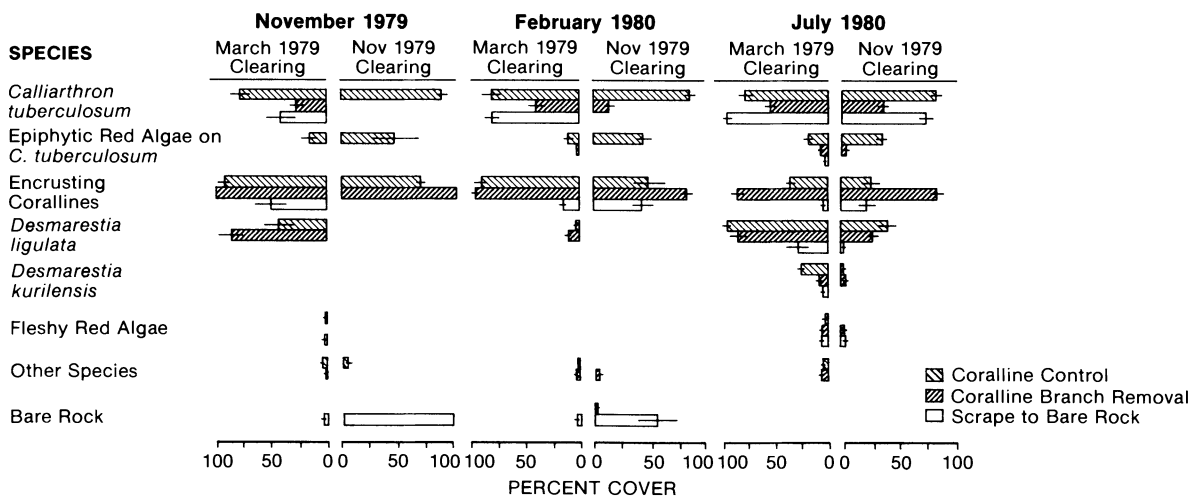


FIG. 6. Understory algal percent cover of quadrats cleared in March 1979 and in November 1979 in the *Pterygophora* removal area;  $n = 5$  quadrats for each treatment.

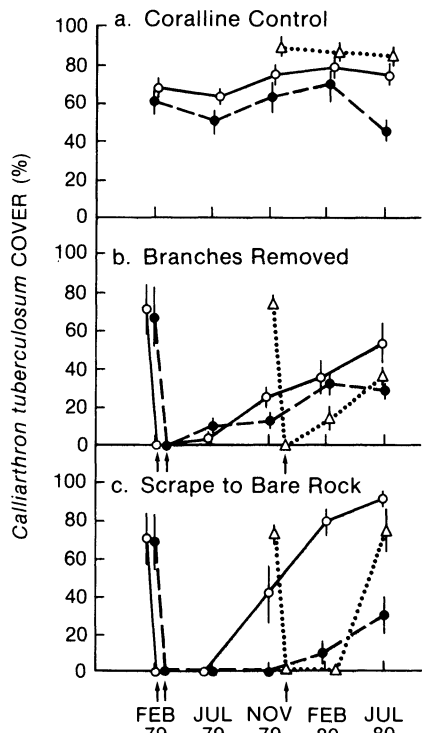


FIG. 7. Percent cover of *Calliarthron tuberculosum* in the three coralline understory treatments (a-c) in the kelp canopy removal and control sites. The coralline understory treatment quadrats in the kelp canopy control area were cleared in March 1979 only. Quadrats in the kelp canopy removal site were cleared in March and November 1979. Coralline algae were not cleared in any coralline control quadrats.  $\uparrow\uparrow$  on abscissa axes indicate times when coralline algae were cleared;  $n = 5$  for the coralline understory treatment quadrats in the kelp canopy removal area cleared in November 1979;  $n = 10$  quadrats for all others.  $\bullet$ — $\bullet$  kelp canopy control/March clearing,  $\circ$ — $\circ$  kelp canopy removal/March clearing,  $\Delta$ — $\Delta$  kelp canopy removal/November clearing.

turing the subtidal algal association in Stillwater Cove. Unlike the *Pterygophora californica* canopy, the persistence and extent of development of the *Macrocystis pyrifera* canopy is greatly affected by local meteorological and hydrographic conditions, and so is more variable from year to year. In a calm year, both the surface *M. pyrifera* and subsurface *P. californica* canopies are well developed by the spring, and consequently are independently capable of inhibiting the major pulse of algal recruitment which normally occurs at this time (Fig. 3). In unusually stormy years, wave surge may remove entire *M. pyrifera* plants and/or a higher proportion of fronds per plant, resulting in a greater reduction in surface canopy. When this occurs, canopy restoration is delayed (Foster 1982b). *Pterygophora californica*, unlike *M. pyrifera*, possesses a thick, "woody" stipe that is very difficult to break. Loss of entire plants after storms is rarely observed at Stillwater Cove (D. C. Reed and M. S. Foster, personal

observation). This characteristic, along with a subsurface habit, increases its persistence through these periods of high wave surge. During winter periods of extreme water motion, large-scale removal of *P. californica* has been observed in other central California kelp forests (G. Van Blaricom, personal communication), and breakage of the substratum caused by excessive wave surge may remove bottom cover species (Foster 1982b). We have never observed these phenomena in Stillwater Cove; therefore, despite the drastic reduction in the *M. pyrifera* canopy by winter storms, springtime recruitment continues to be inhibited by the more persistent *P. californica* and branched coralline canopies (Table 1, and text; see Coralline Understory Effects).

Our observations of the individual and combined effects of the three major canopies on algal recruitment show that recovery from disturbance is affected by all canopies. Although we have not observed the natural removal of *Pterygophora californica* or branched corallines by storms, the above observations suggest that the removal of different vegetation layers occurs along a disturbance gradient. Thus, analyzing the inhibitory effects of the different algal layers allows the prediction of community development under different intensities of disturbance.

If greater storm-associated disturbance occurred in Stillwater Cove, removing both *Macrocystis pyrifera* and *Pterygophora californica*, our results indicate that both of these perennials would recruit simultaneously (Table 1). We did not experimentally examine their interactions after recruitment, but a number of observations suggest they compete for light, and their competitive abilities differ. *Macrocystis pyrifera* forms a surface canopy during the 1st yr, with small *P. californica* below. We predict that, as both canopies develop during successive years, fewer and fewer plants recruit into these areas. In time, as the *M. pyrifera* plants are lost due to removal by storms, the more persistent *P. californica* continues to develop, and a dense, monospecific stand is formed, inhibiting further algal recruitment. Inhibitory effects of *P. californica* shading on recruitment have been suggested by others (McPeak 1981, Pace 1981). Our observations at Stillwater Cove indicate that *P. californica* only forms dense stands in certain habitat types, usually on the tops of high-relief areas and flat terraces. The reason(s) for the particular distribution is(are) unknown to us, but as a result, *M. pyrifera* can grow and form an overlying canopy in areas where *P. californica* is sparse or absent.

Continual removal of the dominant canopy species led to a significant increase in annual algal cover, consisting primarily of *Desmarestia* spp., and to a lesser extent, *Nereocystis luetkeana* and fleshy red algae (Fig. 5). Foster (1982b) found a similar increase in *D. ligulata* following the natural removal of *Macrocystis pyrifera* canopy by storms. The opportunistic characteristics of *D. ligulata* appear similar to those of the kelp

*Alaria fistulosa* found in some Alaskan kelp forests inhabited by sea otters (Dayton 1975a, Duggins 1980). Both *D. ligulata* and *A. fistulosa* seem unable to invade established stands of other kelps, but rapidly colonize areas when other kelp canopies are removed. In addition, Duggins (1980) noticed abundant *N. luetkeana* when a *Laminaria groenlandica* canopy was absent, and Dayton (1975a), Pearse and Hines (1979), and Foster (1982b) observed similar increases in fleshy red understory algae following the removal of kelp canopy species.

Coralline branches also inhibited algal recruitment, and although no measurements were taken, this effect was probably caused by reduced light. Removal of branches did not increase primary space, because coralline holdfasts were left intact, and clearly provided suitable space for recruitment. Furthermore, if space were limiting, one would expect the highest recruitment on quadrats scraped to bare rock, not the lowest as actually observed. However, this could have resulted from some toxic materials (metals?) leaching from the new exposed rock, or may reflect the presence of "dormant" algal stages which are not removed when the upright branches are removed. The former hypothesis is unlikely, as benthic diatoms quickly colonized the scraped areas. Further experiments are underway to resolve this question.

Inhibition of settlement caused by the abrasive action of algae has been documented in intertidal (Black 1974, Dayton 1975b), and subtidal communities (Velimirov and Griffiths 1979). That the subtidal articulated corallines produce a similar whiplash effect is unlikely, as their branches are stiff, intertwined, and not subject to the extremes of water motion found in the intertidal zone. Furthermore, if abrasion were important, one would not expect the observed common occurrence of uncalcified epiphytes on *Calliarthron tuberculosum*. Hruby and Norton (1979) found that a thick turf of *Enteromorpha intestinalis* significantly reduced the number of algal spores reaching the underlying substratum. However, the *C. tuberculosum* mats are far less dense than *E. intestinalis* turf. Thus, it is also unlikely that our results reflect the effects of a barrier to spore settlement on the bottom.

Articulated coralline algae do inhibit algal recruitment, but it is unlikely that any natural storm disturbance common to Stillwater Cove could remove the tough thalli of these low-growing plants. If such a disturbance did occur, the results show that unless all adult kelp were removed so there was no source of spores, kelp recruitment and growth would quickly lower light to predisturbance levels, and coralline branches would probably slowly regenerate from remaining holdfasts (Fig. 7b). If holdfasts were also removed, coralline recovery to predisturbance levels would simply take longer (Fig. 7c).

A diverse assemblage of small invertebrates, some of which are grazers, occurs in the coralline mats (Reed

1981). Because of the difficulties encountered in trying to remove these animals from the mats without disturbing the plants, their impact was not directly determined. However, the evidence available suggests that their effects on recruitment are small relative to the effects of the coralline branches. There was substantial algal recruitment on coralline mats in the kelp canopy removal area, and essentially none in the kelp canopy control (Fig. 5), but the invertebrates associated with the mats were undisturbed in both sites. It is possible that the invertebrate fauna differed in mats due to changes in water flow or predators as a result of our kelp canopy manipulations. We did not measure water motion, but qualitative observations indicated that the abundance of potential fish and invertebrate predators was similar in both kelp canopy removal and control areas, and that the coralline mat fauna was similar. However, all of the possible ways coralline mats and their associated fauna may be affected by canopy manipulations that, in turn, affect algal recruitment warrant further experimentation.

The only large invertebrate grazers commonly found in Stillwater Cove are sea hares (*Aplysia californica*), bat stars (*Patiria miniata*), and turban snails (*Tegula* spp.). Sea urchins (*Strongylocentrotus* spp.), abalone (*Haliotis* spp.), and kelp crabs (*Pugettia* spp.), important herbivores in many California kelp forests, are rare. The few large sea urchins and abalone present are restricted to crevices, where they probably feed on drift algae (Lowry and Pearse 1973). The low densities of these latter, potentially important, large herbivores may be attributed to the presence of the sea otter, *Enhydra lutris*, which has inhabited the cove since 1956 (Ebert 1967). These grazers are important prey of the sea otter in California (Ebert 1968, Wild and Ames 1974), and a variety of evidence suggests that sea otters can be important in structuring near-shore algal communities by limiting herbivore densities (Estes and Palmisano 1974, Estes et al. 1978, Duggins 1980). Little is known about the structure of the algal community in Stillwater Cove prior to the re-establishment of sea otters. *Macrocystis pyrifera* was present (Andrews 1945), but perhaps, as shown by Duggins (1980) in southeastern Alaska, under conditions of intense grazing, other perennials were less abundant. If cortical rings in *Pterygophora californica* are annual (as proposed by Frye 1918), then the time since the re-establishment of sea otters in Stillwater Cove closely parallels the proposed age of the older *P. californica* stands based on our ring counts. As many as 18 rings were counted in plants that were removed from the study site in May 1978,  $\approx 22$  yr after the re-introduction of sea otters into the cove. These dense stands may have developed after sea otters removed large grazers.

The giant kelp forest at Stillwater Cove experiences low levels of biological and physical disturbance. Under these conditions, perennial algal species are able to monopolize light, and thus exclude other algae as

well as inhibit their own recruitment. In contrast, nearby giant kelp forests located 45–60 km north on a more wave-exposed coast experience greater and more frequent levels of both physical and biological disturbance (Cowen et al. 1982, Foster 1982*b*). These exposed forests grow on a soft mudstone bottom that is easily eroded by the high water motion experienced throughout much of the year. Shifting patches of sand also bury and abrade the substratum. Consequently, plants are frequently removed. In addition, sea urchin (*Strongylocentrotus franciscanus*) densities are relatively high, as the area is beyond the present range of sea otters. Grazing by these urchins affects algal composition and abundance, and may lead to a higher species richness (Cowen 1979). This combined physical and biological disturbance appears to reduce the survival of long-lived, slow-growing perennial species. The understory, in the absence of continual overstory shading but disturbed by water motion, sand abrasion/burial, and sea urchin grazing is characterized by a relatively rich assemblage of rapidly growing, apparently annual species which flourish during periods of abundant light.

Experimentally induced disturbances (i.e., selective canopy removals) allowed annual algal species to invade the otherwise perennial algal assemblage at Stillwater Cove (Fig. 5). The composition of the understory (*Desmarestia* spp. and fleshy red algae) soon began to resemble that of nearby kelp forests, which are typified by greater disturbance. Only under conditions of frequent disturbance might this annual algal assemblage be maintained, particularly because the recruitment of slower-growing perennials was also high. Without their periodic removal, long-lived perennials become re-established, increasing competition for light and reducing chances for survival of other species.

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