

Effects of shade from multiple kelp canopies on an understory algal assemblage

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ABSTRACT: We examined the effects of shade from multiple kelp canopy layers (surface *Macrocystis pyrifera* canopy, understory *Pterygophora californica* canopy), both individually and in combination, on an understory algal assemblage in a central Californian kelp forest. The removal of both kelp canopies resulted in a dense recruitment of the understory brown alga *Desmarestia ligulata* that formed a third canopy layer, which significantly decreased bottom light and the abundance of understory red algae. We subsequently created an additional canopy treatment by removing this third canopy layer. In general, the understory red algae fluctuated seasonally with winter swell intensity, changes in kelp canopy cover, and grazing; and although species richness increased significantly with increased bottom light, red algal bottom cover did not respond significantly to the canopy clearings until 2 yr after the canopies were initially cleared. Red algal cover within the *Pterygophora* canopy treatment was similar to that in the control treatment. In the absence of *Pterygophora*, the *Macrocystis* canopy treatment and 'no canopy' treatment were found to have greater red algal cover and species richness. Individual understory species were rare, which resulted in small effects sizes and thus low statistical power. However, when grouped post hoc, according to how they responded to the canopy clearings (i.e. response groups), we were able to detect canopy treatment effects as much as 1 yr earlier. This method identified that some understory red algae adapted to areas of canopy removal (light-adapted), and others adapted to a variety of light regimes (shade-tolerant). We were able to classify the light-adapted algae into 2 subgroups: the high-light species and the intermediate-light species. Although this method of grouping was done post hoc, our results indicate that it may provide the clearest assessment of how understory algae respond to shading from kelp canopies.

KEY WORDS: Canopy shading · Community structure · Kelp forest · Light-adapted · *Macrocystis* · *Pterygophora* · Red algae · Shade-tolerant

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INTRODUCTION

Competitive dominance by canopy-forming plants plays an important role in structuring forest communities (Brokaw & Scheiner 1989, Connell 1989, Spies & Franklin 1989, Hubbell et al. 1999). Disturbance-mediated removal of only a few canopy dominants can therefore prevent the competitive exclusion of many

understory species, promoting greater diversity (Pickett & White 1985, Brokaw & Scheiner 1989, Whitmore 1989). In temperate marine communities, where shading by thick canopies of kelp (order: Laminariales) can, in part, regulate understory algal abundance in shallow (<30 m) water (Pearse & Hines 1979, Foster 1982, Reed & Foster 1984, Kennelly 1987a, Harrold et al. 1988, Dayton et al. 1992), the removal of the dominant

kelp canopies typically results in increased bottom light and a corresponding increase in the abundance of opportunistic species (Dayton et al. 1984, 1992, Reed & Foster 1984, Kennelly 1987b, Cecchi & Cinelli 1992, Graham 1996, Edwards 1998). As a consequence, variation in algal assemblages within and among kelp forests can be attributed partly to differences in the primary canopy-disturbing agent, ocean wave exposure (Foster 1975a,b, Cowen et al. 1982, Foster 1982, Dayton et al. 1984, 1992, Breda & Foster 1985, Harrold et al. 1988, Seymour et al. 1989, Graham 1997). Along parts of the west coast of North America, where large ocean waves associated with winter storms typically result in maximum kelp canopies in summer and minimum canopies in winter (Kimura & Foster 1984, Reed & Foster 1984, Dayton et al. 1992), competitive interactions between the canopy-forming kelps and understory algae can vary temporally, further increasing the overall variation in kelp forest community composition (Pearse & Hines 1979, Gerard 1984, Kennelly 1987a,b, Harrold et al. 1988, Dayton et al. 1999).

Given that understory algal assemblages are commonly complex mosaics of multiple species, responses to environmental perturbations can be ambiguous, especially where these responses vary among species. Furthermore, many understory algal assemblages contain numerous rare species that, when examined individually, may show only small (possibly undetectable) responses to environmental perturbations. As a consequence, many studies on the effects of shading by kelp canopies have simplified matters by limiting their focus to either the most common species (e.g. Edwards 1998, Dayton et al. 1999) or groups of species (e.g. Reed & Foster 1984, Santelices & Ojeda 1984, Kennelly 1987b, 1989). One method commonly used for grouping species has been to combine those with similar morphologies (e.g. foliose red algae vs articulated coralline algae; Littler & Littler 1980, Reed & Foster 1984, Dayton et al. 1999). Although this 'functional group' approach (sensu Littler & Littler 1980) may simplify patterns in complex multi-species systems, it may be inappropriate if the ecologies of the various species within each group differ substantially (Padilla & Allen 2000). In such cases, it may be better to group species according to similarities in how they respond to changes in a particular aspect of their environment. This 'ecological-response group' approach has been widely used by terrestrial plant ecologists to classify individual species according to how they respond to changes in their light environment and has been very useful in studies on canopy shading (e.g. Collins et al. 1985, Whitmore 1989, Kursar & Coley 1999).

The logic behind the response-group approach is straightforward; if canopy shading regulates an understory assemblage, canopy removal should elicit posi-

tive responses in recruitment and/or growth for species that require high irradiances, negative responses for species that require low irradiances, and no responses for species adapted to a variety of irradiances (Brokaw & Scheiner 1989, Spies & Franklin 1989, Whitmore 1989, Kursar & Coley 1999). Those species, then, that remain rare under dense canopies but rapidly recruit into canopy gaps following widespread canopy removal, have typically been referred to as 'light-adapted', 'gap-requiring' or 'shade-intolerant' and are often considered to represent fugitive species. On the other hand, those species that occur under forest canopies but do not markedly respond to canopy loss have typically been referred to as 'light-flexible' or 'shade-tolerant' species and are often considered to represent climax species (Whitmore 1989). Whereas light-flexible species are generally numerically more abundant than light-adapted species, both under canopies as well as in canopy gaps, their ability to withstand low-light environments may result in a decreased ability to rapidly respond to sudden increases in light (Canham 1989). As a consequence, light-adapted species, through greater recruitment and growth, typically dominate areas following canopy loss. There are numerous examples of response groups for terrestrial plants which have been used successfully in marine systems to discern the effects of physical disturbance on understory algae (Hay 1994). Other examples can be discerned from published studies of marine macroalgal assemblages (e.g. Pearse & Hines 1979, Kastendiek 1982, Santelices & Ojeda 1984, Edwards 1998), but this approach has not been widely applied. Classification of response groups may be particularly useful for grouping understory algae in subtidal kelp forests where, due to the synergistic effects of a floating surface canopy and a stipitate understory canopy, light regimes are highly variable in space and time (Reed & Foster 1984, Edwards 2004, the present study).

Along the Californian coast, thick surface canopies of the giant kelp *Macrocystis pyrifera* (hereafter *Macrocystis*) and understory canopies of the stipitate kelp *Pterygophora californica* (hereafter *Pterygophora*) occur over rocky substrates from 2 to >30 m depth (Foster & Schiel 1985). Both individually and together, these canopies, along with the water column itself, can decrease bottom irradiance to <1% of that at the surface and thereby reduce the abundance of understory algae (Reed & Foster 1984, Edwards 1998). While numerous studies have examined the effect of shading from kelp canopies on understory algae, few have simultaneously examined the effects of shading from both individual and combined canopy layers (see however Reed & Foster 1984, Dayton et al. 1999). Here, we investigate the effects of shading from individual

and combined canopy layers on understory algae by manipulating *Macrocystis* and *Pterygophora* canopies over a 2 yr period in a central Californian kelp forest, and then examining changes in the abundance of understory algae. We show that while both assemblage-wide and individual species responses to the canopy manipulations may be small, certain groups of species within the understory assemblage may exhibit stronger responses than other groups due to differences in their adaptation to specific light regimes. These response-groups can then be used to elucidate otherwise cryptic responses in the understory algal assemblages to complex changes in the benthic light environment.

MATERIALS AND METHODS

Study site. The study was carried out in Stillwater Cove, California (36° 34' N, 121° 56' W) from December 1991 to January 1994 (see Fig. 1). Stillwater Cove faces south and is relatively protected from the large north-west swells that are associated with winter storms, although less frequent southwest winter swells periodically reduce the surface *Macrocystis* canopies (Foster 1982, Kimura & Foster 1984, Reed & Foster 1984). These canopies typically recover during the following spring and become fully developed by mid to late summer. Thus, *Macrocystis* exhibits a seasonal cycle with a maximum surface canopy in summer and a minimum canopy in winter. A uniform understory canopy (1 to 2 m above the substratum) of *Pterygophora* is common in the cove and exhibits a similar but less pronounced seasonality to the *Macrocystis* canopy. The substratum beneath these canopies is dominated by a dense turf composed of several species of geniculate coralline algae, primarily *Calliarthron tuberosum* and *Bossiella californica*, that covers almost all available substrate not occupied by kelp, the foliose red algae *Plocamium cartilagineum* and *Laurencia subopposita*, which commonly grow as epiphytes on the geniculate coralline algae, and a variety of brown algae, primarily *Dictyoneuropsis reticulata*, *Cystoseira osmundacea*, and the seasonal *Desmarestia ligulata* (Foster 1982, Reed & Foster 1984, Konar & Foster 1992, Leonard & Clark 1993, Edwards 1998). Numerous other species of red macroalgae also occur in the cove but comprise only a small portion (<1% individually and <5% combined) of the understory assemblage.

Canopy clearing. In January 1992, *Macrocystis* and *Pterygophora* canopies were manipulated, both individually and in combination, at three 10 to 12 m deep sites within Stillwater Cove. Canopy clearings were established in an orthogonal block design (Fig. 1A). These sites were selected following a series of survey

dives in December 1991 and were chosen based on the presence of both *Macrocystis* and *Pterygophora* canopies, a predominance of low-relief rock, and limited sand cover. The sites were initially established as 30 m radius circles around a center marker buoy, and were divided into 2 regions of equal area: a 20 m radius inner circle surrounded by a 10 m radius outer torus. Each region was subsequently divided in half and canopy-manipulation treatments were allocated within each section (Fig. 1B). After the initial December 1991 winter sampling (pre-treatment baseline), *Macrocystis* were cleared from each inner circle by

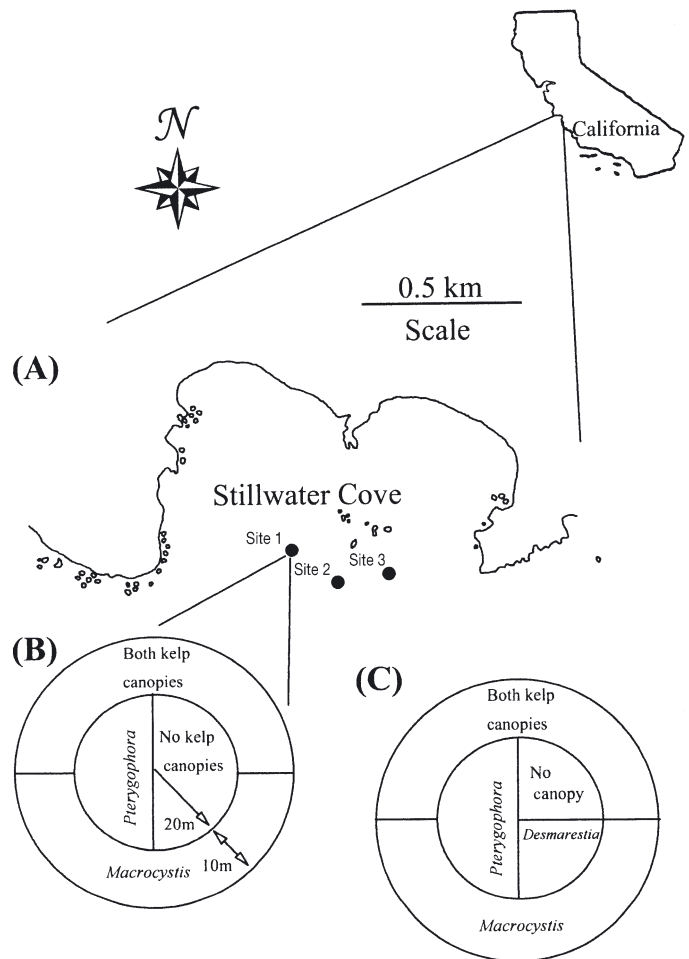


Fig. 1. (A) Study area at Stillwater Cove showing location of the 3 replicate sites. (B) Canopy clearing design showing the 20 m radius inner circles and 10 m radius outer tori. Canopy clearings were allocated in a blocked design. Treatments include 'no kelp canopies' = both *Macrocystis* and *Pterygophora* removed, '*Pterygophora* canopy' = *Macrocystis* removed and *Pterygophora* left unmanipulated, '*Macrocystis* canopy' = *Pterygophora* removed and *Macrocystis* left unmanipulated (also considered as control treatment). (C) Canopy clearings showing the placement of the *Desmarestia* removal (redefining the 'no canopy' treatment) and the '*Desmarestia* canopy' = *Desmarestia* left unmanipulated within the previous 'no kelp canopies' treatment

cutting their stipes at their holdfasts below the primary dichotomy. Holdfasts were not removed in order to minimize disturbance to the substratum and no *Macrocystis* were removed from the outer tori. All *Pterygophora* were removed from half of each inner circle and half of each outer torus by cutting them at their holdfasts. Canopy treatments are hereafter referred to by the name of the kelp canopies present (i.e. *Macrocystis* canopy, *Pterygophora* canopy, no canopy and both canopies treatments; Fig. 1B). All canopy treatments were maintained for 2 yr by removing all *Macrocystis* and *Pterygophora* recruits from their corresponding treatments before they formed a canopy. Giant kelp canopy abundance was then monitored from March 1992 to November 1993 by visually estimating kelp canopy abundance (expressed as wet weight) during aerial surveys (data provided by D. Glantz, Kelco, ISP Alginates, San Diego, CA).

In the summer following the initial canopy removal (June 1992), the seasonal understory alga *Desmarestia ligulata* (order: Desmarestiales; hereafter *Desmarestia*) developed a thick bottom cover (i.e. a third canopy layer) within the no kelp canopies treatment (see also Edwards 1998). To examine the effects of this third canopy layer on understory algae, all *Desmarestia* were cleared from half of each no kelp canopies treatment but were allowed to produce a thick seasonal canopy in the other half. This subdivided the no kelp canopies treatment into 2 treatments: a *Desmarestia* canopy treatment where *Macrocystis* and *Pterygophora* were both removed but *Desmarestia* remained, and a no canopy treatment where *Macrocystis*, *Pterygophora* and *Desmarestia* were all removed (Fig. 1C).

To quantify the difference in available light among treatments and sampling seasons, benthic irradiance was estimated at 6 positions within each canopy treatment during March, May and September 1993. Estimates were made at 5 m intervals along each of 3 radial transects within one of the replicate sites using a Li-Cor 4 π quantum sphere collector (sample rate = 2 Hz) attached to a hand-held CTD (Seabird Electronics-Sea Cat[®]). On each date, irradiance measurements were also made at 1 position within each canopy treatment at the other 2 replicate sites to check for consistency. All measurements were made on cloudless days at ~1200 h and were averaged over 2 min intervals. Because surface irradiance differed among sample dates, it was necessary to standardize the irradiance values. The average benthic irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$) within each treatment was standardized to that of the no canopy treatment (average treatment irradiance/average no canopy treatment irradiance) and expressed as 'percent ambient light'.

Holes within each kelp canopy (patch-gaps), associated with natural variability in kelp canopies, were

estimated using the percent cover of *Desmarestia*, which requires close to full benthic irradiance to grow (Edwards 1998). The area influenced by patch-gaps was estimated as '% cover of patch-gaps' = % cover *Desmarestia* for a treatment/% cover of *Desmarestia* within the *Desmarestia* treatment (optimal cover) \times 100%.

Effects of the canopy clearing on understory algae.

The abundance of understory algae was estimated within each canopy treatment seasonally from December 1991 to December 1993, except in the *Desmarestia* treatment where understory algae was first estimated in September 1992. A random point quadrat (RPQ) (Leonard & Clark 1993) was used to identify algal species at 20 points within each of the 15 quadrats that were randomly placed in each canopy treatment during each season. This technique estimated the percent bottom cover of individual algal species to 5% resolution within each quadrat (Goodall 1952, Foster 1982, Greig-Smith 1983, Leonard & Clark 1993). The percent bottom cover of individual species within each canopy treatment was determined at each site from these 15 quadrats, and the overall percent bottom cover of each species was then estimated for each canopy treatment from the 3 sites ($n = 3$). The December 1991 sampling estimated initial algal bottom cover prior to canopy manipulations. Total algal bottom cover within a quadrat often exceeded 100% due to layering.

Because RPQs often underestimate rare species (<1% cover) (Dethier et al. 1993, Leonard & Clark 1993), we measured how frequently rare species occurred within 18 to 0.25 m² quadrats that were randomly placed in each canopy treatment. Here, individual species were classified as being either present or absent in each quadrat and their frequency of occurrence then determined by dividing the number of quadrats in which each species occurred by the total number of quadrats sampled (Greig-Smith 1983). This technique offered an additional estimate of community structure (species richness), which was estimated both as average number of species observed per quadrat, and as the total number of species per canopy treatment.

Response groups. Individual understory algal species generally occurred in low abundances (<5% bottom cover) in all canopy treatments and continued to do so throughout the study. As a result, statistical power to detect changes in abundance for any one species following canopy removal was consistently problematic (see 'Results'). Therefore, to increase our ability to discern otherwise weak canopy effects, we combined individual species into larger groups, which were subsequently examined for changes in (combined) bottom cover. We first grouped all understory species together (i.e. total red algae), and then classified species post hoc according to similarities in the

way they responded to the canopy manipulations. As has been observed in terrestrial forests, this latter method yielded 2 response groups: light-adapted and light-flexible species. Individual species were considered to be light-adapted if they exhibited a response in cover which resulted in there being at least twice the bottom cover in the no canopy treatment as that of the both kelp canopy treatment in September 1993. The rarity of many of the species mandated this approach, rather than a statistical one. Species were considered to be light flexible if they occurred in all canopy treatments but did not respond (greater than twice the control) following any of the canopy removals. To identify possible subgroups within the light-adapted group (e.g. those species that responded differently to the removal of a single canopy layer than to the removal of both canopy layers), the light-adapted species were further divided into 2 subgroups: high-light-adapted species and intermediate-light-adapted species. Algae were considered high-light species if they increased (greater than twice the control) following the removal of both kelp canopies but not following the removal of only a single canopy, and intermediate-light species if they increased following the removal of either kelp canopy alone as well as both kelp canopies together.

We examined how each group changed in the canopy treatments over the course of the study (1991 to 1993). We are careful to point out that this response-group classification scheme was developed from evaluating changes in species abundance post hoc, and is therefore not intended to make generalizations about the ecology of any one species, but rather to simplify a number of complex responses in multiple species to the experimental treatments. If the interest is in examining the ecology of any one species in this study, proper unbiased experimental protocols need to be followed. We do, however, pose these groups as a means of elucidating how the understory algal assemblage in our study sites changed following canopy manipulation, and suggest that they can be used to increase statistical power in future studies.

Statistical analyses. All statistical analyses were done using SYSTAT (Windows version 8.0). Prior to analyses, data were examined for homogeneity of variances using an *F*-test or Cochran's *C*-test, and for normality by graphical examination of residuals. If percent cover data were heteroscedastic they were arcsine transformed ($\text{Arcsine } \sqrt{x+1}$) and retested. There is increasing risk of making a Type I error when inferences are simultaneously drawn from multiple statistical tests (Peres-Neto 1999). Therefore, in cases where this was done (e.g. *a priori* treatment contrasts following ANOVA), we applied the Bonferroni method of controlling for error inflation (Simes 1986). However, in cases where separate statistical tests were per-

formed on individual species or for different dates, and where the inferences drawn for these tests were independent, we adopt the argument of McCullagh & Nelder (1989), Hilborn & Mangel (1997) and Dayton et al. (1999) and do not correct for α -error inflation. Given the rarity of individual species, the statistical power of detecting differences among the canopy treatments for any one species or group was considered to be inherently low, and the corresponding α -error reduction would too greatly increase the risk of making a Type II error. We, however, report the uncorrected p-values, degrees of freedom and mean square estimates and allow the reader to decide for themselves the relative importance of Type I versus Type II errors, as well as evaluate the significance of each test accordingly.

To determine if kelp canopy removal affected the bottom cover of individual understory species or the combined bottom cover of the different algal groups, separate 1-way blocked ANOVAs, with canopy treatment blocked within site, were done for each species and algal group on each survey date. The effects of different canopy treatments on individual species and algal groups were tested by contrasting algal bottom covers within each canopy treatment to that in the appropriate control using Bonferroni-adjusted planned comparisons. On each sample date, the *Macrocystis* canopy, *Pterygophora* canopy and no canopy treatments were each compared to the both canopies treatment, while the *Desmarestia* canopy treatment was compared to the no canopy treatment.

RESULTS

Canopy clearing and bottom irradiance

Bottom irradiance within the no canopy treatment (hereafter referred to as ambient light) was used to represent available bottom light and was the standard against which light levels in the other treatments were compared. Percent of ambient light in all other canopy treatments was greatest in late winter to early spring when kelp canopies were at their minimum, and then decreased during the summer and fall (Fig. 2) as kelp canopies recovered from the winter storms (Fig. 3A). Specifically, the *Macrocystis* canopy alone was capable of reducing bottom light to ~60% of ambient during the spring and ~45% of ambient during the fall, while the *Pterygophora* canopy, either alone or in combination with the *Macrocystis* canopy, was capable of reducing bottom light to ~25% of ambient during the spring and ~2% of ambient during the fall. Finally, although it only occurred seasonally (spring to fall), the *Desmarestia* canopy alone had the greatest effect on bottom light, decreasing bottom light to <1% of ambient by the fall

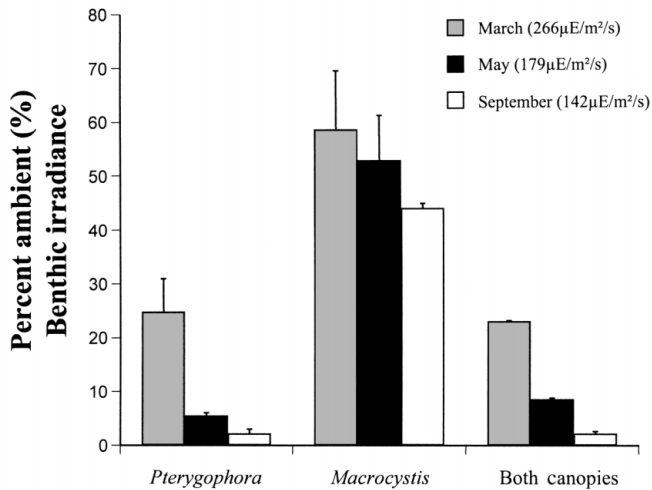


Fig. 2. Percent of ambient bottom light (mean + SE) under each canopy type individually and combined throughout the summer growth season. Data represent the amount of light relative to that observed at the same depth in the no canopy treatment (provided as $\mu\text{E m}^{-2} \text{s}^{-1}$). Kelp species identified refers to the canopy present in that treatment ($n = 4$)

when its cover was at a maximum (see also Edwards 1998). Furthermore, spatial heterogeneity in bottom light (i.e. differences in benthic irradiance among sample positions along each transect) within each area varied significantly among the 4 canopy treatments in the spring and summer (Cochran's tests: $p < 0.05$ and 0.01 respectively, $n = 5$, $df = 4$) but not in the fall (Cochran's tests: $p > 0.05$). Spatial heterogeneity in bottom light (as estimated by standard error) declined markedly in the summer and fall, indicating that patch-gaps (areas within each canopy treatment with greater irradiance than the surrounding area which likely resulted from beaks in the canopy; Connell 1989) decreased in size and number for each canopy treatment as the kelp canopies became more established (Fig. 2).

Effects of the canopy clearing on understory algae

The most conspicuous biological response to the canopy manipulations was a large springtime recruitment of the annual alga *Desmarestia* into the areas cleared of all kelp canopies. As a result, *Desmarestia* bottom cover varied significantly among the 4 canopy treatments in September 1992 (ANOVA: $F = 7.07$; $df = 3, 6$; $p = 0.018$; Fig. 3B). Specifically, bottom cover was significantly or near significantly greater in the no canopy treatment (Bonferroni: no canopy vs both canopies, $p = 0.021$; no canopy vs *Macrocystis* canopy, $p = 0.058$; no canopy vs *Pterygophora* canopy, $p = 0.032$) but was not significantly different between any of the other pairs of canopy treatments. However, there

was a trend in which *Desmarestia* bottom cover appeared greater in the *Pterygophora* canopy treatment than in the *Macrocystis* canopy treatment, both of which appeared greater than in the both canopies treatment (Fig. 3B). The general effect of the *Desmarestia* canopy was 2-fold: first it reduced benthic light by greater than 99% relative to adjacent areas without *Desmarestia*, and second it reduced the size and branch density of at least one of the more common understory red alga, *Plocamium cartilagineum*, through physical abrasion (Clark 1996).

Total red algae

Total red algal abundance varied seasonally within Stillwater Cove, exhibiting maximum bottom cover in the spring and minimum cover in the winter (Fig. 3C). Following its spring maximum, total red algal cover declined in all canopy treatments between June and September each year (Fig. 3C), coincident with increasing kelp canopies (Fig. 3A). These declines were particularly large in 1992, apparently enhanced by intense grazing from large numbers (400 to 500 ind. site^{-1}) of the Opisthobranch *Aplysia californica* (R. P. Clark pers. obs.; Fig. 3C). Following the *A. californica* outbreak (*A. californica* densities declined by January 1993; R. P. Clark pers. obs.), total red algal abundance increased in all canopy treatments, returning to pre-manipulation cover by June 1993, before again decreasing in all but the no canopy treatment as the canopies again approached their annual maximum (Fig. 3C). Total red algal cover in the no canopy treatment continued to increase through December 1993. Surprisingly, however, differences in total red algal cover between the canopy treatments were significant only on the last sample date (December 1993; ANOVA: $F = 4.09$; $df = 4, 8$; $p = 0.043$) (Table 1a, Fig. 3C). At this time, total red algal cover was significantly greater in the no canopy treatment ($43 \pm 6\%$, mean \pm SE) than in the both canopies treatment ($24 \pm 5\%$; Bonferroni: $p = 0.05$) and the *Pterygophora* canopy treatment ($22 \pm 5\%$, $p = 0.03$) but was not significantly different than in the *Macrocystis* canopy treatment ($33 \pm 6\%$, $p = 0.5$), again suggesting that the *Macrocystis* canopy alone was less efficient at reducing benthic irradiance than either the *Pterygophora* canopy alone or both canopies combined. The overall lack of significant canopy effects across sample dates, however, was surprising given the large body of literature suggesting that kelp canopies exert significant effects on understory algae (e.g. Foster 1975a,b, Foster 1982, Reed & Foster 1984, Kenelly 1987a, Harrold et al. 1988, Dayton et al. 1992), and we therefore examined species responses individually as well as for potential response-groups.

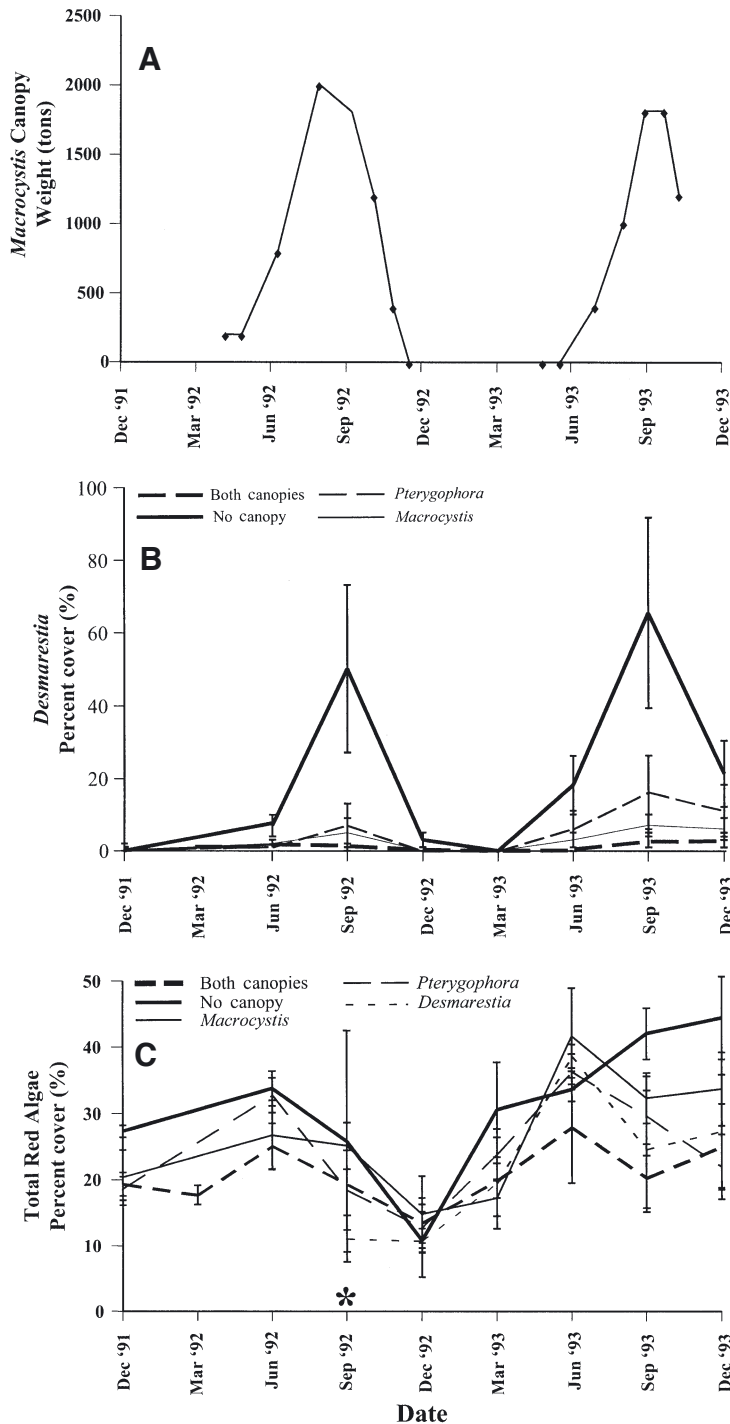


Fig. 3. (A) Kelp canopy abundance in Stillwater Cove during study period (March 1992 to December 1993). Data for kelp abundance are presented as wet weight (tons) for the surface *Macrocyctis pyrifera* canopy as estimated from aerial surveys by D. Glantz (ISP Alginates, San Diego, CA) and are used to show relative changes in canopy abundance. (B) Bottom cover of *Desmarestia ligulata* in the canopy treatments (mean \pm SE). Data were determined as the average bottom cover per canopy treatment in the 3 sites ($n = 3$). (C) Bottom cover (mean \pm SE) of understory red algae (as a group) in the different canopy treatments (December 1991 to December 1993). Data for the *Desmarestia* canopy treatment begin in September 1992, following the removal of the *Desmarestia* canopy ($n = 3$). Note the asterisk denoting the time of intense *Aplysia* grazing

Individual species

With few exceptions, we were unable to detect statistically significant responses of individual understory species to the canopy manipulations (Table 1b). We attributed this surprising result, at least in part, to low statistical power resulting from the small effect sizes caused by the rarity of individual species, even though some species had proportionally large changes in bottom cover relative to the both canopies treatment (Table 2). In fact, in September 1993, all species except *Plocamium cartilagineum*, *Laurencia subopposita*, *Callophyllis crenulata*, and geniculate corallines exhibited their greatest bottom cover in the no canopy treatment and their lowest cover in the both canopies treatment (Table 3). Similarly, species richness was also highest in the no canopy treatment (Table 3). In contrast, the availability of bare space (i.e. rock and nongeniculate coralline algae) was greatest in the both canopies treatment and lowest in the no canopy treatment (excluding the *Desmarestia* canopy treatment where bare space was difficult to measure due to the dense cover of *Desmarestia*; Table 3). The effects of the canopy manipulations on the rare understory species, which are commonly under-represented using a point quadrat method, were analyzed separately based on their frequencies of occurrence (see section Rare species and richness).

Response groups

Changes in cover of individual understory species in each of the canopy treatments were assessed post hoc in September 1993 and the species then regrouped according to how they responded to the canopy manipulations. Grouping the individual species in this manner yielded 2 general response groups, light-adapted species and light-flexible species (Table 2), and identified canopy treatment effects up to 8 mo earlier than did the total red algae or individual species approaches (Table 1a–c). Specifically, responses to the canopy manipulations for the total red algae group (Table 1a) were not observed to be statistically significant until December 1993, whereas responses for the light-adapted species were observed as early as March 1993 (Table 1c). At that time, bottom cover of light-adapted species was significantly greater in the no canopy treatment than in the *Desmarestia* canopy treatment (Bonferroni: $p < 0.01$), the both canopies treat-

Table 1. p-values and mean square estimates obtained from ANOVA for canopy treatment effects on understory red algae (both combined and individual) for each sample date. Columns are organized as p-values (p) followed by the mean square (ms) estimates (numerator/denominator) for each test. Significant treatment effects are denoted by p-values in bold face. Degrees of freedom for each test were 3, 6 for June 92, and 4, 8 for each remaining date. Results show both the prevalence and timing of significant treatment effects as identified by the different grouping approaches

Species or groups	Jun 92		Sep 92		Dec 92		Mar 93		Jun 93		Sep 93		Dec 93	
	p	(ms)	p	(ms)	p	(ms)	p	(ms)	p	(ms)	p	(ms)	p	(ms)
(a) Total understory	0.6	(43.3/64.9)	0.28	(213.0/138.6)	0.57	(56.1/71.9)	0.14	(234.6/97.9)	0.32	(215.0/155.8)	0.31	(238.3/168.4)	0.04	(421.2/102.9)
(b) Individual species														
<i>Plocamium cartilagineum</i>	0.12	(57.2/19.3)	0.87	(18.6/61.5)	0.98	(0.8/8.4)	0.56	(13.8/18.9)	0.34	(31.3/23.6)	0.75	(13.0/26.9)	0.82	(10.4/28.2)
<i>Laurencia subopposita</i>	0.16	(2.5/22.7)	0.62	(27.3/39.2)	0.65	(5.3/8.3)	0.63	(10.3/15.2)	0.43	(12.7/12.0)	0.88	(2.4/8.5)	0.06	(31.0/80.5)
<i>Chondracanthus corymbifera</i>	0.16	(2.5/22.7)	0.62	(27.3/39.2)	0.65	(5.3/8.3)	0.63	(10.3/15.2)	0.43	(12.7/12.0)	0.51	(1.8/1.9)	0.05	(31.0/8.1)
<i>Prionitis lanceolata</i>	0.76	(0.1/0.2)	0.89	(0.1/0.5)	0.24	(0.08/0.05)	0.60	(0.06/0.08)	0.54	(0.5/0.5)	0.67	(0.1/0.2)	0.07	(0.2/0.1)
<i>Rhodomenia californica</i>	0.45	(0.1/0.1)	0.51	(0.1/0.1)	0.75	(0.1/0.3)	0.65	(0.1/0.2)	0.20	(0.03/0.02)	0.28	(2.3/1.5)	0.47	(0.1/0.1)
<i>Cryptopleura farlowiana</i>	0.19	(2.7/1.3)	0.28	(0.5/0.4)	0.73	(0.5/0.9)	0.03	(22.2/4.9)	0.34	(3.4/2.6)	0.32	(24.0/17.0)	0.26	(25.3/15.8)
<i>Callophyllis crenulata</i>	0.06	(0.9/0.2)	0.78	(1.0/2.3)	0.69	(0.7/1.2)	0.09	(1.1/0.4)	0.91	(1.0/4.5)	0.47	(2.2/2.2)	0.51	(0.9/0.9)
<i>Faucheia laciniata</i>	0.92	(0.1/0.7)	0.11	(7.4/2.8)	0.48	(1.0/1.1)	0.98	(0.01/0.12)	0.16	(11.5/5.2)	0.15	(4.5/2.0)	0.37	(0.7/0.6)
<i>Weeksia reticulata</i>	0.68	(0.6/1.1)	0.62	(0.8/1.1)	0.57	(0.1/0.1)	0.36	(0.03/0.02)	0.25	(0.7/0.4)	0.21	(0.2/0.1)	0.83	(0.01/0.03)
(c) Response groups														
Light-adapted	0.41	(15.6/13.7)	0.17	(7.2/3.5)	0.95	(0.6/3.6)	0.01	(21.1/3.3)	0.15	(31.2/13.8)	0.04	(120.0/27.1)	0.05	(50.7/13.2)
High-light	0.74	(1.1/2.7)	0.10	(6.6/2.3)	0.55	(0.8/1.0)	0.98	(0.01/0.15)	0.10	(16.4/5.7)	0.21	(14.2/7.7)	0.32	(0.8/0.6)
Intermediate-light	0.33	(8.5/6.1)	0.55	(1.6/1.9)	0.91	(0.2/1.0)	0.02	(21.0/3.6)	0.33	(7.5/5.5)	0.16	(56.1/25.9)	0.12	(40.8/16.0)
Light-flexible	0.65	(52.6/90.1)	0.49	(15.83/166.1)	0.56	(50.6/63.4)	0.20	(159.7/82.7)	0.54	(128.8/154.7)	0.30	(159.4/108.4)	0.16	(226.4/104.5)

ment (p = 0.05) and the *Pterygophora* canopy treatment (p = 0.05), and was significantly greater in the *Macrocystis* canopy treatment than in the *Desmarestia* canopy treatment (p = 0.048). Bottom cover, however, did not differ between any of the other canopy treatments. In contrast, canopy treatment effects were not observed for the light-flexible group on any of the sample dates (Table 1c). We are careful to point out that this method was done post hoc and that intentionally grouping those species with the greatest responses, and then statistically testing the response of this group to the canopy manipulations will undoubtedly result in artificially high power and therefore should be viewed with caution. However, we think this method elucidated otherwise weak or cryptic responses by certain algae that responded in consort to the canopy manipulations, while other algae did not. Furthermore, this method allowed us to quantitatively assess the magnitude of these different responses, and therefore can provide critical information into the overall responses by the understory assemblage that would otherwise not have been determined.

Within the light-adapted group, differences in the way the individual species responded to the canopy treatments suggested that 2 subgroups could be discerned: high-light species and intermediate-light species. High-light species were those that only responded to removal of all canopy layers, while intermediate-light species were those that responded to removal of either kelp canopy layer as well as all (including *Desmarestia*) canopy layers (Table 2), and ultimately exhibited at least twice the bottom cover in the corresponding canopy treatment than in the both canopies treatment (Table 3). Dividing the light-adapted group into these subgroups differentiated responses to the canopy treatments for the high-light species in September 1992 and the intermediate-light species in March 1993 (Table 1c). This grouping method identified responses to the canopy treatments as much as a year earlier than for any of the other grouping methods and identified responses on at least 3 sample dates when none of the other methods did (Table 1a–c). Furthermore, it suggested that some species were strongly affected by canopy shading, some species were weakly affected by shading, and some species were unaffected by shading.

Rare species and richness

Although numerous understory species occurred in the study sites in consistently low abundances during this study, only 2 were classified as rare. Cover of these, *Fryeella gardneri* and *Neoptilota densa*, never exceeded 1% in any of the canopy treatments, making

Table 2. Understory algal response groups based on percent cover relative to the both kelp canopies treatment in September 1993. Relative percent cover (treatment % cover/both kelp canopies % cover) represents the response of each alga or group to the corresponding treatment, compared to the control treatment. Light-adapted species responded to the clearing of 1 or more canopies (greater than twice the control). Maximum light species responded when both canopies layers were cleared. Intermediate light species responded when 1 or more canopy layers were cleared. Light-flexible species have cover approximately equal to the controls

Light requirement categories	Relative percent cover		
	No canopy	<i>Macrocystis</i>	<i>Pterygophora</i>
Light adapted (combined)	5.8	2.5	2.4
High light spp. (combined)	4.7	1.1	0.7
<i>Fauchea laciniata</i>	28.0	2.0	1.0
<i>Chondracanthus corymbiferus</i>	3.1	0.6	0.6
<i>Prionitis lanceolata</i>	2.0	1.3	0.3
<i>Weeksia reticulata</i>	2.7	1.8	1.4
Intermediate light spp. (combined)	6.5	3.5	3.5
<i>Callophyllis crenulata</i>	5.7	7.0	8.0
<i>Rhodymenia californica</i>	7.0	3.0	2.5
<i>Cryptopleura farlowiana</i>	6.5	2.9	2.9
Light-flexible spp. (combined)	1.1	1.1	1.2
<i>Plocamium cartilagineum</i>	1.4	1.6	1.4
<i>Laurencia subopposita</i>	1.3	1.3	1.2
Geniculate corallines	1.0	1.0	1.2

them too rare to be included in any of the algal groups with confidence (Table 3). Instead, these species were included in the estimation of species richness in each canopy treatment, both for the average number of species per unit area (sample quadrat) as well as the total number of species observed per canopy treatment. The number of species observed per unit area differed significantly among the canopy treatments (ANOVA: $p < 0.01$), with the no canopy treatment > the *Macrocystis* canopy treatment > the *Pterygophora* canopy treatment > the both canopies treatment > the *Desmarestia* canopy treatment (Table 3). In addition, the total number of species observed in each canopy treatment followed a similar pattern with the no canopy treatment > the *Macrocystis* canopy treatment > the *Pterygophora* canopy treatment = the both canopies treatment = the *Desmarestia* canopy treatment (Table 3). Together, these 2 measures indicated that spe-

Table 3. Percent bottom cover of understory algae in each canopy treatment in September 1993 (fleshy red algae = total red algae-geniculate corallines). Significant differences of blocked ANOVA: ns = not significant. na = not applicable, nd = not determined, ns = not significant. Bold face indicates treatments with the highest value for each category. Species richness and percent patch gaps determined as described in text

Canopy treatment % surface irradiance	% cover by canopy treatment					Effect	
	No canopy 9.10%	<i>Macrocystis</i> 4.00%	<i>Pterygophora</i> 0.20%	<i>Desmarestia</i> 0.02%	Both canopies 0.20%	Treatment	Site (block)
Fleshy red algae combined	41.8	32.9	29.3	24.9	20.2	ns	<0.05
<i>Plocamium cartilagineum</i>	13.6	15.7	13.6	11.3	9.9	ns	<0.05
<i>Laurencia subopposita</i>	8.1	8.2	7.4	6.3	6.4	ns	<0.05
<i>Chondracanthus corymbifera</i>	2.2	0.4	0.4	0.7	0.7	ns	ns
<i>Prionitis lanceolata</i>	0.6	0.4	0.1	0.1	0.3	ns	ns
<i>Rhodymenia californica</i>	2.8	1.2	1	1.2	0.4	ns	ns
<i>Cryptopleura farlowiana</i>	9.1	4	4	3.6	1.4	<0.1	<0.05
<i>Callophyllis crenulata</i>	1.7	2.1	2.4	1	0.3	ns	ns
<i>Fauchea laciniata</i>	2.8	0.2	0.1	0	0.1	ns	ns
<i>Weeksia reticulata</i>	0.6	0.4	0.3	0.2	0.22	ns	ns
Geniculate corallines	63.3	67.5	76.9	75.9	64.3	ns	<0.05
Rare species	0.4	0.2	0	0.1	0	nd	nd
<i>Neoptilota densa</i>	0.2	0.2	0	0.1	0	nd	nd
<i>Fryeella gardneri</i>	0.2	0	0	0	0	nd	nd
Clear substrate/nongeniculate corallines	7.9	9	9.9	6.2	17.9	ns	ns
Sand	1.6	0.8	1.7	1.4	2.9	ns	<0.01
Total species/quadrat	12*	10	9	9	9	nd	nd
Richness (# species/quadrat)	3.5	2.7	1.9	1.3	1.4	<0.01	ns
# with highest bottom cover in treatment	9.5	3.5	2	0	2	nd	nd
% cover of patch gaps	na	11.7	25.5	na	4.3	nd	nd

cies richness tended to increase with increasing bottom light, but the trend was not significant (Spearman rank correlation: $r = 0.9$; $k = 5$; $p = 0.084$).

DISCUSSION

Few studies have simultaneously examined the effects of shading from both individual and combined kelp canopies (see Reed & Foster 1984, Dayton et al. 1992). This experiment found that removal of the dominant kelp canopies lead to complex responses in the benthic light regimes and corresponding responses in the benthic algal communities. Higher cover of red algae in spring and subsequent decreases by late summer 1993 in all treatments with canopies (Fig. 3C) supports previous observations that understory plants undergo early spring growth before canopy layers mature (Pearse & Hines 1979, Foster 1982, Breda & Foster 1985, Collins et al. 1985, Harrold et al. 1988). The continued increase in cover of red algae through September 1993 in the no canopy treatment indicates that these algae have greater growth potential than was observed under the canopies, but shading causes their early declines in abundance.

The effects of increased bottom light in the no canopy treatment did not persist without the subsequent removal of the seasonal *Desmarestia* canopy. *Desmarestia* ultimately covered as much as 90% of the substrate in this treatment and reduced bottom light far below that observed in the unmanipulated canopy areas. This suggests that a single benthic canopy of *Desmarestia* is more effective at shading the bottom and influencing benthic algal composition than the combined surface and subsurface kelp canopies. Summertime benthic irradiance and understory algal composition in the *Pterygophora* canopy treatment was similar to that in the both canopies treatment, suggesting that the *Pterygophora* canopy, where present, is the dominant canopy regulating benthic algal composition. In contrast, in the absence of *Pterygophora*, the *Macrocystis* canopy was not able to reduce bottom light to levels similar to those observed under both canopy layers and was found to have greater red algal cover and species richness. Regardless, each canopy type, either individually or in combination, is capable of decreasing bottom light to levels that reduce recruitment of other species of macroalgae, including the dominant kelps themselves (Reed & Foster 1984, Foster & Schiel 1985, Dayton et al. 1992, Edwards 1998).

The canopy treatments also differed with regard to homogeneity and intensity of gap irradiance. Thus, while benthic irradiance varied as a function of canopy type (associated with capabilities to shade the understory), it also varied substantially as a function of

canopy uniformity. In sum, our results show that shading from *Macrocystis* canopy provided a more uniform intermediate light environment (45% of ambient in September 1993) and *Pterygophora* provided greater shading (2% of ambient in September 1993) but with greater heterogeneity (calculated 25% patch-gaps in September 1993).

Response to intermediate shading and canopy variability are evident within the 2 single canopy treatments (Tables 2 & 3). The greater species richness (2.7 species per quadrat) and intermediate algal cover (32% fleshy red algae) of the *Macrocystis* canopy treatment in comparison to the control and *Desmarestia* canopy treatments suggest that a single canopy *Macrocystis* forest can support a greater abundance of turf algal species than a 2 canopy forest. As suggested by Kennelly (1987a), some species respond to clearing 50% of the canopy layer. Three such species have been identified here (Table 2). Because *Pterygophora* is capable of excluding light-adapted red algae by reducing irradiance by 20 times that measured under the *Macrocystis* canopy, holes (patch-gaps) within the canopy most likely provide favorable microhabitats for growth of these species under a single *Macrocystis* canopy.

Without a surface canopy of *Macrocystis*, these gaps within the *Pterygophora* would receive full ambient light and be dominated by *Desmarestia* (>15% cover of *Desmarestia* in September 1993). The *Desmarestia* would decrease understory species abundance and diversity and negate higher light associated with gaps in single canopy treatments. This study suggests that the abundance and diversity of turf red algae within the natural 2 canopy environment of Stillwater Cove is most likely attained through variability in the *Pterygophora* canopy beneath a canopy of *Macrocystis*. Such a habitat allows increased light within *Pterygophora* patch-gaps sufficient for growth of the intermediate light-adapted red algae while restricting the dense *Desmarestia* canopy, which would recruit in the absence of a *Macrocystis* canopy and exclude a majority of red algal species.

One of the most surprising results of this study was the weak response of the red algae as a whole to the kelp clearings, a response that was only significant on the last sample date (December 1993). An inherent problem, however, with grouping large numbers of individual species when measuring a manipulative effect, is the masking of treatment differences from a variety of responses of separate taxa. The various responses of individual red algae in this study suggest that grouping algal species into broad groups such as total red algae can obscure rather than illuminate community organization regarding light requirements. The classification of species into functional groups is

used to develop general models and to increase the statistical robustness of data. When applied in this study, this technique similarly masked important single species attributes and interactions. Several subgroups of understory algae responded differently to the canopy disturbance; such inferences were lost if the subgroups were combined within the commonly used total and fleshy red functional groups.

We found that grouping the individual species according to similarities in how they respond to changes in their environment enhanced the ability to discern community-level effects of the canopy manipulations, and we devote the remainder of our discussion to inferences drawn from this method.

Similar to observations in terrestrial forests, the most abundant understory species, namely geniculate coralline algae, *Plocamium cartilagineum* and *Laurencia subopposita*, did not exhibit marked responses to the canopy manipulations and were therefore categorized as light-flexible algae. Moreover, *P. cartilagineum* and *L. subopposita* are perhaps the foliose red algae best adapted to the understory environment of Stillwater Cove; they are relatively unaffected by low light regimes and they are both adapted to dispersal via dislodgement, fragmentation and subsequent entanglement with the coralline turf (Downing 1995), the single most abundant understory in the cove. In contrast, those species that increased substantially following the removal of the kelp canopies, namely *Fauchea laciniata*, *Chondracanthus corymbifera*, *Prionitis lanceolata*, *Weeksia reticulata*, *Callophyllis crenulata*, *Rhodymenia californica* and *Cryptopleura farlowiana* were categorized as light-adapted species. These species were more abundant and exhibited greater richness within the no canopy treatment than in any of the other treatments. Furthermore, by subdividing the light-adapted species into 2 subgroups, high-light and intermediate-light species, we were able to discern that some species responded to the removal of a single canopy layer (intermediate-light species) while others required the removal of both kelp canopy layers (high-light species). It is interesting that, other than an initial bleaching of encrusting and articulated corallines which recovered rapidly, no alga responded negatively (i.e. were classified as shade loving) to the clearing of canopy layers.

The various mechanisms by which the different species responded to the canopy clearings are unclear and may have varied from species to species. For example, Edwards (1998) observed that the increases in *Desmarestia* abundance following kelp-canopy removal was due to the enhanced recruitment of its sporophytes (by means of reproduction of its microscopic gametophytes; Edwards 2000), while Watanabe et al. (1992) observed that *Pterygophora* exhibited a positive

physiological response (increased growth, fecundity and photosynthesis) following removal of the *Macrocystis* canopy. Similarly, Roberts (1996) observed that at least some red algae (e.g. *Bossiella californica*) can shift photosynthetic pigments throughout their thalli and alter reproductive patterns in response to changes in the light regime. Whether such abilities allow some species to shift from one response group to another is unclear, and we believe warrants further investigation.

The wide range in the responses of these various species of red algae foster a diverse and complex understory algal community in Stillwater Cove. To address such complex responses, it is necessary to not only fully describe the light regime within this multi-canopy community, but also to more completely appreciate the differences in the way each species responds to changes in the light environment. While similar results on the effects of canopy shading have been observed in other studies, most notably the dramatic positive response of *Desmarestia* following the removal of both canopies (e.g. Foster 1982, Reed & Foster 1984, Dayton et al. 1992, 1999, Edwards 1998), we believe our study is unique in that it offers greater insight into the complex nature of how multiple species, or groups of species, respond to canopy shading. As such, we argue that adopting the ecological response-group approach may elucidate otherwise cryptic responses by the benthic algal assemblages to changes in the canopy structure.

To adopt response groups composed of these species for future research, however, is premature. Independent studies testing the expected response to canopy removal (both single and multiple canopies) is warranted. These groupings may not hold true for different locations, different canopy structures, or for different depths. For instance, Kain (1987) classified *Plocamium cartilagineum* as a 'shade loving' species which failed to thrive under full irradiance at a depth of 0.5 m. Further field experimentation (additional clearing experiments and transplants) and laboratory studies are necessary before such classifications are adopted for generalization of response. A primary conclusion of this study is that variation in response among species occurs and should be taken into account to properly understand the complexity of an understory algal assemblage.

While this study was designed to investigate the competitive effects of canopy shading, other competitive effects were also apparent. The limited community changes after canopy removal (still dominated by geniculate corallines, *Plocamium cartilagineum* and *Laurencia subopposita*) suggests that shading is not the only factor structuring this system. The effects of proximity of spore sources, grazer abundance, substrate availability, sand cover, etc. likely also affect algal distribution and abundance, as has been

observed in other studies (e.g. Foster 1982, Reed et al. 1988, Dayton et al. 1992, 1999, Edwards 1998). The reduction in red algal abundance from the 1992 *Aplysia californica* recruitment episode demonstrates the importance of rare but intense grazing events on understory composition. While some of the observations are speculative, the species response trend characterized in this study does add insight into the relative importance of other processes regulating this kelp forest system, and calls for further investigation. While variability within the understory assemblage does not allow for competitive exclusion of these species, significantly lower abundance under canopy layers are evident.

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