



Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F)

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Abstract

Experiments in a central California *Macrocystis pyrifera* (L.) C.A. Agardh forest examined the effects of long-term (six year) kelp canopy exclusion on the abundance of the annual brown alga *Desmarestia ligulata* (Light F). Exclusion of both surface and subsurface kelp canopies from replicate clearings within Stillwater Cove, CA, USA showed that *D. ligulata* sporophyte recruitment is opportunistic, with more sporophytes occurring in areas where canopies were excluded than under control canopies. Kelp canopy exclusion also increased spring and summer bottom irradiances, and resulted in a steady increase of perennial turf algae over the six-year study. This, in turn, led to a decrease in the availability of nongeniculate coralline algae (the primary substratum on which *D. ligulata* recruits). Subsequently, the annual maximum abundance of *D. ligulata* sporophytes decreased in the canopy clearings, but did not change under control canopies. Removal of turf algae from experimental plots further increased bottom irradiances and significantly enhanced *D. ligulata* recruitment. When released from apparent competition for light and space, *D. ligulata* sporophytes exhibited an annual life history, with recruitment occurring during a two-week period (April 4–April 17) in the spring, and maximum bottom cover occurring in the summer (July). The onset of *Desmarestia* sporophyte recruitment was closely associated with seasonal increases in daylength and rapid decreases in ocean temperature. These results indicate that the *Desmarestia* sporophyte life history is both annual and opportunistic, with the onset of recruitment stimulated by predictable, seasonal changes in environmental conditions, and the magnitude of recruitment modified by stochastic processes that affect the availability of light and space. Comparison of these results with those from similar studies indicate that they are robust and suggest that they may be generalized over broad temporal and spatial scales. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: *Desmarestia ligulata*; Disturbance; Kelp canopy exclusion; Kelp forest; *Macrocystis pyrifera*; *Pterygophora californica*; Recruitment; Seaweed; Storm; Turf algae

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1. Introduction

Field studies on marine macroalgae have indicated that, within given locations, responses to disturbances, such as large waves, may differ greatly among species (McLean, 1962; Foster, 1982; Dayton and Tegner, 1984; Reed and Foster, 1984; Harrold et al., 1988) or among individuals of the same species (Watanabe et al., 1992). While some environmental factors, such as daylength (Lüning, 1986, 1993; tom Dieck, 1991; Lüning and Kadel, 1993), solar irradiance (Gerard, 1984), ocean temperature and seawater nutrient concentration (Jackson, 1977; Zimmerman and Kremer, 1984) vary seasonally and, therefore, may induce annual patterns in algal life histories, other factors, such as grazing (Dean et al., 1988; Watanabe and Harrold, 1991; Leonard, 1994), El Niño events (Dayton and Tegner, 1984; Dayton et al., 1992; Foster and Schiel, 1993; North et al., 1993) and severe storms (Foster, 1982; Dayton et al., 1984, 1992; Ebeling et al., 1985) are relatively unpredictable, and their effects on algal populations may vary in space and time (Dayton and Tegner, 1984; Santilices and Ojeda, 1984; Ebeling et al., 1985; Kennelly, 1987a,b). Relatively few studies, however, have simultaneously examined the relative roles of both predictable and stochastic process in the regulation of marine macroalgal populations.

Large ocean waves associated with winter storms are a major factor regulating subtidal algal populations along the California coast, USA (Rosenthal et al., 1974; Foster, 1982; Dayton et al., 1984, 1992; Ebeling et al., 1985; Seymour et al., 1989). The nearshore environment of this region is dominated by dense forests of the surface canopy-forming kelps *Macrocystis pyrifera* and *Nereocystis luetkeana*, and the subsurface kelp *Pterygophora californica*. These forests occur on rocky substrata at depths of 2 to over 30 m (Foster and Schiel, 1985) and support diverse assemblages of benthic algae that vary both geographically and temporally, at least in part due to differences in wave exposure (Foster, 1982; Breda and Foster, 1985; Harrold et al., 1988; Graham et al., 1997). This is particularly true for the brown alga *Desmarestia ligulata* var. *ligulata* (Light F) (hereafter *Desmarestia*), which commonly occurs in wave-exposed areas during spring and summer, but remains uncommon during the rest of the year and in protected areas (Foster, 1982).

Desmarestia is an annual alga that occurs from the low intertidal to a depth of 15 m and is widely distributed in the eastern Pacific, from Alaska to South America (Abbott and Hollenberg, 1976). In central California, *Desmarestia* sporophytes recruit in the spring, grow during the summer (attaining lengths of up to 2 m), reproduce in early-to-mid winter and then disappear (Edwards, 1996). *Desmarestia* is also an opportunistic alga that remains rare in established kelp stands, but recruits in high densities (multiple sporophyte blade layers producing > 100% cover 0–20 cm above the bottom) in areas where the dominant canopy-forming kelps have been removed experimentally or by winter storms (Foster, 1982; Reed and Foster, 1984; Dayton et al., 1992). In a two-year study on the effects of kelp-canopy removal on benthic algal communities, Reed and Foster (1984) observed that *Desmarestia* sporophytes recruited within a narrow time period in the spring, and were more abundant in areas where turf algae had been removed. Although many studies have documented a positive relationship between kelp canopy loss and *Desmarestia* recruitment, none have examined the

effect of kelp canopy exclusion on the year-to-year variation in sporophyte abundance, or evaluated what environmental factors are responsible for the timing of sporophyte recruitment.

The effects of long-term canopy exclusion may be particularly important to *Desmarestia* populations occurring in exposed areas where large ocean waves frequently remove kelp canopies. Graham (1996) observed that frequent removal of *Macrocystis pyrifera* canopies from an exposed area along the Monterey Peninsula, CA, led to increased cover of perennial, geniculate coralline algae. Similarly, Kennelly (1987a) and Kennelly and Underwood (1993) observed that exclusion of kelp canopies from experimental plots along the Australian coast resulted in a significant increase in turf algae, which subsequently led to increased sediment entrapment. These factors can negatively affect *Desmarestia* sporophyte recruitment (Reed and Foster, 1984; Edwards, 1996).

I examined the effects of long-term (six year) kelp canopy exclusion on the annual maximum abundance of *Desmarestia* sporophytes in a central California *Macrocystis pyrifera* forest, as well as the relationship between sporophyte recruitment and long-term changes in bottom cover of turf algae. I also evaluated year-to-year variability in the timing of sporophyte recruitment, and its relationship to seasonal changes in daylength and ocean temperature, and to a lesser degree, changes in ocean nutrient concentration. Finally, my results are compared to those from similar studies (Foster, 1982; Reed and Foster, 1984; Dayton et al., 1992) to evaluate their robustness over broad temporal and spatial scales.

2. Materials and methods

2.1. Study site

Field experiments were done from January 1992 to July 1997 in Stillwater Cove, located at the north end of Carmel Bay, California, USA (36°34'N, 121°56'W). This cove is characterized by moderate-relief granite, sandstone and conglomerate terraces that are separated by cobble and sand channels at depths from 6–14 m, and supports a surface canopy of *Macrocystis pyrifera*, a subsurface canopy of *Pterygophora californica* and a diverse assemblage of turf algae (primarily, *Calliarthron tuberculosum*, *C. cheilosporioides*, *Bossiella californica*, *Plocamium cartilagineum*, *Laurencia subopposita* and *Cryptopleura farlowianum*). The Cove opens to the south and is relatively protected from large northern swells associated with winter storms. *M. pyrifera* canopies reach their surface maxima in early-to-mid summer and minima in late winter (Reed and Foster, 1984).

2.2. Effects of variation in light and space on *Desmarestia* abundance

2.2.1. Kelp canopy exclusion

Complete removal of kelp canopies by severe winter storms was simulated in January 1992 by clearing all surface and subsurface canopies from two 20 m radius half circles

(628 m²) located approximately 200 m apart at a depth of 12 m, near the middle of the Cove. An unmanipulated control area of equal size was established adjacent to each clearing. To examine the effect of kelp canopy exclusion on the variation in annual maximum abundance of *Desmarestia* sporophytes, as well as to determine the timing of sporophyte recruitment, the clearings were maintained weekly until July 1997. The effect of kelp canopy exclusion on bottom irradiance was determined by measuring light intensity (photon flux density; $\mu\text{Em}^{-2} \text{s}^{-1}$) in three bare patches on the bottom in each canopy treatment during winter (February), early spring (March) and early summer (May) 1995 within each canopy treatment using a Li-cor 4 π quantum sphere collector (sample rate = 2 Hz) attached to a hand held CTD (Seabird Electronics-Sea Cat[®]). The three irradiance estimates in each canopy treatment on each sample date were determined from the average of ~40 measurements, taken over approximately a 20-s period.

Maximum cover of *Desmarestia* sporophytes (used as a measure of plant abundance) was estimated weekly during the spring and summer each year (1992–1997) in ten 0.25 m² quadrats that were haphazardly placed within each canopy clearing and control area. To ensure this haphazard sampling method did not bias bottom-cover estimates (Krebs, 1989), a subset of these data were compared to data simultaneously collected from a random sampling method. Here, ten quadrats were randomly placed within a randomly chosen replicate of each canopy treatment on three sampling dates during this study. Analysis of variance (ANOVA) determined that haphazard and random sampling methods did not yield differences in bottom cover estimates ($p = 0.63$; Table 2; see Section 2.3 for test description). In addition, the cover of nongeniculate coralline algae (the primary bare space within the cove) and perennial turf algae was estimated each spring within the canopy clearings and control areas using point contacts. Here, three transects were established along randomly selected compass headings in each treatment replicate, and a 2-m-long PVC bar attached to a piece of string with ten knots tied in it was placed at each of five randomly selected positions along each transect. The string was pulled taut on both sides of the bar and the substratum/algal species each of the knots contacted was identified. The bottom cover of bare space and perennial turf algae was then estimated for each bar position from these twenty point contacts (Cowen et al., 1982), and within each canopy treatment replicate from the average of the fifteen bar locations. Bottom cover of bare space and perennial turf algae was then estimated for each canopy treatment from the average of the two treatment replicates ($n = 2$).

2.2.2. Effects of turf algae

To assess the potential effects of loss of turf algae by severe winter storms on *Desmarestia* recruitment, all turf algae were removed from three 0.25 m² replicate plots within one of the kelp canopy clearings in February 1993. Three 0.25 m² unmanipulated control plots were interspersed among the turf-removal plots. Sporophyte recruitment was then estimated by counting all new *Desmarestia* sporophytes in the plots on five dates during the following spring and summer. To examine the effects of turf algae on bottom light, irradiances in bare spaces and under turf algae were estimated within one of the canopy clearings on the sample dates described in Section 2.2.1. Irradiances in bare spaces (no turf) were determined in the three locations described above, and

irradiances under turf algae were estimated by removing the turf algae from three haphazardly selected locations, placing the CTD's quantum sphere collector on the exposed substratum, and then covering it with the turf algae removed from that location. Irradiance in the three locations (replicates) of each turf treatment was determined from the average of ~40 measurements taken over a 20-s period.

Qualitative observations made in spring 1993 suggested that *Desmarestia* sporophyte recruitment was greater on nongeniculate coralline algae than on other available substrates (i.e., geniculate coralline algae, fleshy algae, bryozoans and sponges). To determine if this relationship was significant, in April 1993, all new *Desmarestia* sporophytes occurring within 25 0.25 m² quadrats randomly placed within the canopy clearings were examined, and the substrate they were growing on was identified. On the same date, bottom cover of available substrates occurring within the clearings was estimated using point contacts. In addition, in spring 1994, the relationship between sporophyte recruitment and the exposure of nongeniculate coralline algae was examined by estimating the bottom cover of nongeniculate coralline algae within twelve 0.25 m² quadrats that were randomly placed in each of the clearings, and then counting the number of young *Desmarestia* sporophytes within each quadrat.

2.2.3. Onset of sporophyte recruitment

The year-to-year variability in the timing (onset) of *Desmarestia* sporophyte recruitment was evaluated by examining the date of sporophyte recruitment each year between 1993 and 1997. Each year, new sporophytes were sampled for in twenty haphazardly placed 0.25 m² quadrats within each canopy clearing, and in ten quadrats within each control area. Since recruitment occurs in the spring (Reed and Foster, 1984), sites were sampled more frequently (~three times per week) between early March and late June, and less frequently (~once per week) during other months. The date sporophytes were first observed in sampling quadrats identified the date of recruitment for that year. Data provided by R.P. Clark (unpubl.) provided the date of sporophyte recruitment (\pm one week) for 1992.

To examine possible factors responsible for stimulating *Desmarestia* sporophyte recruitment, the relationships between the onset of recruitment and seasonal changes in daylength, ocean temperature and seawater nutrient concentration were evaluated. Daylength and ocean temperature in Stillwater Cove were estimated between January 1992 and June 1997, while seawater nutrient concentration was estimated in 1995 only. Daylength in the Cove was modeled using the equation [daylength = 12 - 2.2 · Cos(2 π (date + 10)/365)] (Zimmerman et al., 1984); where 12 is mean daylength, in hours, 2.2 is the amplitude of the curve, in hours (set for the appropriate latitude and with maximum and minimum values occurring in summer and winter, respectively), date + 10 sets the minimum daylength at December 21, and dividing by 365 sets the date to the Julian day. Daily ocean temperatures were recorded within the Cove on 335 days between April, 1993 and October, 1994 using a Ryan[®] J90TM thermograph placed at a depth of 6 m near the middle of the cove, and on 139 days between March 1996 and May, 1997 using an Onset Computer Corporation[®] Optic Stow AwayTM temperature logger, which was placed at a depth of 12 m within one of the canopy clearings. Temperatures for the remainder of the study period were modeled using daily ocean

temperatures recorded at Granite Canyon Laboratories, approximately 20 km south of Stillwater Cove (regression equation; $SC = 0.85 \times GCL + 0.733$; $r^2 = 0.91$; $n = 335$). Measurements of seawater nitrate concentration were then used to estimate of nutrient concentration in the Cove. Here, water samples were collected from the study site at a depth of 10 m by hand in 25 ml scintillation vials on 39 occasions during 1995 using SCUBA. Vials were immediately placed on ice, transported to the laboratory, frozen, and later analyzed with a modified Strickland and Parsons nitrate/nitrite analysis method on an Alpkem 300[®] nutrient analyzer using flow analysis (Strickland and Parsons, 1972). Relationships between the onset of *Desmarestia* sporophyte recruitment and changes in daylength, ocean temperature and seawater nutrient concentration were analyzed graphically.

2.3. Statistical analyses

All statistical analyses were done using SYSTAT (Windows version 7.0). The effect of canopy removal on bottom irradiance was examined with a two-way mixed-model analysis of variance (ANOVA), with canopy treatment as a fixed factor and season as a random factor. Subsequent Bonferroni-adjusted planned pairwise comparisons (Simes, 1986) on the significant season \times canopy treatment interaction were used to examine differences between canopy clearings and control areas during each season separately. Differences between haphazard and random sampling methods were examined with a three-way mixed-model ANOVA, with sample method as a fixed factor, canopy treatment and date as random factors, and canopy treatment blocked within date. Due to multiple random factors in the statistical linear model ($X_{ijk_r} = \mu + D_i(\text{date}) + C_j(\text{canopy treatment}) + M_k(\text{method}) + DM_{ik} + CM_{jk} + e_{ijk_r}$), a precise test of sample method could not be done (Underwood, 1997). Therefore, the model mean square error was pooled with the nonsignificant date \times method, and canopy treatment \times method interaction terms and the differences between sample methods were retested under the reduced linear model ($X_{ijk_r} = \mu + D_i + C_j + M_k + e_{ijk_r}$; Underwood, 1997; Table 1 Table 2). Changes in maximum annual *Desmarestia* abundance among years were compared between the

Table 1

Analysis of variance (mixed-model; method = fixed, date and canopy treatment = random) of the effects of sample date, canopy treatment and sample method (haphazard vs. random) on *Desmarestia* sporophyte abundance estimates

Source of variation	SS	df	Mean square	F-statistic	P-value
Date	0.634	2	0.317	4.831	0.010
Canopy treatment	1.840	1	1.840	28.039	< 0.001
Method	0.015	1	0.015	No test
Date \times method	0.008	2	0.004	0.061	0.941
Canopy treatment \times method	0.008	1	0.008	0.119	0.731
Error	7.351	112	0.066		

Full linear model; $X_{ijk_r} = \mu + D_i(\text{date}) + C_j(\text{canopy treatment}) + M_k(\text{method}) + DM_{ik} + CM_{jk} + e_{ijk_r}$.

Due to multiple random factors, a precise test of method was not possible (see Table 2 for reduced model test). $N = 10$ (quadrats per sample method per canopy treatment per date).

Table 2

Analysis of variance (reduced model) of the effects of sample method (haphazard vs. random) on *Desmarestia* sporophyte abundance estimates in the two canopy treatments on three sample dates

Source of variation	SS	df	Mean square	F-statistic	P-value
Date	0.634	2	0.317	4.955	0.009
Canopy treatment	1.840	1	1.840	28.755	< 0.001
Method	0.015	1	0.015	0.229	0.630
Error	7.351	115	0.064		

Non significant date \times method and canopy treatment \times method interactions under the full linear model (see Table 1) allowed for pooling of their mean squares with the model mean square error and subsequent removal from the statistical linear model (Underwood, 1997).

Reduced model; $X_{ijk_r} = \mu + D_i + C_j + M_k + e_{ijk_r}$.

$N = 10$ (quadrats per sample method per canopy treatment per date).

canopy treatments by examining the homogeneity of slopes (canopy treatment \times year interaction) with analysis of covariance (ANCOVA). After failing to meet the assumption of parallelism (see Section 3.1.1), differences in maximum sporophyte abundance among years were compared between canopy treatments using a two-way model I ANOVA, with year and canopy treatment as fixed factors (Underwood, 1997). Independent regressions, with Bonferroni-adjusted probabilities, were then used to examine changes in maximum sporophyte abundance among years within each canopy treatment separately.

Changes in bottom cover of nongeniculate coralline algae among years were compared between the canopy treatments by examining the homogeneity of slopes (canopy treatment \times year interaction) with ANCOVA. After failing to meet the assumption of parallelism (see Section 3.1.1), independent regressions, with Bonferroni-adjusted probabilities, were used to examine changes in bottom cover among years within each canopy treatment separately. Statistical analysis of *Desmarestia* sporophyte recruitment in the turf-removal and control plots was problematic. Due to the lack of fully nested, independent residuals, within-subject \times between-subject interactions could not be tested using repeated measures ANOVA (Underwood, pers. comm.). Therefore, the date of maximum sporophyte density was chosen, and differences in *Desmarestia* recruitment between the turf-removal and control plots were analyzed with a *t*-test.

Heterogeneity χ^2 determined that sporophyte recruitment and substrate availability data obtained from the 25 quadrats sampled in April 1993 were homogeneous and, therefore, the results were pooled ($\chi^2 = 30.18$; $df = 48$; $p = 0.98$; Zar, 1984). Subsequently, a single χ^2 analysis (with $n = 321$) was used to determine if the frequency in which *Desmarestia* sporophytes recruited onto nongeniculate coralline algae was significantly different than expected, given the substrate's availability. Finally, the relationships between *Desmarestia* sporophyte recruitment and the availability (cover) of nongeniculate coralline algae in the two canopy clearings were compared by examining the homogeneity of slopes (clearing \times cover interaction) with ANCOVA. After meeting the assumption of parallelism (see Section 3.1.2), the overall relationship between sporophyte recruitment and availability of nongeniculate coralline algae in the canopy clearings was examined with a single linear regression.

Prior to all statistical tests, data were examined for homogeneity of variances using an *F* test or Cochran's *C* test, and for normality by graphical interpretation of frequency distributions of residuals. The appropriate transformations were applied to those data that did not meet either of these assumptions, and subsequent retesting determined that problems were corrected. All percent-cover data were arcsin transformed (Sokal and Rohlf, 1995) and power analysis was performed on appropriate nonsignificant results (Winer, 1971).

3. Results

3.1. Effects of variation in light and space on *Desmarestia* abundance

3.1.1. Kelp canopy exclusion

The effect of kelp canopy exclusion on bottom irradiance varied seasonally in 1995 (ANOVA: season \times canopy treatment interaction; $p < 0.001$; Fig. 1 Table 3). Kelp canopy removal simulated the effects of storm-induced canopy loss on winter bottom light levels, with no differences observed between the canopy clearings and control areas (Bonferroni; $p = 0.378$; Table 4 Fig. 1). Control canopies began to recover in early spring, significantly reducing bottom irradiance (to approximately 70%) relative to the canopy clearings (Bonferroni; $p = 0.004$). Control canopies became well established by early summer, further reducing bottom irradiance (to approximately 25%) relative to those in the canopy clearings (Bonferroni; $p < 0.001$).

Maximum abundance of *Desmarestia* sporophytes occurred in the summer (July) each

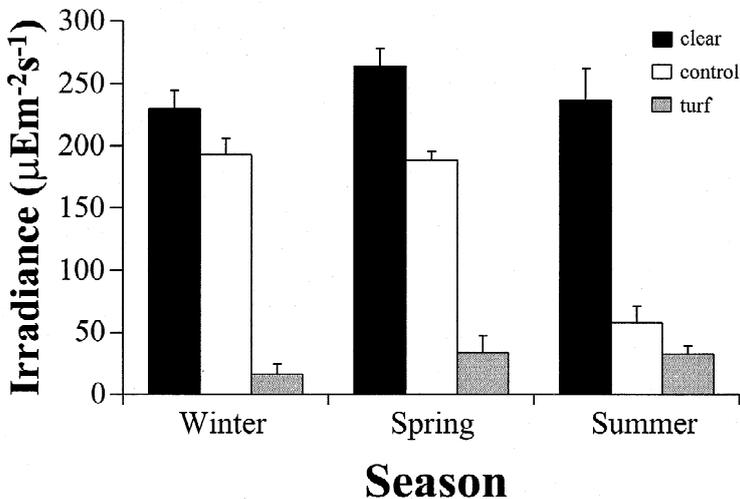


Fig. 1. Bottom irradiances (photon flux density; $\mu\text{Em}^{-2} \text{s}^{-1}$; means + standard error) in canopy clearings (clear), control areas (control) and under turf algae (turf) in winter, spring and summer 1995. $N = 3$ irradiance estimates per treatment per season.

Table 3

Analysis of variance (mixed-model; canopy treatment = fixed, season = random) of the effects of kelp canopy exclusion and turf algae (treatments) on bottom irradiance among seasons (winter, spring and summer) in 1995

ANOVA table					
Source of variation	SS	df	Mean square	F-statistic	P-value
Season	9930.227	2	4965.113	10.016	0.002
Treatment	181 164.965	2	90 582.482	18.767	0.009
Season × treatment	19 306.807	4	4826.702	9.736	< 0.001
Error	7931.833	16	495.740		

$N = 3$ (irradiance estimates per treatment per season).

year and was significantly greater in areas where kelp canopies had been removed (ANOVA: $F = 277.553$; $df = 1, 5$; $p < 0.001$; Fig. 2). Furthermore, among-year changes in maximum sporophyte abundance differed between the canopy treatments (ANCOVA: canopy treatment × year interaction; $p = 0.036$; Table 5). Subsequent independent regressions determined that annual sporophyte abundance steadily decreased in the canopy clearings ($p = 0.012$), but did not change in the control areas ($p = 0.84$; Table 4). Regardless, in all years, *Desmarestia* sporophytes exceeded 100% bottom cover within localized areas of the canopy clearings, but remained consistently rare (< 10% bottom cover) within the control areas.

Among-year changes in the exposure of nongeniculate coralline algae differed significantly between the canopy treatments over the course of this study (ANCOVA: canopy treatment × year interaction; $F = 12.575$; $df = 1, 6$; $p = 0.012$). Independent regressions indicated that exposure of nongeniculate coralline algae decreased significantly within the canopy clearings ($p < 0.001$) but did not change in the control areas ($p > 0.05$; Fig. 3A). The primary cause of this decrease was a significant increase in bottom cover of perennial turf alga (*Calliarthron tuberculosum*) that occurred in the canopy clearings ($p < 0.05$) but not in the control areas ($p > 0.05$; Fig. 3B) over this period.

Table 4

Bonferroni-adjusted planned comparisons on the season × treatment interaction, testing differences in irradiance between canopy clearings vs. control areas, and under turf vs. open space in each season separately

Bonferroni-adjusted comparisons		
Comparison	Difference between means ($\mu\text{Em}^{-2} \text{s}^{-1}$)	P-value
Kelp clearing vs. control		
Winter	36.33	0.378
Spring	75.67	0.004
Summer	167.67	< 0.001
Under turf vs. open space		
Winter	– 214.00	< 0.001
Spring	– 231.33	< 0.001
Summer	– 204.83	< 0.001

$N = 3$ (irradiance estimates per treatment per season).

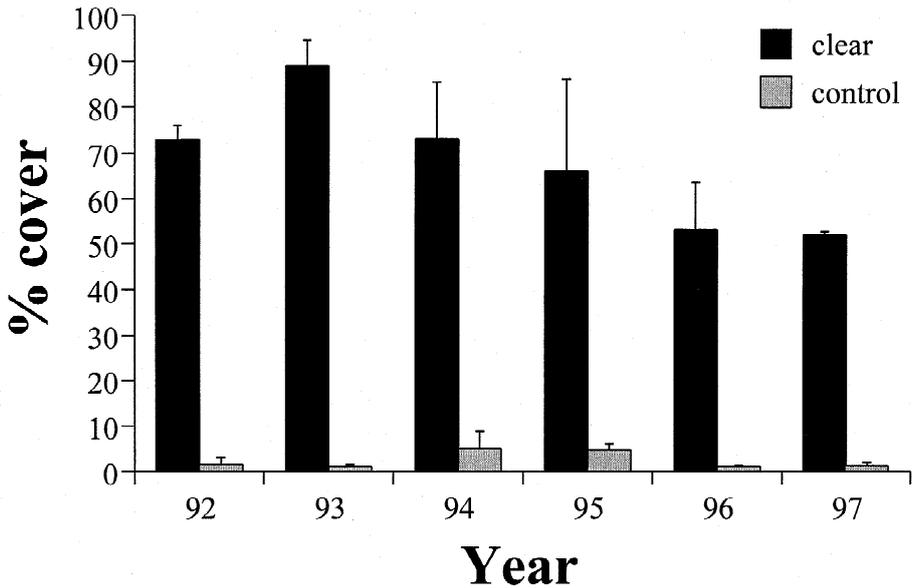


Fig. 2. Annual maximum abundance (cover) of *Desmarestia* sporophytes (means + standard error) in canopy clearings (clear) and control areas (control) from 1992–1997. Ten 0.25 m² quadrats, haphazardly placed in each canopy treatment replicate, were used as subsamples to estimate average cover per replicate. The mean cover per treatment per year was estimated from the replicate averages ($n = 2$). Maximum sporophyte abundance occurred in July each year.

3.1.2. Effects of turf algae

Removal of turf algae from experimental plots within the canopy clearings (1) exposed underlying nongeniculate coralline algae and (2) increased bottom irradiances by as much as ten times (from $< 20 \mu\text{Em}^{-2} \text{s}^{-1}$ to $> 200 \mu\text{Em}^{-2} \text{s}^{-1}$; Table 4 Fig. 1). *Desmarestia* sporophytes recruited into the plots in early April 1993 reached their

Table 5

(A) Analysis of covariance (canopy treatment = fixed, year = covariate) testing for parallelism in regression slopes of the relationships between the maximum abundance of *Desmarestia* sporophytes and year (1992–1997) within the two canopy treatments. (B) Independent regressions with Bonferroni-adjusted probabilities of year vs. *Desmarestia* abundance in the canopy clearings and controls areas

Source of Variation	SS	df	Mean square	F-statistic	P-value
Year	0.081	1	0.081	5.847	0.025
Canopy treatment	0.091	1	0.091	6.529	0.019
Year \times canopy treatment	0.070	1	0.070	5.026	0.036
Error	0.278	20	0.014		
B. Regressions					
Treatment	Slope	y-intercept	F-statistic	P-value	r ²
Canopy clearings	-0.112	11.579	30.123	0.012	0.91
Control areas	-0.005	0.617	0.048	0.840	0.02

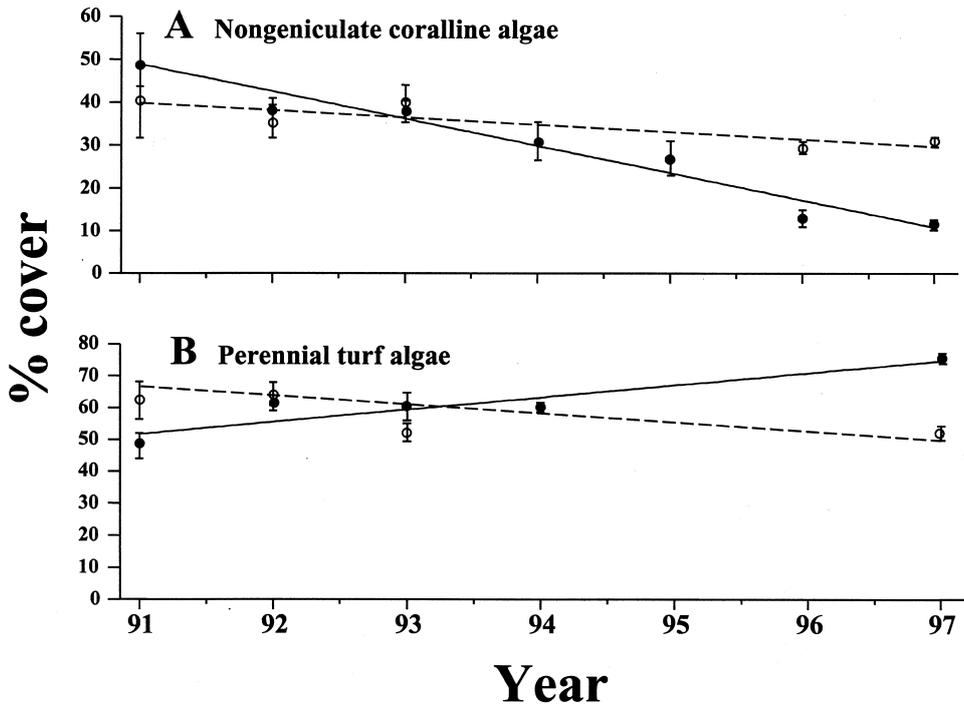


Fig. 3. (A) Linear regressions of springtime exposure of nongeniculate coralline algae (cover; mean \pm standard error) vs. year in the canopy clearings (\bullet) and control areas (\ominus) from 1992–1997. Regression equations: Canopy clearings, cover = $-6.33 \times \text{year} + 48.85$; $r^2 = 0.91$; $n = 7$; $p < 0.05$; control areas, cover = $-1.67 \times \text{year} + 39.94$; $r^2 = 0.80$; $n = 5$; $p > 0.05$. Mean cover per canopy treatment per date was estimated from the averages of the two replicates ($n = 2$). (B) Linear regressions of springtime cover of perennial turf algae vs. year, in canopy clearings and control areas from 1992–1997. Regression equations: Canopy clearings, cover = $-1.67 \times \text{year} + 39.94$; $r^2 = 0.80$; $n = 5$; $p > 0.05$; control areas, cover = $-1.81 \times \text{year} + 61.56$; $r^2 = 0.57$; $n = 4$; $p = 0.24$.

maximum density by late April and were more abundant in turf-removal plots (128.67 ± 36.04 recruits 0.25 m^{-2} ; mean \pm SE) than in control plots (14.67 ± 8.68 recruits 0.25 m^{-2} ; mean \pm SE; $t_{2(2)} = 3.07$; $p = 0.037$).

Of the 321 recruits sampled in spring 1993, a significantly greater number occurred on nongeniculate coralline algae than expected, given the substrate's availability ($\chi^2 = 2121.509$; $df = 2$; $p < 0.001$, Table 6). Furthermore, in spring 1994, cover of nongeniculate coralline algae, which varied between zero and 82% (per 0.25 m^2) within the clearings, was positively related to *Desmarestia* recruitment ($p < 0.001$; Fig. 4). This relationship was not significantly different between the canopy clearings (ANCOVA: clearing \times cover interaction; $F = 0.432$; $df = 1, 20$; $p = 0.519$).

3.2. Onset of sporophyte recruitment

The onset of *Desmarestia* sporophyte recruitment occurred within a two-week period

Table 6

Occurrence of *Desmarestia* sporophytes on available substrata vs. substratum availability within Stillwater Cove

Substrate type	Available substratum (%)	Percentage of recruits on substrate (no. of recruits)
Nongeniculate coralline algae	16.0	91.0 (291)
Geniculate coralline algae	52.5	6.5 (21.0)
Other (sponges, bryozoans, non-coralline algae, rock)	31.5	2.5 (9)
Total	100	100 (321)

Sporophyte substrates were identified by close examination of all *Desmarestia* holdfasts within 25 randomly placed quadrats in the two canopy clearings in April 1993, and substratum availability was estimated by point contacts. Note: Data from the 25 quadrats were homogeneous and are pooled (see Section 3.1.2).

(April 4 to April 17) each year (average, April 9; SE, 2.6 days) with little year-to-year variability (average date was determined by transforming dates to the Julian day). No sporophytes were observed to recruit after mid-May in any year, and maximum sporophyte density was attained within a few weeks of the onset of recruitment (unpubl.

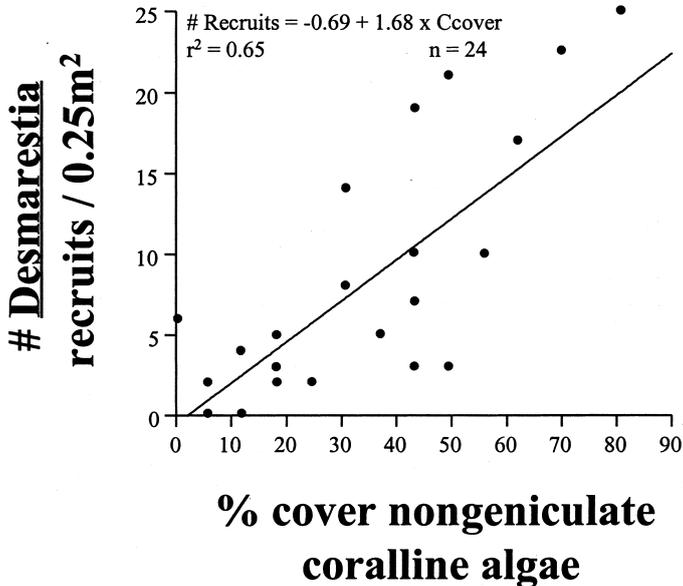


Fig. 4. Linear regression of exposure of nongeniculate coralline algae (cover) vs. *Desmarestia* sporophyte recruitment (recruits) within the two canopy clearings in spring 1994. Cover was estimated using point contacts within twelve 0.25 m² quadrats that were randomly placed in each clearing replicate, and sporophyte recruits were counted within each quadrat.

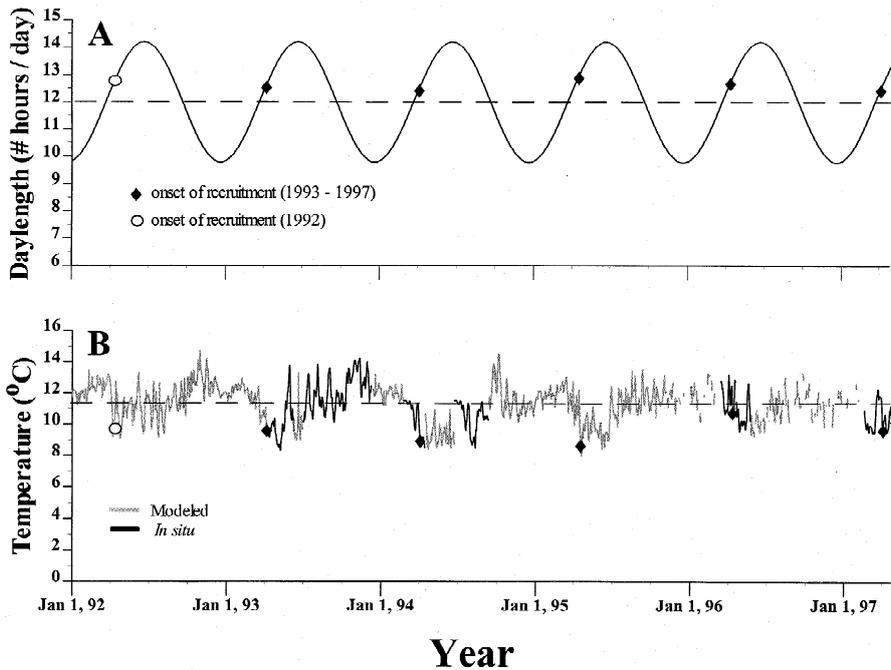


Fig. 5. (A) Daylength in Stillwater Cove vs. onset of sporophyte recruitment (1992–1997). Hatched line denotes the mean daylength (12 h/day). (B) Ocean temperatures within the Cove (measured in situ and modeled) vs. onset of sporophyte recruitment. Hatched line denotes the mean temperature (11.34°C).

data). Sporophyte recruitment was closely associated with increasing daylength (Fig. 5a) and rapid decreases in ocean temperature (Fig. 5b), with recruits first observed at daylengths of 12.7 ± 0.1 h day⁻¹ (mean \pm SE) and ocean temperatures of 9.9 ± 0.4 °C (mean \pm SE).

Although *Desmarestia* sporophyte recruitment also occurred when seawater nutrient concentration was highest, nutrient levels within Stillwater Cove were highly variable (ranging between 2 and 21 μ M NO₃), and were consistently higher than those typically observed during the spring in southern California (Jackson, 1977; Zimmerman and Kremer, 1984) when *Desmarestia* recruits. This suggests that the onset of recruitment was not closely associated with changes in seawater nutrient concentration itself, but that this weak association was probably the result of a significant negative relationship between nutrient concentration and ocean temperature (Regression: $r^2 = 0.28$; $p = 0.006$; $n = 25$).

4. Discussion

Exclusion of the canopy-forming kelps *Macrocystis pyrifera* and *Pterygophora californica* from experimental clearings within Stillwater Cove over a six-year period

resulted in significantly greater annual maximum abundance of *Desmarestia* sporophytes within the canopy clearings relative to control areas. These results are similar to those obtained over a decade earlier by Reed and Foster (1984) from another site in Stillwater Cove, indicating that they are robust and suggesting that they may be generalized over broad temporal scales. These results also support those of Foster, (1982, Santa Cruz, CA) and Dayton et al., (1992, San Diego, CA), who observed that *Desmarestia* sporophytes typically recruit in high densities in exposed areas where canopies are removed by winter storms, but remain uncommon both in wave-protected areas and during mild years, when kelp canopies persist. This similarity suggests that these results may also be generalized over broad spatial scales. In fact, similar patterns of *Desmarestia* recruitment have been observed in Bahía Tortugas, Mexico (I. Patron, pers. comm.) and Shemya, Aleutian Islands, AK, USA (unpubl. data). Although winter storms typically thin kelp canopies in Stillwater Cove, the canopies recover rapidly relative to more wave-exposed areas in this region (Cowen et al., 1982; Foster, 1982), thereby allowing the canopies to become reestablished prior to *Desmarestia* recruitment, possibly explaining why *Desmarestia* sporophytes still remain uncommon in the Cove. During years in which storms occur late in the winter, however, recovery of kelp canopies within the Cove may be delayed, allowing *Desmarestia* to become abundant in the following spring and summer (Foster and Schiel, 1985). Taken together, this suggests that *Desmarestia* exhibits an opportunistic life history, becoming locally abundant in areas where kelp canopies are removed by large ocean waves, but remaining uncommon in protected areas where canopies are more persistent.

This opportunistic life history of *Desmarestia* sporophytes is not surprising considering that some species of *Desmarestia* require relatively high irradiances for sporophyte production (Peters and Müller, 1986). Although the removal of both surface and subsurface kelp canopies within Stillwater Cove increased spring and summer bottom irradiances by as much as 400% relative to control areas, removal of the *Macrocystis pyrifera* canopy alone only increased irradiances by 133% relative to those under both canopy layers (R.P. Clark, unpubl. data). Most likely because of this added effect of the *Pterygophora californica* canopy, removal of both canopy layers significantly enhances *Desmarestia* recruitment relative to areas where only the *M. pyrifera* canopy is removed (Reed and Foster, 1984; Clark, 1996; pers. obs.). The removal of *M. pyrifera*, but persistence of *P. californica*, represents the effects of typical winter storms in Stillwater Cove, while removal of both canopy layers is representative of more severe storms (Reed and Foster, 1984). This also may explain why *Desmarestia* becomes abundant following severe winter storms, but remains uncommon following typical storms, even though the *M. pyrifera* canopies are significantly thinned.

Damage from severe winter storms can also result in the removal of large amounts of turf algae (Foster, 1982), thereby increasing the exposure of nongeniculate coralline algae (bare space). Here, I observed a positive relationship between *Desmarestia* recruitment and the availability of nongeniculate coralline algae within the canopy clearings. Furthermore, consistent with Reed and Foster (1984), I observed that removal of turf algae from experimental plots, in combination with kelp canopy removal, greatly increased the recruitment of *Desmarestia* sporophytes. This appeared to be the result of increased bottom irradiance, as light levels under the turf algae varied between 5 and 20

$\mu\text{Em}^{-2} \text{ s}^{-1}$. At these low irradiances, *Desmarestia* gametophytes remain dormant and do not produce sporophytes (Edwards, 1996). In areas without turf algae, however, bottom irradiances often exceeded $200 \mu\text{Em}^{-2} \text{ s}^{-1}$.

The results from this study are similar to those of Kennelly (1987b), who observed that continuous exclusion of kelp canopies in an Australian *Eklonia radiata* forest resulted in increased cover of turf algae relative to unmanipulated areas. Here, within the *Macrocystis pyrifera*–*Pterygophora californica* forest in Stillwater Cove, I observed that, over the six years of kelp canopy exclusion, bottom cover of perennial turf algae (primarily *Calliarthron tuberculosum*) increased from ~40 to ~80% within the canopy clearings, but did not change in the control areas. As a result, exposure of nongeniculate coralline algae decreased within the canopy clearings. The subsequent decrease in maximum annual sporophyte abundance in the canopy clearings between 1993 and 1997 is believed to be due to three factors that were associated with the changes in perennial turf algae. First, exposure of nongeniculate coralline algae decreased annually over this period, leading to a decrease in the availability of substrate that was suitable for sporophyte recruitment. Second, as bottom cover of perennial turf increased within the canopy clearings, the amount of substrate with adequate irradiance for sporophyte production no doubt decreased, leading to decreased sporophyte abundance. Finally, increased cover of turf algae in the canopy clearings appeared to increase sediment entrapment (pers. obs.; see also Kennelly, 1987a; Kennelly and Underwood, 1993) and, thereby, may have negatively affected sporophyte recruitment and survivorship (Edwards, 1996; Devinnny and Vorse, 1978; Deysher and Dean, 1986 for data on sedimentation vs. *M. pyrifera* recruitment). In contrast, the slight increase in *Desmarestia* sporophyte abundance observed between 1992 and 1993 is believed to be due to a smaller propagule source (i.e. a lower abundance of sporophytes) prior to the initial kelp canopy removal, as *Desmarestia* was rare in 1991 (Clark, unpubl. data) but was abundant in the following years. No significant among-year differences in cover of perennial turf algae or *Desmarestia* abundance were observed in the control areas. Although the above factors, in combination, were observed to significantly affect *Desmarestia* recruitment, the individual importance of each still remains unclear.

In the absence of kelp canopies, *Desmarestia* clearly exhibited an annual life history, with sporophyte recruitment occurring within a two-week period (April 4 to April 17) each year, with little year-to-year variability. This is consistent with the observations made by Reed and Foster (1984), who observed that *Desmarestia* sporophytes recruited in Stillwater Cove in early April during 1979 and 1980. Thus, the timing of recruitment appears to be consistent among years and over broad (> ten years) temporal scales. My results further indicate that the onset of sporophyte recruitment is closely associated with increases in daylength and decreases in ocean temperature, but not with increases in seawater nutrient concentration (although a weak association was observed due to a significant negative correlation between nutrient concentration and ocean temperature). Although the importance of these factors was not examined individually, it appears that the timing of sporophyte recruitment is closely tied to predictable, seasonal changes in these environmental factors. My results further show that the magnitude of sporophyte recruitment is then modified by stochastic processes (e.g., disturbance from large waves), which alter the physical and biological environment, and affect competition for light and

space. Comparisons with the results from other studies, in addition to the temporal scale of this study, suggest that these results can be generalized over broad spatial and temporal scales. Few studies have documented a robustness of this nature over similar scales.

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