FACTORS REGULATING THE RECRUITMENT OF THE ANNUAL ALGA *DESMARESTIA LIGULATA* ALONG THE CENTRAL CALIFORNIA COAST

A thesis submitted to the faculty of
San Francisco State University
in partial fulfillment of the
requirements for the
degree

Master of Science
in
Marine Science

by

Matthew Sean Edwards

San Francisco, California

September, 1996

FACTORS REGULATING THE RECRUITMENT OF THE ANNUAL ALGA *DESMARESTIA LIGULATA* ALONG THE CENTRAL CALIFORNIA COAST

Matthew Sean Edwards
San Francisco State University
1996

Within Stillwater Cove, CA, sporophytes of the annual alga *Desmarestia ligulata* recruit in high densities (>100% bottom cover) into areas where kelp canopies have been removed experimentally or by winter storms. Continuous exclusion of canopies over a five year period indicated a seasonal pattern of sporophyte recruitment in spring, maximum abundance in summer and disappearance the following winter, with little temporal variation among years. Removal of turf algae enhanced *D. ligulata* recruitment by increasing bottom irradiances and the availability of nongeniculate coralline algal substrate. The timing of sporophyte recruitment was closely associated with increases in daylength and decreases in temperature. Microscopic gametophytes persist during periods of sporophyte absence, allowiug sporophytes to reoccur yearly. Gametophyte survivorship was negatively affected by sedimentation and grazing, and positively related to nongeniculate coralline algae.

ACKNOWLEDGMENTS

I would like to thank my committee members: Drs. Mike Foster, Dan Reed and Tom Niesen for reviewing and commenting on this manuscript. I want to thank Dan Reed for his guidance with this project, and for introducing me to subtidal research before it ever started. I would especially like to thank Mike Foster for his friendship, guidance and for showing me the beauty of the kelp forests along our coast. I want to thank John Heine for his friendship and for running a superior dive program that made doing a subtidal thesis possible. As with any subtidal project, I could not have done it without the help of my dive buddies. Although they were numerous, I would like to extend my warmest appreciation to a few that hauled tanks, shivered in the cold water and then lamented with me about it all afterwards at Taco Bell more times than I can remember. Thank you Ross Clark, James Downing, Stewart Lamerdin, Mark Pranger, Michelle Jacobi and Brad Colvin. I want to thank Mike Graham for those late night discussions that brought about an understanding of statistics that otherwise would not have been possible. Finally I want to extend my most sincere appreciation to the faculty of Moss Landing who made my time here so much easier; specifically to Gail Johnston and Sandy Yarbrough for fixing it when I "forgot to dot the i's and cross the t's". This project could not have been done without the financial assistance of the Dr. Earl H. and Ethyl M. Meyers Oceanographic and Marine Biology Trust or The Phycological Society of America's Grants-in-Aid of Research.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF APPENDICES

Table Page

CHAPTER 1

FACTORS REGULATING THE RECRUITMENT OF THE ANNUAL ALGA *DESMARESTIA LIGULATA* ALONG THE CENTRAL CALIFORNIA COAST

ABSTRACT

Within Stillwater Cove, CA, sporphytes of the annual alga *Desmarestia ligulata* recruited in high densities (>100% bottom cover) into areas where kelp canopies were removed either experimentally or by winter storms. Continuous exclusion of the canopies over a five year period indicated a seasonal pattern existed in which macroscopic sporophytes recruited during the spring, with little year-to-year variation in timing, attained maximum bottom cover during the summer and disappeared the following winter. Removal of turf algae increased both bottom irradiance and the availability of nongeniculate coralline algal substrate, both of which significantly enhanced *D. ligulata* recruitment. The timing of sporophyte recruitment was closely associated with seasonal (predictable) increases in daylength and rapid decreases in ocean temperature, and to a lesser degree, with increased in nutrient concentration. Thus it appears that *D. ligulata* exhibits a life history that is both annual and opportunistic, with sporophyte recruitment being stimulated by both seasonal (predictable) changes in environmental conditions as well as unpredictable disturbances to kelp canopies and turf algae.

INTRODUCTION

The relationship between environmental factors and the recruitment, growth and mortality of marine macroalgae has been a focus of recent field studies in algal demography (Foster 1982; Mathieson 1982; Dayton *et al.* 1984; Reed & Foster 1984; Schiel 1985; Deysher & Dean 1986; Santilices 1990; Underwood & Kennelly 1990; Konar & Foster 1992). Within a given location, responses to factors such as swell exposure may differ greatly among species (McLean 1962; Dayton & Tegner 1984; Harrold *et al.* 1988) or among individuals of the same species (Watanabe *et al.* 1992). Factors regulating the recruitment and mortality of marine algae may also differ among geographic locations. For example, although along both the central and southern California coasts mortality of the giant kelp *Macrocystis pyrifera* occurs during winter storms, increased water motion during these storms appears the be the main factor controlling sporophyte mortality in central California (Foster 1982; Graham 1996) whereas in southern California, *M. pyrifera* sporophytes senesce during the summer due to warm water and low nutrients (North 1971; Jackson 1977; Zimmerman & Kremer 1984). Factors such as changes in photoperiod (Lünning 1986 & 1993; Lünning & Kadel 1993; tom Dieck 1991), solar irradiance (Gerard 1984), temperature and nutrients (Jackson 1977; Zimmerman & Kremer 1984), vary seasonally and may induce annual patterns in marine algal demography, while other factors such as grazing (Dean *et al.* 1988; Watanabe & Harrold 1991; Leonard 1994), El Niño events (Dayton *et al.* 1992; North *et al.* 1993; Schroeter *et al.* 1995) and severe storms (Foster 1982; Dayton *et al.* 1984; Ebeling *et al.* 1985) are

unpredictable and their effects depend on timing (Kennelly 1987a), location (Santelices & Ojeda 1984) and severity (Dayton & Tegner 1984; Ebeling *et al.* 1985).

One of the more important factors influencing algal populations along the California coast is increased water motion from winter storms (Rosenthal *et al.* 1974; Ebeling *et al.* 1985; Foster & Schiel 1985; Seymour *et al.* 1989). Nearshore rocky substrates in this region are dominated by kelp forest communities at depths of 2 m to over 30 m. These forests support diverse assemblages of benthic algae (Abbott & Hollenberg 1976; Dawson & Foster 1982; Foster & Schiel 1985) that vary both spatially and temporally at least in part due to differences in substratum and water motion (Breda & Foster 1985; Foster 1982; Harrold *et al.* 1988). This is particularly true for the brown alga *Desmarestia ligulata* var. *ligulata*, an opportunistic species that is uncommon in established kelp stands (Reed & Foster 1984), but recruits in high densities when canopy-forming kelps are removed experimentally or by winter storms (Foster 1982; Reed & Foster 1984; Dayton *et al.* 1992; Clark 1996). *D. ligulata* can form a complete cover on the bottom (Foster & Schiel 1985; *pers obs.*) and can exclude other algae by inhibiting their recruitment through shading (Dayton *et al.* 1992) or by increasing their mortality through physical abrasion (Clark 1996).

Species of the genus *Desmarestia* occur as secondary species in temperate Laminarian forests, and as dominant species in Polar regions (Pease 1920). These species have heteromorphic life histories that alternate between microscopic gametophytes and macroscopic sporophytes (Chapman & Burrows 1971; Anderson 1982; Nakahara 1984;

Peters & Müller 1986; Anderson & Bolton 1989). Sporophytes, which attain lengths of greater than 2 meters, reproduce after vegetative growth ceases and unilocular sporangia arise from transformation of single cells in the cortical tissue (Peters & Müller 1985). Zoospores are then released, settle on the bottom and germinate into male or female gametophytes, that in turn undergo sexual reproduction and produce new sporophytes directly attatched to the female gametophytes (Chapman & Burrows 1971; Müller & Lüthe 1981). *D. ligulata* (hereafter referred to as *Desmarestia*) is an annual that occurs from the low intertidal to a depth of 15 m, from Alaska to South America, and is widely distributed throughout the Northern Hemisphere (Abbott & Hollenberg 1976). Macroscopic sporophytes recruit in the spring and disappear the following winter, leaving several months each year when they are absent (*pers obs*). Along the central California coast, *Desmarestia* occurs in high densities in exposed areas where the canopy-forming kelps *Macrocystis pyrifera*, *Nereocystis luetkeana* and *Pterygophora californica* are periodically removed by large ocean swells, and in low densities in protected areas where these kelps remain abundant. The specific processes that allow *Desmarestia* to recruit in the absence of spore producing plants are not fully understood.

Although studies have noted the effects of canopy removal on recruitment of *Desmarestia*, they have not examined the effects of excluding canopies for several years on the persistence of *Desmarestia* populations. Kennelly and Underwood (1993) observed that continuous exclusion of kelp canopies may lead to significant increases in turf algae and sedimentation. However, it remains unknown if these factors interact to

affect *Desmarestia* reoccurence or persistence along central California. The objectives of this study were to 1) determine the effect of continuous exclusion of kelp canopies over a period of several years (i.e. from frequent severe storms) on *Desmarestia* sporophyte recruitment and persistence, 2) examine the effect of the removal of turf algae by winter storms on *Desmarestia* recruitment and 3) describe seasonal cues that stimulate springtime recruitment of *Desmarestia* sporophytes along the central California coast.

METHODS

Study site

Field experiments were done in Stillwater Cove (36° 34'N, 121° 56'W), located at the north end of Carmel Bay, California. The algae, invertebrates and fish in this area have been well described in (Reed & Foster 1984; Foster & Schiel 1985). Moderate relief terraces, separated by cobble and sand channels, occur from depths of 6 m to 14 m and support a surface canopy of *Macrocystis pyrifera*, a subsurface canopy of *Pterygophora californica* and a rich mosaic of turf algae, primarily *Calliarthron tuberculosum*, *C. cheiosporioides*, *Bossiella californica*, *Plocamium cartilaguneum*, *Laurencia subopposita* and *Cryptopleura farlowianum*. Kelp canopies reach a maximum in early summer and a minimum during winter. *Desmarestia* occurs in the cove seasonally from spring to early winter.

Effects of canopy removal on recruitment and persistence of *Desmarestia* sporophytes

Loss of kelp canopies

Loss of kelp canopies from winter storms was simulated in winter, 1992 by clearing all surface and subsurface canopies from two 20 meter radius semicircles at a depth of 12 m near the middle of the cove . To examine both seasonal and year-to-year differences in the effects of long term canopy exclusion on reoccurence of *Desmarestia* sporophytes, the clearings were maintained until May, 1996. An unmanipulated control

area of equal size was established adjacent to each clearing in a block design. The effect of canopy removal on bottom irradiance was examined by periodically measuring light intensity within each canopy treatment during 1994 and 1995 with a Seabird Electronics-Sea Cat® battery operated CTD equipped with a Li-cor 4π quantum sphere collector (sample rate = 2Hz). A paired t-test was used to determine differences in irradiance between canopy types.

Bottom cover of *Desmarestia* sporophytes was estimated seasonally between spring, 1992 and spring, 1996 in 10-0.25m^2 quadrats placed haphazardly in each canopy removal and control area. Quadrats were subdivided into 25-5cm^2 subquadrats, percent cover estimated within each and then averaged for the entire quadrat to obtain greater accuracy. Because haphazard sampling can potentially bias results (Krebbs 1989), these percent cover estimates were compared to those simultaneously collected from the same number of randomly placed quadrats within the four locations on two sampling dates. Data were arcsin transformed and means tested with a three-way nested ANOVA, (with method and date as fixed factors, and location nested within date). There was no significant difference between the haphazard and simple random sampling ($p=0.692$; Appendix Table 1). To examine the effects of canopy exclusion on sporophyte cover, percent cover data were arcsin transformed and the maximum sporophyte cover each year was compared between canopy types and among years using a two-way mixed-model ANOVA, with year as a random factor and canopy type as a fixed factor.

Loss of turf algae

Loss of turf algae from winter storms was simulated in February, 1993 by removing all turf algae from three $0.25m^2$ plots within an area where the kelp canopies had been removed. Three $0.25m^2$ unmanipulated control plots were interspersed among the turf-removal plots. In addition, three $0.25m^2$ plots where the substrate was sterilized were interspersed among the turf-removal and control plots as part of a related study (see Chapter two). To control for among-study alpha error inflation, data from all plots were analyzed together. New sporophytes were counted within all plots the following spring, and differences between treatments tested for on the date of greatest plant density with a one-way ANOVA. A Bonferoni adjusted pairwise comparison was then used to test for differences between control and turf-removal plots.

The removal of turf algae increased the availability of nongeniculate coralline algae, and initial qualitative observations made in spring, 1993 suggested that sporophyte recruitment of *Desmarestia* was greater on nongeniculate coralline algae than other substrates. To examine this relationship further, 321 recruits were randomly chosen in spring, 1993 and the substrate they were growing on identified. Percent cover of available substrate types occurring within the sites was estimated using a point quadrat method (Cowen *et al.* 1982), and chi-square used to determine if young sporophytes occurred disproportionately on nongeniculate coralline algae than other available substrates. In addition, in spring, 1994, twenty four $0.25m^2$ randomly placed quadrats were sampled in the two kelp canopy removal areas. Within each quadrat the percent availability of

nongeniculate coralline algal substrate was estimated using a point quadrat and the number of recruits counted. Substrate data were arcsin transformed and an analysis of covariance (ANCOVA) was used to determine the relationship between nongeniculate coralline algal cover and sporophyte recruitment at the two sites.

Seasonal cues that stimulate sporophyte recruitment

To determine if the timing of sporophyte recruitment varies from year to year or if it follows a predictable pattern, the timing of recruitment was examined between 1993 and 1996 by sampling new sporophytes within 30 haphazardly placed $0.25m^2$ quadrats within each treatment. Since sporophyte recruitment occurs in the spring, sites were sampled more frequently (~3 times per week) between early March and late June, and less frequently (~1 to 3 times per week) during the remainder of each year. The date sporophytes first appeared in any one quadrat was considered the date of recruitment for that year. Observations by Clark (1996) yielded the recruitment date(+\- 1 week) for 1992.

To examine possible factors responsible for the initiation of sporophyte recruitment, the relationship of recruitment to changes in photoperiod (daylength) and sea temperature was examined over the five year period (1992 - 1996). In addition, the relationship between nutrient concentration and sea temperature was examined in 1995 to determine how closely nutrients are associated with temperature, and if they subsequently could be responsible for the timing of sporophyte recruitment.

Photoperiod in Stillwater Cove was modeled over the five year period using the equation daylength = 12-2.2*Cos(2π(date+10)/365); where 12 = mean daylength in hours, 2.2 = the amplitude of the curve in hours (with maximum and minimum values occurring in summer and winter), (date + 10) set the minimum daylength at December 21 and dividing by 365 sets date to the Julian day. The relationship between the timing of sporophyte recruitment and changes in photoperiod was then analyzed graphically.

Sea temperatures were recorded within the cove for 335 days between April, 1993 and October, 1994 using a Ryan® J90 thermograph placed at a depth of 6 m approximately 40 m from site one. Daily temperatures were also recorded between March and June, 1996 using an Onset Computer Corp.® Optic Stow Away™ temperature logger placed at a depth of 12 m within the cove. Sea temperatures within the cove were subsequently modeled for the remainder of the period between January, 1992 and March, 1996 using daily temperature observations made at Granite Canyon laboratories, approximately 20 km to the south of Stillwater Cove. Granite Canyon temperatures were considered to be a good predictor of Stillwater Cove temperatures (SWC = 0.85*Gran + 0.733; $r^2 = 0.91$; n=335). To verify that modeled temperatures were not significantly different from those observed in the cove, *in situ* temperatures were recorded on nine days between 1994 and 1995 using the hand held CTD. A paired t-test determined there were no significant differences between modeled and *in situ* temperatures (p = 0.85; power = 0.87). The relationship between the timing of sporophyte recruitment and changes in sea temperature was analyzed graphically.

To examine the relationship between ocean nutrient concentration and sea temperature, water samples were collected by hand at 10 m depth in 25ml scintillation vials on 39 occasions between February and October, 1995 using SCUBA. Samples were immediately placed on ice, transported to the laboratory, frozen, and later analyzed with a modified Strickland & Parsons nitrate/nitrite analysis method (Strickland & Parsons 1972) on an Alpkem 300® nutrient analyzer using sediment flow analysis. The relationship between ocean temperature and nutrient concentration was examined using a linear regression, and the relationship between the timing of sporophyte recruitment and nutrient concentration was analyzed graphically.

Statistical analysis

All data were analyzed on a personal computer using SYSTAT® (version 5.04) statistical software package (Wilkinson 1990). Prior to each test, data were examined for homogeneity of variances using an F test or Cochran's C test, and for normality by graphical interpretation of residual plots. The appropriate transformations were applied to those data not meeting either of these assumptions, and assumptions then retested. All tests were analyzed at 5% confidence levels. Specific tests, multiple comparisons and/or transformations used are presented separately.

RESULTS

Effects of canopy removal on recruitment and persistence of *Desmarestia* sporophytes

Loss of kelp canopies

The removal of *Macrocystis pyrifera* and *Pterygophora californica* canopies within Stillwater cove increased bottom irradiances during spring and summer to 400% of those occurring under unmanipulated canopies. Although still significantly different ($p = 0.002$), canopy thinning by winter storms increased irradiances under the remaining canopies, thus decreasing this ratio to 133%. These canopies however, recovered prior to *Desmarestia* recruitment each year.

Maximum cover of *Desmarestia* sporophytes occurred in the summer (July-August) each year and was significantly greater in areas where kelp canopies had been removed ($F_{1,3} = 87.842$, $p = 0.002$, Figure 1, Appendix Table 2). Sporophytes often exceeded 100% bottom cover in localized areas of the clearings, while cover remained low (< 10%) under the canopies. Sporophyte cover began declining around October each year with the arrival of winter storms (*pers obs*). No differences in sporophyte survivorship were observed between canopy types, and no sporophytes survived through an entire winter, although a few (< 1% cover) from the 1993 cohort persisted until early March, 1994. These however, were reduced to only their holdfasts and a few centimeters of tattered thalli.

Loss of turf algae

Removal of turf algae within the no-canopy areas increased irradiances on the substrate by as much as 40 times (to greater than 200 $\mu Em^{-2}s^{-1}$) as well as the availability of nongeniculate coralline algae, the primary substrate within the cove. *Desmarestia* sporophytes recruited during the spring, reached their maximum density in late April, and were more abundant in turf-removal plots than in control or sterilized ($F_{1,21} = 34.9$, $p = 0.021$, Figure 2, Appendix Table 3a&b). Sporophyte density within the plots then steadily decreased throughout the remainder of the summer.

Of the 321 recruits sampled in spring, 1993, a significantly greater number occurred on nongeniculate coralline algal substrates relative to other available substrates ($X^2 = 2121.509$; $p < 0.001$, Table 1). In spring, 1994, cover of nongeniculate coralline algal substrates within localized areas of the clearings varied between zero and 82% but was not significantly different between sites. There was a significant positive relationship between nongeniculate coralline algal substrate and sporophyte recruitment at both sites ($p < 0.001$, Figure 3, Appendex Table 4) that did not differ between sites.

Seasonal cues that stimulate sporophyte recruitment

The onset of sporophyte recruitment occurred in early April each year with little year-to-year or place-to-place variation (Table 2). When first observed, recruits were small (~1cm tall) but their morphology was similar to adults. No new sporophytes

appeared after mid May in any year, and maximum sporophyte density was attained within a few weeks of the onset of recruitment.

Sporophyte recruitment was strongly associated with increasing daylengths (Figure 4a) in all years of this study, with sporophytes first being observed at daylengths of 12.71 ± 0.10 (mean ± se) hrs. day^{-1}. Recruitment was also a strongly associated with rapid decreases in temperature (below the mean of 11.34°C) during 1993, 1994 & 1995, but not in 1996 (Figure 4b), with new sporophytes first observed at ocean temperatures of 9.65 ± 0.47 °C (mean ± se). Because temperatures fluctuated ± 1°C around the mean during the several weeks prior to recruitment, only temperature decreases of ≥ 2°C (to ≤ 9.34°C) were considered significant in the analysis. Within Stillwater Cove warmer waters (12-14°C) predominate during winter, and colder waters (9-11°C) during spring and summer. On several occasions, however, temperatures exceeded these ranges by ±1°C. Oservations made in spring, 1992 suggested the timing of sporophyte recruitment and its relationship to both increasing photoperiod and rapid decreases in temperature were similar to those observed between 1993 & 1996. Although sea temperature was negatively related to nutrient concentration, it described little of the variability in nutrient concentration ($r^2 = 0.288$). Nutrient levels within the cove varied between 2 - 21 μM during 1995 and, although sporophyte recruitment occurred when nutrients were highest, nutrients were consistently higher than those reported for southern California during the spring (Jackson 1977) when *Desmarestia* recruits.

DISCUSSION

Continuous exclusion of kelp canopies within Stillwater Cove resulted in a clear seasonal pattern of macroscopic *Desmarestia* sporophyte recruitment in the spring, growth during the summer, and disappearance the following winter and, a pattern of significantly greater recruitment in the areas where the canopy-forming kelps *Macrocystis pyrifera* and *Pterygophora californica* were removed. These results were similar to those of Foster (1982), Clark (1996), and Dayton *et al.* (1992) who observed that *Desmarestia* sporophytes recruited in high densities into exposed areas where canopies are naturally removed by winter storms, but sporophytes remained uncommon following winters in which storms were mild and did not sufficiently thin the canopies, and in protected areas where the canopies were more persistent. Although typical winter storms thin canopies within Stillwater Cove, they recover rapidly relative to canopies in more wave-exposed areas, and *Desmarestia* remains relatively uncommon (Cowen *et al.* 1982; Foster 1982). Following winters in which ocean swells are severe however, recovery of the canopies may be delayed, and *Desmarestia* may become abundant (Foster & Schiel 1985). Altogether, this suggests that the effect of winter storms on *Desmarestia* recruitment varies between exposed and protected areas. In exposed areas, where canopies are regularly removed by ocean swells, *Desmarestia* follows a seasonal cycle in which sporophytes become locally abundant each summer, while in protected areas where canopies are more persistent, *Desmarestia* sporophytes remain uncommon. However, if

canopy thinning in such areas is severe or occurs late in the winter, sporophytes may recruit in high densities and produce a dense bottom cover.

The opportunistic behavior of *Desmarestia* is similar to that of the kelp *Alaria fistulosa* (Dayton 1975) in that they both appear to be poor competitors for light, but rapidly recruit in high densities into areas where irradiances are increased by removal of the dominant kelps. This is not surprising considering some species of *Desmarestia* require relatively high light irradiances (greater than those occurring under the canopies) for sporophyte production (Peters & Müller 1986). Similarly, Kennelly (1989) observed that along the Australian coast, the understory algae *Zonaria* sp., *Lobophora* sp. and *Dictyota dichotoma* increase in bottom cover as a result of increased irradiances from removal of the canopy-forming kelp *Ecklonia radiata.* Although the removal of both surface and subsurface canopies within Stillwater Cove increased springtime bottom irradiances by as much as 400% of those occurring in areas with the canopies remaining, the removal of the surface canopy alone increased irradiances to only 200% of those under both canopy layers. Although removal of the *Macrocystis pyrifera* canopy alone significantly enhanced *Desmarestia* recruitment in areas lacking *Pterygophora californica* (Reed & Foster 1984), it did not significantly enhance *Desmarestia* recruitment in areas where *P. californica* was abundant (Clark 1996). The later represented damage from typical to mild winter storms, which remove *M. pyrifera* but leave the more persistent *P. californica* (Reed & Foster 1984). Along central California however, if the storms are severe both species may be removed and *Desmarestia* recruits in high densities (see also

Foster & Schiel 1985). Therefore, it appears that for *Desmarestia* to recruit in high densities within the cove, winter storms must be severe enough to remove both surface and subsurface canopies, and to delay recovery of the canopies.

Damage from winter storms can also extend to the substrate, removing large amounts of turf algae (Foster 1982). I found that, consistent with Reed & Foster (1984), removal of turf algae in combination with the canopy removal greatly increased the recruitment of *Desmarestia* sporophytes within Stillwater Cove. This appeared to be the result of increases in both bottom irradiances and the availability of nongeniculate coralline algal substrate. The turf within the cove may cover up to 100% of the substrate in localized areas, with very low irradiances (5 to 20$\mu Em^{-2}s^{-1}$) occurring under the turf within the no-canopy areas. At these extremely low levels, *Desmarestia* gametophytes do not grow or become fertile, but remain dormant and therefore do not produce sporophytes (see chapter 2). Although the continuous exclusion of kelp canopies may lead to increases in cover of turf algae (Kennelley 1987b), thereby decreasing *Desmarestia* recruitment in subsequent years, the cover of *Desmarestia* sporophytes exhibited little year-to-year variation. This appears to be because sporophytes recruit in greater densities than can be supported as adults, and self thin before achieving maximum bottom cover (*pers obs*). Therefore, although exclusion of kelp canopies may lead to increases in turf algae, *Desmarestia* bottom cover remains unchanged from year to year. Since sporophyte recruitment density was positively related to nongeniculate coralline algal substrate, increases in the availability of this substrate due to turf removal was at least partially

responsible for the increased sporophyte recruitment (see also Reed & Foster 1984). The relative importance of increases in irradiance and proper substrate on sporophyte recruitment, however, remains unclear. What is clear is that storm damage to turf algae as well to the kelp canopies positively influences *Desmarestia* sporophyte recruitment.

Sporophyte recruitment occurred in early to mid April each year with little year-to-year variation in timing. During this period, daylengths increased and, sea temperatures decreased rapidly while nutrient levels increased due to upwelling. Although the timing of recruitment was closely associated with changes in temperature and daylength between 1992 and 1995, observations in 1996 suggest that increases in photoperiod may be the more important factor. Although recruitment in 1996 occurred as nutrient levels increased, nutrient levels varied considerably throughout the year and were generally greater than those observed off southern California. This suggests that the 1995 relationship of recruitment to nutrients was due to nutrients being negatively related to temperature. Changes in daylength, however, follow similar seasonal cycles in both geographic regions. Central California waters are cold and nutrient rich relative to southern California, but *Desmarestia* recruits at approximately the same time in both regions (Reed *pers. com.*). This suggests daylength may be the most important factor stimulating sporophyte recruitment.

In addition, gametophytes of the related *Desmarestia firma* (= *Desmarestia ligulata* var. *firma* in Abbott and Hollenberg, 1976) achieve maximum fertility when cultured under short photoperiods and warm temperatures (15°C), typical of winter

conditions, and then transferred to long daylengths and cold temperatures (9°C), typical of upwelling events in the spring (Anderson & Bolton 1989). These gametophytes become fertile during short (winter) daylengths, and produce sporophytes during spring, when daylengths increase and temperatures suddenly decrease due to upwelling, a response well suited for living in areas where upwelling occurs. My observations suggest *Desmarestia ligulata* var. *ligulata* exhibits a very similar phenology. These environmental factors may act together to initiate sporophyte production, with gametophytes becoming fertile under the short photoperiods and high temperatures observed in winter, then producing sporophytes when photoperiods increase in the spring and temperatures suddenly drop due to upwelling and canopies are reduced due to storms in the previous winter. *Desmarestia*, therefore, appears to exhibit a life history which maximizes recruitment success by responding to environmental cues that both stimulate recruitment and indicate a reduction in dominant competitors. The individual relationships between sporophyte production and these environmental factors, however, still remain unclear.

CHAPTER 2

THE ROLE OF MICROSCOPIC LIFE-HISTORY STAGES IN THE PERSISTENCE OF THE ANNUAL ALGA *DESMARESTIA LIGULATA*

ABSTRACT

Seasonal sampling within Stillwater Cove, CA indicated that macroscopic *Desmarestia ligulata* sporophytes recruit in high densities in the spring, into areas where kelp canopies have been removed, attain maximum cover during the summer, become reproductive in the fall and disappear in early winter. There was a period of two to four months each year when sporophytes were absent. Field experiments indicated sporophyte populations reoccur from year to year from microscopic gametophytes that overwintered during sporophyte absence. Gametophytes grew faster in higher irradiances (75 $\mu Em^{-2}s^{-1}$ > 24 $\mu Em^{-2}s^{-1}$) and appeared to remain dormant under extremely low irradiances (4 $\mu Em^{-2}s^{-1}$), similar to those occurring under dense algal turfs in the field. Growth rates were not significantly different between summer and winter photoperiods. Sporophyte recruitment was lower where gametophytes were exposed to sedimentation and grazing. Dispersal of zoospores declined rapidly within 0.25 m of the parent plants, and sporophyte recruitment was lower in areas where they were absent the previous year.

INTRODUCTION

Environmental variability is one of the main factors controlling the life histories of organisms in both terrestrial and marine environments. Seasonality is an important component of this variability and can result in periods unfavorable to growth and survivorship (Tauber & Tauber 1978). Many organisms must survive these periods with resting stages that remain dormant during unfavorable environmental conditions (Tauber & Tauber 1978; Venable & Lawlor 1980; Grice & Marcus 1981; Levin *et al.* 1984; Keeley 1987; Maier 1990; Hoffman & Santilices 1991; Viitasalo 1992). Most species with dormant stages enter and exit periods of diapause in response to changes in only a few environmental factors, such as temperature, photoperiod, salinity and food abundance (Grice & Marcus 1981). For example, several species of marine diatoms produce resting spores that can remain dormant for up to two years under unfavorable light and temperature regimes, and then germinate when these conditions improve (Hollinbaugh *et al.* 1981). In addition, populations of many terrestrial plants that are periodically exposed to severe disturbances such as fires, recover rapidly by the emergence of new individuals from dormant seeds that survive the disturbance (Keeley 1987; Enright & Lamont 1989; Pierce & Cowling 1991). Many species of marine macroalgae have generations that differ in thallus morphology and size, presumably to better tolerate seasonal changes in environmental conditions (Lubchenco & Cubit 1980; Mathieson 1982; Hawkes 1983; Nakahara 1984). For algal species that alternate between macroscopic and microscopic life-history stages, microscopic thalli may act like

terrestrial seed banks, persisting during periods which are stressful to macroscopic thalli (Hoffman & Santelices 1991). It has not however, been determined if these stages actually serve as resting stages for macroalgal populations.

Some intertidal red algae occur as tetrasporic crusts during periods of increased sand abrasion (Hawkes 1983) or high grazer density (Slocum 1980), and produce upright, fleshy thalli when these pressures are reduced. In addition, several species of marine algae have annual life histories in which macroscopic sporophytes occur during only part of the year. For these species to persist, microscopic stages must maintain populations during the periods of sporophyte absence. Microscopic stages tend to be more tolerant of unfavorable temperature, light and nutrient conditions (Chapman & Burrows 1971; Nakahara 1984; Wienke & Dieck 1989, 1990; Hoffman & Santilices 1991; Peters & Breeman 1992), and produce new macroscopic stages when conditions improve (Kain 1964; Dayton 1975; Hoffman *et al.* 1984; Hoffman & Santilices 1991). The zoospores of many of these algae appear to be short lived (Nakahara 1984; Hoffman 1987; reviewed in Santilices 1990) and germinate immediately upon settlement (Chapman & Burrows 1971; Hoffman & Santilices 1982). In addition, the spores of similar algae but with perennial sporophytes, such as the kelps *Macrocystis pyrifera* and *Pterygophora californica* (Reed *et al.* 1992), *Laminaria hyperborea* (Kain 1964), and several species of intertidal algae (Hoffman & Camus 1989) have been observed to germinate directly in the water column but their settlement competency decreases dramatically within hours to days of release. It thus appears that species with annual

sporophytes must persist on the substrate as attached gametophytes, microscopic sporophytes or as perenniating holdfasts for several months each year. Although it has been broadly hypothesized that gametophytes of annual brown algae overwinter periods of sporophyte absence (Kain 1964; Dayton 1975; Lüning 1980; Anderson 1982; Foster 1982), it has not been demonstrated in the field.

The microscopic stages of the large, perennial brown alga, *Macrocystis pyrifera*, may be more tolerant of unfavorable light, temperature and nutrient conditions than the macroscopic sporophytes, but are easily damaged or killed by sedimentation (Devinny & Volse 1978; Deysher & Dean 1986), invertebrate grazing (Dean *et al.* 1988; Leonard 1994) and/or exposure to toxic effluents (Anderson *et al.* 1990; Reed & Lewis 1994). In addition, although they can live in laboratory cultures for several years (Vadas *et al.* 1992; Neushul *pers. com.*), most survive in the field for a few weeks only (Deysher & Dean 1986). How then do the microscopic stages of annual algae survive in the field for extended periods each year? This may accomplished if the individuals of each generation reproduce just prior to their disappearance, minimizing the time during which these stages must survive, or by exhibiting certain characteristics that reduce their mortality.

One of the most conspicuous species of annual macroalgae occurring within the kelp forests off the west coast of North America is the understory alga *Desmarestia ligulata* var. *ligulata* (order Desmarestiales) (hereafter referred to as *Desmarestia*). Sporophytes of this opportunistic species recruit at high densities in the spring in areas where canopy forming kelps such as *Macrocystis pyrifera* and *Pterygophora californica*

have been removed by winter storms (Foster 1982; Reed & Foster 1984; Dayton *et al.* 1992; Clark 1996), and may attain 100% cover on the bottom (Foster & Schiel 1985). Cover however, remains low under remaining canopies or in years when storms are too mild to remove the canopies (Foster 1982; Chapter 1). The question arises: How do *Desmarestia* sporophytes recruit in high densities into areas where canopies have been removed when few or no sporophytes were present in previous years? Moreover, *Desmarestia* sporophytes recruit in the spring, grow during the summer and die back in the fall and early winter. This leaves a period of several months during winter when sporophytes are absent. Thus, in order for sporophyte populations to reestablish from year to year, microscopic life-history stages must overwinter during these periods or sporophytes must arise from newly settled spores that dispersed long distances from a few perennating sporophytes. The purposes of this study were to 1) examine seasonal patterns of recruitment, reproduction and persistence of *Desmarestia* sporophytes, 2) determine if microscopic life-history stages of *Desmarestia* overwinter periods of sporophyte absence and describe their contribution to sporophyte recruitment, 3) identify the life-history stage(s) that overwinter(s) during these periods, 4) determine the effects of summer and winter photoperiods and increased irradiance from kelp canopy removal on the growth rates of these stages, 5) determine the effects of sedimentation and grazing on survivorship of these stages, 6) determine if *Desmarestia* sporophyte density differs between areas depending on previous year's sporophyte density, and 7) examine dispersal patterns of *Desmarestia* zoospores.

METHODS

Seasonal patterns in recruitment

To examine seasonal patterns in the recruitment and persistence of *Desmarestia* sporophyte populations within areas where kelp canopies had been removed, sporophyte cover and fecundity were estimated within Stillwater Cove, Carmel Bay, CA (see Chapter 1 for a description of the study area) seasonally between January, 1994 and May, 1996. Methods for estimating sporophyte cover are described Chapter 1. To estimate sporophyte fecundity, 8 - 10 haphazardly selected mature sporophytes were periodically collected, brought back to the laboratory and placed in flowing seawater for two hours. Fifty 2.8 cm^2 thallus cores were then obtained from the blades using a cork borer, placed in a refrigerator between layers of moist paper towels and desiccated for one hour (see Reed 1990). Five haphazzardly chosen cores were then reimursed in each of ten petri dishes filled with 100 ml of nutrient enriched sea water (70 ml Alga Grow® solution $liter^{-1}$ filtered sea water) such that no dish had two cores from any one sporophyte, or that any two dishes had cores from the same set of sporophytes. A single glass microscope slide was placed within each dish, and dishes were placed in a dark culture chamber at 8°C for 24 hours. The combination of nutrient and osmotic shocks induced the thalli to release motile zoospores that settled on the slides. Slides were then examined microscopically, and the density of settled zoospores was estimated on each slide by counting the number of spores occurring within each of five haphazardly chosen 0.16 mm^2 fields of view. A mean spore density was determined for each slide, and fecundity estimates based on the

ten slides (n = 10) were standardized to # spores settled (mean ± se) $mm^{-2}cm^{-2}$ thallus. The relationship between the percentage cover of *Desmarestia* sporophytes and fecundity was then analyzed graphically.

Overwintering life-history stages

To examine if *Desmarestia* sporophyte recruitment arises from microscopic life-history stages that overwinter during periods of sporophyte absence, all macroscopic and microscopic algal thalli were removed from three 0.25 m^2 plots in February, 1993 within an area where the canopy-forming kelps *Macrocystis pyrifera* and *Pterygophora californica* had been removed and *Desmarestia* was known to recruit in high densities (see Chapter 1). I sterilized the plots by first scraping away all visible algae and then placing a tent over the substrate into which I injected bleach. Tents made from reinforced plastic tarping attached to PVC frames were bolted to the substrate and sealed with water tight, petroleum-based clay gaskets (Figure 5). To ensure tents were properly sealed to the substrate, 5 ml of Fluoricine dye was injected into each tent with a hypodermic needle. Leaks were identified visually and plugged with additional clay. One liter of bleach was then injected into each tent through a diaphragm, and tents were left for two days before being retrieved. The efficiency of this method of sterilization was examined by removing pieces of substrate from three additional sterilization plots and culturing them in nutrient enriched filtered sea water under ambient light. Substrates from three unsterilized plots were also cultured under these conditions, and all substrates were monitored for algal

growth. In addition to the sterilized plots, three 0.25 m^2 plots were cleared of all turf algae, while taking care not to damage the substrate, and three 0.25 m^2 unmanipulated control plots were interspersed among the sterilized and turf-removal plots as part of a related study (see Chapter one). To control for among-study alpha error inflation, data from all plots were analyzed together. Sporophytes were counted within all plots during the following spring and summer, differences among treatments were examined on the date of maximum sporophyte density (April 28) with a one-way ANOVA. Bonferoni adjusted pairwise comparisons were then used to test for differences between sterilized and turf-removal plots, as well as turf-removal and control plots.

Regrowth from perenniating sporophytes or holdfasts remaining from the previous year's population (as observed for *Desmarestia aculeata*; Chapman & Burrows 1971) was assessed in 20 haphazardly chosen sporophytes marked in winter, 1993 and 25 in winter, 1994. Marking was done using tags of bicycle tape nailed to the substrate 6 cm on either side. This allowed easy identification of the exact holdfast attachment site, but did not affect sporophyte survivorship. Attatchment sites were then monitored during each of the following springs for regrowth from perenniating sporophytes. In addition, in April, 1993, 321 recruits were closely examined and the substrate they were attached to identified.

To identify the life-history stage that persists during sporophyte absence, zoospores were settled onto frosted glass microscope slides in January, 1994, allowed 48 h to germinate and then outplanted to the field. Prior to outplanting, slides were immursed in a 0.01% solution of *Fungi-fluor*® stain (a non-lethal biostain that binds to

cullulose and flouresces red when irradiated with blue light) and filtered sea water for one hour. Ninety slides were subsequently placed on three PVC slide racks (30 per rack) and transported to the field in dark plastic bags, while taking care not to expose them to direct sunlight or desiccation. Racks were then bolted to the substrate at a depth of 12 m. For the remainder of the winter (early January - mid April), three slides per rack were haphazardly selected each week, returned to the laboratory and examined with an epiflourescent microscope. Stained (overwintering) *Desmarestia* thalli were easily identified under blue light and life-history stages under white light.

Effects of photoperiod and irradiance on growth rates of overwintering stages

Bottom-irradiancies within Stillwater Cove varies throughout the year as a function of canopy cover (Clark 1996; Reed & Foster 1984; Chapter 1) as well as season, cloud cover, water clarity and time of day. Irradiance was periodically measured under the canopy were during 1994 and 1995 using a Seabird Electronics-Sea Cat® battery operated CTD equipped with a Li-cor 4π quantum collector (sample rate = 2Hz). All sampling was done at 1200 hrs on days of no cloud cover and good water clarity. During the winter, when canopies were thinned by storms, bottom-irradiance varied between approximately $24\mu Em^{-2}s^{-1}$ in areas where removal of canopies was minor, to approximately $75\mu Em^{-2}s^{-1}$ in areas where canopy loss was more complete. Irradiance reached $> 200\mu Em^{-2}s^{-1}$ in areas where the canopies had been completely removed.

Irradiances under the turfing algae within these areas varied between $4\mu Em^{-2}s^{-1}$ and $16\mu Em^{-2}s^{-1}$.

Shading effects of the canopy and turf algae on the growth rates of the overwintering stages were examined using zoospores settled onto glass microscope slides and placed in glass culture dishes filled with 200 ml nutrient enriched sea water (70 ml Alga Grow® per liter filtered sea water). Four dishes were then randomly allocated to each of six laboratory treatments consisting of three irradiances ($4\mu Em^{-2}s^{-1}$, $24\mu Em^{-2}s^{-1}$ & $75\mu Em^{-2}s^{-1}$) within each of two photoperiods (16:8 & 8:16 LD) at 10°C and cultured for three weeks. Treatments were chosen to estimate naturally occurring irradiances under the different canopy treatments, and to isolate effects of winter and summer photoperiods. To prevent diatom contamination, GeO_2 (0.2 ml saturated solution per liter culture media) was added to the culture medium, but was not added in subsequent weekly media changes. Zoospores germinated into microscopic gametophytes within 48 hours of settlement. Gametophyte growth rates were then estimated by measuring five haphazardly chosen filaments per slide using a ocular micrometer on a compound microscope at 100X. A mean filament length (± 1 se) within each dish was determined, and filament lengths after three weeks were compared among treatments using a three-way ANOVA, with photoperiod as a fixed factor, and irradiance and time as random factors. Bonferoni adjusted pairwise comparisons were subsequently used to determine the effects of irradiance on growth rates of the microscopic thalli.

Laboratory growth experiments suggested that microscopic stages have the ability to become dormant under extremely low irradiances and then begin growing when irradiances increase. To investigate this, zoospores were settled onto glass microscope slides within four culture dishes and then incubated under $4\mu Em^{-2}s^{-1}$ and short day (8:16 LD) conditions at 10°C. Due to logistical constraints, only one dish per treatment was monitored (n = 1). The results from this experiment were used to describe a pattern, rather than to test if gametophytes can remain dormant. One of the dishes was subsequently transferred to $24\mu Em^{-2}s^{-1}$ within the same photoperiod on day one, one on day 40 and one on day 59. The fourth dish was left at $4\mu Em^{-2}s^{-1}$ for the duration of the experiment. Dishes were incubated for a total of three months, during which time growth rates for the gametophytes were determined as above. Due to difficulties in making accurate measurements of large gametophytes, measurements within a dish ceased once average thalli length exceeded 400μm.

Survivorship of the overwintering stages

Because *in situ* measurements of survivorship of the microscopic thalli were not technically possible, sporophyte recruitment was used to estimate it. The effects of invertebrate grazing on survivorship of the microscopic thalli were examined in December, 1993 by settling zoospores onto fifteen $24cm^2$ rock slates, transporting the slates to the field and bolting them to the substrate at 12 m depth. Spore settlement occurred in a large well mixed tank to ensure spore density was similar on all slates. Slates were then

randomly allocated to one of three treatments with five replicates each; completely enclosed in a 1cm^2 stainless steel mesh cage to exclude gastropod and echinoid grazers; partially enclosed (i.e. two sides and a roof) to determine possible cage effects other than absence of grazers; and uncaged. Slates were monitored for sporophyte recruitment during the following spring.

The relationship between sedimentation and sporophyte recruitment was examined at Site 1 in May, 1994 within forty randomly placed 0.25m^2 quadrats. Within each quadrat, the amount of sediment covering substrate suitable for sporophyte recruitment was estimated using a twenty point point-quadrat method (Cowen *et al.* 1982), and the number of recruits determined. Quadrats placed over sand channels were discarded due to the unsuitable nature of the substrate for *Desmarestia*. Sediment data were arcsin transformed and the relationship between recruitment density and sediment cover was analyzed using a linear regression.

Effects of sporophyte density on the following year's sporophyte recruitment, and dispersal patterns

To determine if sporophyte recruitment differs between areas where sporophytes were abundant the previous year and where they were rare all *Desmarestia* sporophytes were removed from one-half of each of two of the 20 m radius canopy clearings discussed in Chapter 1 before the onset of zoospore production in early summer, 1993. Maximum sporophyte density was then estimated seasonally within the treatments during the

following two years by counting the number sporophytes occurring within ten haphazardly placed $0.25m^2$ quadrats within each treatment. To determine if the haphazard placement of quadrats introduced bias (Krebbs 1989), density data were compared to those simultaneously obtained from the same number of randomly placed quadrats within four locations on two dates during this study. A three-way nested ANOVA, with method and date as fixed, and location nested within date, found no significant differences between the haphazard and simple random methods ($p = 0.769$, Appendex Table 5). Therefore, a two-way mixed-model ANOVA, with date as a random factor and treatment as a fixed factor, was used to determine the effects of *Desmarestia* removal on subsequent sporophyte recruitment.

To examine dispersal patterns in *Desmarestia* zoospores, two frosted glass microscope slides were mounted on each of thirteen PVC slide holders, transferred to the field, and bolted to the substrate at 12 m depth in November, 1994. The distance from each slide holder to the nearest sporophyte was determined, and slide holders were left in the field for two weeks before being collected and returned to the laboratory. Slides were then examined microscopically and the density of settled *Desmarestia* spores was estimated using the same methods described for fecundity estimates. Although the morphologies of settled *Desmarestia* spores and gametophytes are similar to other locally abundant species (i.e. the kelps *Macrocystis pyrifera* and *Pterygophora californica*), they are slightly smaller (5.5 - 6.5μm vs. 8 - 12μm diameter). Therefore, settled *Desmarestia* spores were identified on basis of both morphology and size, and the

relationship between distance from the nearest sporophyte (spore source) and spore settlement density was determined using a non-linear power regression.

RESULTS

Seasonal patterns in recruitment

Seasonal sampling indicated that *Desmarestia* sporophytes recruit in the spring, attain maximum cover in summer, and then disappear the following winter (Figure 6). Except for a few heavily grazed, tattered individuals (< 1 sporophyte 400 m^{-2}) from the 1993 cohort that survived until mid March the following year, all sporophytes that recruited in 1993, 1994 and 1995 disappeared by mid February the following year. Sporophytes became fertile in late September, reached maximum fecundity in November - December, and remained fertile until they disappeared (Figure 6). A period of at least two to three months existed each year between the end of sporophyte reproduction (zoospore release), and recruitment of new sporophytes the following spring.

Overwintering life-history stages

The addition of bleach into the tents killed all microscopic algal thalli within the sterilization plots. No macroalgae or diatoms were observed growing on any of the sterilized substrates within the culture dishes, while both macroalgae and diatoms were observed on all the non sterilized substrates. In addition, no algae were observed to recruit into any of the sterilized field plots for three to four weeks after the tents were removed, while a few recruits, mostly *Macrocystis pyrifera*, *Pterygophora californica* and a few species of turf algae were observed in the turf-removal plots within two weeks after the tents had been removed from the sterilized plots. After five to six weeks, both kelp and turf algae were observed within both the sterilization and turf-removal plots in similar

densities. By contrast, *Desmarestia* sporophytes recruited in significantly greater numbers in turf-removal plots (169 ± 56.67 plants / .25m^2 mean ± se) than in sterilization plots (0.33 ± 0.32 plants / .25m^2 mean ± se) ($p = 0.001$); *Desmarestia* recruits were also more abundant in in turf-removal plots than control plots (28 plants / 0.25m^2 ± 26 mean ± se) ($p = 0.021$) ($F_{2,6} = 17.252$, Figure 2, Appendix Table 6 a&b). No sporophytes recruited into two of the sterilization plots, while a few (maximum = ten on April 28) were observed in the third plot (discussed below).

None of the holdfasts marked in 1993 or 1994 persisted through the entire winter, and no sporophytes recruited to any holdfast positions the following spring. In addition, of the 321 recruits examined in 1993, none recruited onto persisting holdfasts or regrew from perrniating sporophytes.

Microscopic *Desmarestia* filaments were easily identified on outplanted slides by the presence of red fluorescence when examined under blue light with epiflourescent microscopy (Figure 7a). Subsequent identification under white light indicated that all stained thalli examined were gametophytes (Figure 7b). These observations were consistent on all slides and on all sampling dates (February - April, 1994).

Effects of photoperiod and irradiance on gametophyte growth and fertility

Gametophyte growth rates were significantly greater in higher irradiances ($F_{2,18} = 24.04$, $p < 0.001$), but not significantly different between summer and winter photoperiods ($F_{1,18} = 2.869$, $p = 0.106$) (Figure 8a&b, Appendix Table 7a&b). Growth rates of

gametophytes cultured under 8:16 LD photoperiods and 75 $\mu Em^{-2}s^{-1}$ were similar to those growing on microscope slides within the cove under similar conditions (Figure 8c). Although no sporophytes were produced in any of the dishes, gametophytes became fertile, bearing large club shaped oogonia in dishes cultured under 75 $\mu Em^{-2}s^{-1}$ and 24 $\mu Em^{-2}s^{-1}$ within both long and short day photoperiods (16:8 & 8:16 LD). No gametophytes became fertile in dishes cultured under 4$\mu Em^{-2}s^{-1}$ in either photoperiod. Gametophytes cultured under these extremely low light levels did not grow, but appeared to be alive.

Gametophytes initially cultured at 4 $\mu Em^{-2}s^{-1}$ did not grow for extended periods (> 60 days) until they were transferred to 24 $\mu Em^{-2}s^{-1}$, at which time they began growing immediately (Figure 9). Gametophytes initially cultured under 24 $\mu Em^{-2}s^{-1}$ conditions began growing immediately and obtained an average size of > 1 mm within 40 days, at which time they were too large to accurately measure and therefore not censused on subsequent days. Once transferred to the higher irradiance, growth rates resembled those observed in gametophytes initially cultured at the higher irradiance, suggesting that gametophytes can remain dormant for up to 60 days without altering their growth potential.

Survivorship of overwintering stages

The cages effectively excluded the bat star *Asterina miniata*, the gastropods *Tegula brunnea*, *T. puligo*, *Calliostoma annulatum*, *C. canaliculatum* and *C. ligatum* and

the sea hare *Aplysia californica*, the most abundant large grazers in the study site (*pers. obs.*) No grazers were ever observed on any of the caged slates, while grazers were often observed on the non-caged and cage-control slates. No sporophytes were observed on any of the slates that allowed access to grazers, while moderate recruitment (6 ± 3.1 mean ± se recruits / slate) was observed on three of the slates which excluded grazers, and on the stainless steel mesh of a fourth caged slate. Sedimentation, defined here as a fine layer of sediment covering substrate suitable for sporophyte attatchment, was negatively associated with sporophyte recruitment ($n = 40$, $p < 0.001$, $r^2 = 0.28$, Figure 10, Appendex Table 8).

Effects of sporophyte density on the following year's sporophyte recruitment, and dispersal patterns

The removal of sporophytes from areas within the clearings in 1993 significantly reduced sporophyte cover during the following two years ($p = 0.020$; Appendix Table 9). Sporophyte cover in 1994 was higher (42.7% ± 30.4 mean ± se) in areas where the previous year's sporophytes remained than areas where they had been removed (4.45% ± 0.45 mean ± se). Although not significantly different, observations suggested cover within both treatments increased in 1995 (66.9% ± 28.9 in areas where 1993 sporophytes remained and 41.1% ± 22.2 in areas where they were removed). Although *Desmarestia* zoospores dispersed distances of at least 1.5 m, the number of spores settling on

outplanted microscope slides rapidly declined within 0.25m of the nearest sporophyte ($p < 0.001$, $r^2 = 0.518$, Figure 11, Appendix Table 10).

DISCUSSION

Within Stillwater Cove, *Desmarestia* sporophytes recruit in the spring, obtain their maximum cover on the bottom during the summer, become reproductive in early winter and then disappear. Similar patterns previously have been reported for *Desmarestia* in Stillwater Cove and other areas of central California (Foster 1982). Sprophyte recruitment was closely associated with increasing daylength and upwelling (see Chapter 1), while sporophyte disappearance appeared to result from removal by increased water motion during winter storms, increased grazing by gastropods, and/or natural senescence (*pers. obs*). To maintain annual sporophyte populations from year to year, microscopic stages must persist during sporophyte absence each winter, and produce new sporophytes each spring. Although they remained fertile until their disappearance, most of the sporophytes disappeared during September and October each year. Furthermore, maximum sporophyte fecundity occurred during November and December suggesting that the bulk of zoospore release occurs between October and December. Microscopic stages then must overwinter for a minimum of two months, and quite possibly as long as four or six months each year.

The method of sterilizing the substrate developed for this study was effective at removing both macroscopic and microscopic algal thalli from the plots, and did not appear to have any residual toxic effects. Results from this experiment showed that sporophyte recruitment originated from microscopic life-history stages that were on the substrate prior to the February sterilization, and then persisted on the substrate during the winter.

Although no sporophytes recruited into two of the sterilized plots, ten recruits were observed within the third plot on the date of maximum sporophyte density (April 28), possibly the result of nearby overwintering stages that dispersed embryos after fertilization. This process, although uncommon, was observed by Nakahara (1984). Another possibility for this recruitment was that an incomplete sterilization occurred within this tent. In either case, it is still apparent that microscopic life-history stages of *Desmarestia* overwinter periods of sporophyte absence, and thereby allow populations to persist from year to year.

Examination of fluorescently labeled microscopic thalli identified the overwintering life-history stages as gametophytes. These observations were consistent throughout the entire sampling period (January - April) suggesting that the gametophytes remain the overwintering stage throughout the entire winter, and that gametophyte sexual reproduction does not occur until just prior to sporophyte appearance in the spring. Monitoring holdfast positions and young sporophytes indicated that recruits do not arise from perenniating sporophytes or holdfasts from the previous year's population as observed in other species of annual algae. Therefore, it appears that overwintering gametophytes are the sole source of spring sporophyte recruitment for *Desmarestia*. These gametophytes thus act like terrestrial seed banks, persisting during periods when sporophytes are absent, and produce new adults when conditions improve. In contrast, whereas terrestrial seeds represent a period of dormancy, gametophytes behave like microscopic algae, growing throughout the winter. Therefore, it may be more appropriate

to consider these gametophytes as "maintaining populations" rather than as resting stages that "overwinter" during sporophyte absence.

Oceanographic conditions during typical central California winters are dominated by relatively warm water (11 - 13 °C), low nutrients (3 - 10 μM) and short photoperiods (10 - 12 hrs of light day^{-1}) (see also Breaker & Broenkow 1989). Although the gametophytes of several species of *Desmarestia* are more tolerant of these conditions than sporophytes (Chapman & Burrows 1971; Anderson 1982; Wiencke & tom Dieck 1990), they may, like kelp gametophytes, be easily killed by sedimentation, grazing and industrial discharges (reviewed in Foster & Schiel 1985). Sedimentation negatively affected sporophyte recruits, but it explained pnly 28% of the associated variability, suggesting that other factors may be more important. Kennelly & Underwood (1993) observed that continuous exclusion of kelp canopies for several years may lead to significant increases in the cover of turf algae, which in turn increase sedimentation. Although observations within areas of the cove where kelp canopies were excluded suggested both sedimentation and turfing algae increased relative to under the remaining canopies, there was no significant year-to-year variation in *Desmarestia* sporophyte recruitment (Chapter 1). Within the no-canopy areas, sufficient substrate apparently remained for zoospores to settle and gametophytes to survive such that *Desmarestia* sporophytes recruited each spring in high enough densities to attain >100% cover on the bottom in localized areas (Chapter 1). In fact, within these areas sporophyte density at the time of recruitment each

year was greater than that observed at the time of maximum bottom cover, suggesting that sporophytes undergo self thinning before attaining maximum bottom cover.

Leonard (1992) observed that within Stillwater Cove, the bat star *Asterina miniata* effectively grazes 100% of the available substrate every 90 days, killing all *Macrocystis pyrifera* gametophytes. *M. pyrifera* sporophytes therefore, must recruit from recently settled spores that quickly germinate and reproduce. Results from this study indicate that, at least on outplanted substrates, *Desmarestia* gametophytes are also effectively eliminated by grazers during the winter, and therefore do not produce sporophytes. The question remains, how do gametophytes on natural substrates survive grazing through the winter? It may be that high densities of gametophytes occur under dense algal turfs where they are protected from large grazers. Gametophytes cultured under irradiances similar to those occurring under these turfs ($4\mu Em^{-2}s^{-1}$) remained dormant until transferred to irradiances similar to those where the turf algae has been removed ($24\mu Em^{-2}s^{-1}$), and subsequently produced sporophytes. Remaining smaller may increase survivorship as seen in many species of terrestrial seeds (Harper 1977). Turf algae may thus act as a refuge from invertebrate grazing for at least part of the winter by inhibiting gametophyte growth and/or physically excluding grazers. Furthermore, gametophyte growth rates were significantly lower under irradiances similar to those occurring under kelp canopies than in areas where the canopies were removed, and, although not significantly different (power = 0.98), there was a general trend of lower growth rates in winter photoperiods than summer ones. These results suggest that gametophytes may grow slowly under kelp

canopies during the winter, thereby remaining smaller and increasing survivorship, and then grow rapidly towards the end of the winter once the kelp canopies have been removed by storms and daylengths increase. Increased growth rates toward the end of the winter may allow gametophytes to become larger and produce more oogonia and spermatangia, thereby increasing chances of successful reproduction. Likewise, Kain (1964) proposed that by growing filamentously during unfavorable environmental conditions, *Laminaria hyperborea* gametophytes increase filament size, allowing for production of more gametes per gametophyte once conditions improved. This was not yet tested for *Desmarestia*, although future experiments are planned.

When kelp canopies that have persisted for several years are suddenly removed (i.e. by severe winter storms or experimental manipulation), *Desmarestia* sporophytes may attain 100% cover on the bottom during the following year (Reed & Foster 1984; Foster & Schiel 1985; Clark 1996; Chapter 1). My results show that if these sporophytes survive to reproduce, and the canopies remain absent, sporophytes will again attain high bottom cover the following year. If these sporophytes are removed before they reproduce however, sporophytes will be rare during the following year. *Desmarestia* zoospores were observed to disperse distances of at least 1.5 m, but settlement density rapidly decreases within 0.25 m of the parent plants. This is consistent with Venable & Lawlor's (1980) observation that in desert annuals, seed dispersability was lower in plants that exhibited high prevelence of dormancy. Although gametophyte densities observed 1.5 m from the parent plants were greater than those required for *Macrocystis pyrifera* and

Pterygophora californica gametophytes to reproduce successfully (Reed 1990), it appears that sporophyte recruitment within the *Desmarestia*-removal areas was limited by gametophyte availability. This is in contrast to the idea that generalist species typically exhibit high propagule dispersability. It therefore appears that *Desmarestia* exhibits gametophyte overwintering as an alternate strategy to propagule dispersion in order to maintain sporophyte populations from year to year. In areas where kelp canopies persist from year to year and *Desmarestia* sporophytes remain rare, however, gametophytes may accumulate over successive reproductive seasons and attain high enough densities to produce dense sporophyte populations if canopies are removed. This is consistent with Pake & Vanable's (1996) observation that only a small portion of the seeds of desert annual plants that live in a temporaly variable environment germinate during unfavorable years, while the remaining seeds remain dormant until future years when conditions improve. During years when environmental conditions are favorable however, a high portion of the seeds germinate. *Desmarestia* gametophytes may thus act much like terrestrial seed banks, increasing in density over time and persisting until years when conditions favor germination. Although gametophytes of some species of kelp may survive in laboratory culture for several years (Vadas *et al.* 1992; Neushul *pers. com.*), they generally survive in the field for only a few weeks (Deysher & Dean 1986; Reed 1990; Reed *et al.* 1994). *Desmarestia* gametophytes, however, survive in the field for considerably longer than this, allowing for months between sporophyte generations.

LITERATURE CITED

Abbott, I. A. & G. H Hollenberg, 1976. *Marine algae of California.* Stanford University Press, Stanford, California. 827 pp.

Anderson, B. S., J. W. Hunt, S. L. Turpen, A. R. Coulon & M. Martin, 1990. Copper toxicity to microscopic stages of giant kelp *Macrocystis pyrifera*: interpopulation comparisons and temporal variability. *Mar. Ecol. Prog. Ser.*, Vol. 68, pp. 147-156.

Anderson, R. J., 1982. The life history of *Desmarestia firma* (C. Ag.) Skottsb. (Phaeophyceae, Desmarestiales). *Phycologia*, Vol. 21, pp. 316-322.

Anderson, R. J. & J. J. Bolton, 1989. Growth and fertility, in relation to temperature and photoperiod, in South African *Desmarestia firma* (Phaeophyceae). *Bot. Mar.*, Vol. 32, pp. 149-158.

Breaker, L. C. & W. W. Broeknow, 1989. The circulation of Monterey Bay and related processes. Moss Landing Marine Laboratories Technical Publication. Vol. 89, pp. 48-51.

Breda, V. A. & M. S. Foster, 1985. Composition, abundance, and phenology of foliose red algae associated with two central California kelp forests. *J. Exp. Mar. Biol. Ecol.*, Vol. 94, pp. 115-130.

Chapman, A. R. O. & E. M. Burrows, 1971. Field and culture studies of *Desmarestia aculeata* (L.) Lamour. *Phycologia*, Vol. 10, pp. 63-76.

Clark, R. P., 1996. Effects of multiple kelp canopies on understory algal composition. M.S. thesis, San Francisco State University.

Cowen, R. K., C. R. Agegian & M. S. Foster, 1982. The maintenance of community structure in a central California giant kelp forest. *J. Exp. Mar. Biol. Ecol.*, Vol. 64, pp. 189-201.

Dawson, E. Y. & M. S. Foster, 1982. *Seashore plants of California*, edited by A. Smith, California Press, Berkeley, California. 226 pp.

Dayton, P. K., 1975. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchiyka Island, Alaska. *Fish. Bull.*, Vol. 78, pp. 230-237.

Dayton, P. K., V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal & D. Ven Tresca, 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.*, Vol. 54, pp. 253-289.

Dayton, P. K. & M. J. Tegner, 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. *Science*, Vol. 224, pp. 283-285.

Dayton, P. K., M. J. Tegner, P. E.Parnell & P. B. Edwards, 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.*, Vol. 62, pp. 421-445.

Dean, T. A., F. R. Jacobsen, K. Thies & S. L. Lagos, 1988. Differential effects of grazing by white sea urchins on recruitment of brown algae. *Mar. Ecol. Prog. Ser.*, Vol. 48, pp. 99-102.

Devinny, J. S. & L. A. Volse., 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Mar. Biol.* Vol. 48, pp. 343-348.

Deysher, L. E. & T. A. Dean, 1986. In situ recruitment of sporophytes of the giant kelp, *Macrocystis pyrifera* (L.) C.A. Agardh: effects of physical factors. *J. Exp. Mar. Biol. Ecol.*, Vol. 103, pp. 41-63.

Ebeling, A. W., D. R. Laur & R. J. Rowley, 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Mar. Biol.*, Vol. 84, pp. 287-294.

Enright, N. J. & B. B. Lamont, 1989. Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *J. Ecol.*, Vol. 77, pp. 1111-1122.

Foster, M. S., 1982. The regulation of macroalgal associations in kelp forests. In, *Synthetic and Degredative Processes in Marine Macrophytes*, edited by L Srivastava, W. de Gruyter, Berlin, pp. 185-205.

Foster, M. S. & D. R. Schiel, 1985. The ecology of giant kelp forests in California: a community profile. *U.S. Fish & Wildlife Biol. Rep.*, Vol. 85.

Foster, M. S. & W. P. Sousa, 1980. Succession. In, *Handbook of Phycological Methods; Ecological Field Methods: Macroalgae*, edited by Littler, M. M. & D. S. Littler, Cambridge University Press, New York, pp. 269-290.

Gerard, V. A., 1984. The light environment in a giant kelp forest: influence of *Macrocystis pyrifera* on spatial and temporal variability. *Mar. Biol.*, Vol. 84, pp. 189-195.

Graham, M. H., 1995. Regulation of the shallow limit of giant kelp, *Macrocystis pyrifera*, at three sites along the Monterey peninsula. M.S. thesis, San Jose State University.

Grice, G. D. & N. H. Marcus, 1981. Dormant eggs of marine copepods. *Oceanogr. Mar. Biol. Ann. Rev.*, Vol. 19, pp. 125-140.

Harper, J. L., 1977. *Population Biology of Plants*. Academic Press, London.

Harrold, C., J. Watanabe, S. Lisin, 1988. Spatial variation in the structure of kelp forest communities along a wave exposure gradient. P.S.Z.N.I. *Mar. Ecol.*, Vol. 9, pp. 131-156.

Hawkes, M. W., 1980. *Hummbrella hydra* (Rhodophyta, Gigartinales): seasonality, distribution and development in laboratory culture. *Phycologia*, Vol. 22, pp. 403-413.

Hoffman, A. J., 1987. The arrival of seaweed propagules at the shore: a review. *Bot. Mar.*, Vol. 30, pp. 151-165.

Hoffman, A. J., M. Avila & B. Santilices, 1984. Interactions of nitrate and phosphate on the development of microscopic stages of *Lessonia nigrescens* Bory (Phaeophyta). *J. Exp. Mar. Biol. Ecol.*, Vol. 78, pp. 177-186.

Hoffman, A. J. & P. Camus, 1989. Sinking rates and viability of spores from benthic algae in central Chile. *J. Exp. Mar. Biol. Ecol.*, Vol. 126, pp. 281-291.

Hoffman, A. J. & B. Santilices, 1982. Effects of light intensity and nutrients on gametophytes and gametogenesis of *Lessonia nigrescens* Bory (Phaeophyta). *J. Exp. Mar. Biol. Ecol.*, Vol. 60, pp. 77-89.

Hoffman, A. J. & B. Santilices, 1991. Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. *Mar. Ecol. Prog. Ser.*, Vol. 79, pp. 185-194.

Jackson, G. A., 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. *Limnol. Ocean.*, Vol. 22, pp. 979-995.

Kain, J. M., 1964. Aspects of the biology of *Laminaria hyperborea*. III. Survival and growth of gametophytes. *J. Mar. Biol. Ass, U.K.*, Vol. 44, pp. 415-433.

Keeley, J. E., 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology*, Vol. 68, pp. 434-443.

Kennelly, S. J., 1987a. Physical disturbances in an Australian kelp community. I. Temporal effects. *Mar. Ecol. Prog. Ser.*, Vol. 40, pp. 145-153.

Kennelly, S. J., 1987b. Physical disturbances in an Australian kelp community. II. Effects on understory species due to differences in kelp cover. *Mar. Ecol. Prog. Ser.*, Vol. 40, pp. 155-165.

Kennelly, S. J., 1989. Effects of kelp canopies on understory species due to shade and scour. *Mar. Ecol. Prog. Ser.*, Vol. 50, pp. 215-224.

Kennelly, S. J. & A. J. Underwood, 1993. Geographic consistencies of effects of experimental physical disturbance on understory species in sublittoral kelp forests in central New South Wales. *J. Exp. Mar. Biol. Ecol.*, Vol. 168, pp. 35-58.

Konar, B. & M. S. Foster, 1992. Distribution and recruitment of subtidal geniculate coralline algae. *J. Phycol.*, Vol. 28, pp. 273-280.

Krebbs, C. J., 1989. *Ecological methodology*, edited by C.M Wilson & S. Pisano, New York, New York. 654 pp.

Leonard, G. H., 1994. Effect of the bat star *Asterina miniata* (Brandt) on recruitment of the giant kelp *Macrocystis pyrifera* C. Agardh. *J. Exp. Mar. Biol. Ecol.*, Vol. 179, pp. 81-98.

Lobchenco, J. & J. Cubit, 1980. Hetermorphic life histories of certain marine algae as adaptions to variations in herbivory. *Ecology*, Vol. 63, pp. 676-687.

Lüning, K., 1986. New frond formation in *Laminaria hyperborea* (Phaeophyta): a photoperiodic response. *Br. Phycol. J.*, Vol. 21, pp. 269-273.

Lüning, K., 1993. Environmental and internal control of seasonal growth in seaweeds. *Hydrobiologia*, Vol. 260/261, pp. 1-14.

Lüning, K. & P. Kadel, 1993. Daylength range for circannual rhythmicity in *Pterygophora californicornica* (Alariaceae, Phaeophyta) and synchronization of seasonal growth by daylength cycles in several other brown algae. *Phycologia*, Vol. 32, pp. 379-387.

Maier, G., 1990. Spatial distribution of resting stages, rate of emergence from diapause and times to adulthood and to the appearance of the first clutch in 3 species of cyclopoid copepods. *Hydrobiologia*, Vol. 206, pp. 11-18.

Mathieson, A. C., 1982. Field ecology of the brown alga *Phaeostrophion irregulare* Setchell *et* Gardner. *Bot. Mar.*, Vol. 25, pp. 67-85.

McLean, J. H., 1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biol. Bull.*, Vol. 122, pp. 95-114.

Müller, D. G. & N. M. Lüthe, 1981. Hormonal interaction in sexual reproduction of *Desmarestia aculeata* (Phaeophyceae). *Br. Phycol. J.*, Vol. 16, pp. 351-356.

Nakahara, H., 1984. Alternation of generations of some brown algae in unialgal and axenic cultures. *Scientific Papers of the Institute of Algological Research*, Vol. 7, pp. 91-184.

North, W.J., 1971. *The biology of giant kelp beds in California*, edited by W.J. North, Lehre, Germany, pp. 1-96.

North, W. J., James, & L. G. Jones, 1993. History of kelp beds (*Macrocystis*) in Orange and San Diego counties, California. *Hydrobiologia*, Vol. 260/261, pp. 277-283.

Pake, C. E. & D. L. Venable, 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, Vol. 77, pp. 1427-1435.

Pease, V.A., 1920. Taxonomy and morphology of the ligulate species of the genus *Desmarestia*. *Pub. Puget Sound Biol. Sta.*, Vol. 2, pp. 313-366.

Peters, A. F. & D. G. Müller, 1986. Life-history studies-a new appraoch to the taxonomy of ligulate species of *Desmarestia* (Phaeophyceae) from the Pacific coast of Canada. *Can. J. Bot.*, Vol. 64, pp. 2192-2196.

Pierce, S. M. & R. M. Cowling, 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos. *J. Ecol.*, Vol. 79, pp. 731-747.

Ramirez, M. E., D. G. Müller & A. F. Peters, 1986. Life history and taxonomy of two populations of ligulate *Desmarestia* (Phaeophyceae) from Chile. *Can. J. Bot.*, Vol. 64, pp. 2948-2954.

Reed, D. C., 1990. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology*, Vol. 71, pp. 776-787.

Reed, D. C., C. D. Amsler & A. W. Ebeling, 1992. Dispersal in kelps: factors affecting spore swimming and competency. *Ecology*, Vol. 73, pp. 1577-1585.

Reed, D. C. & M. S. Foster, 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology*, Vol. 65, pp. 937-948.

Reed, D. C. & R. J. Lewis, 1994. Effects of oil and gas-production effluent on the colonization potential of giant kelp (*Macrocystis pyrifera*) zoospores. *Mar. Biol.*, Vol. 119, pp. 277-283.

Reed, D. C., R. J. Lewis & M. Anghera, 1994. Effects of an open-coast oil-production outfall on patterns of giant kelp (*Macrocystis pyrifera*) recruitment. *Mar. Biol.*, Vol. 120, pp. 25-31.

Rosenthal, R. J., W. D. Clarke & P. K. Dayton, 1974. Ecology and natural history of a stand of giant kelp, *Macrocystis pyrifera*, off Del Mar, California. *Fish. Bull.*, Vol. 72, pp. 670-684.

Santilices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Ann. Rev.*, Vol. 28, pp. 177-276.

Santilices, B. & F. O. Ojeda, 1984. Effects of canopy removal on the understory algal community structure of coastal forests of *Macrocystis pyrifera* from southern South America. *Mar. Ecol. Prog. Ser.*, Vol. 14, pp. 165-175.

Schiel, D. R., 1985. A short-term demographic study of *Cystoseira osmundacea* (Fucales: Cystoseiraceae) in central California. *J. Phycol.*, Vol. 21, pp. 99-106.

Schiel, D. R. & M. S. Foster, 1986. The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Ann. Rev.*, Vol. 24, pp. 265-307.

Seymour, R. J., M. J. Tegner, P. K. Dayton & P. E. Parnell, 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuarine, Coastal and Shelf Science*, Vol. 28, pp. 277-292.

Slocum, C. J., 1980. Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. *J. Exp. Mar. Biol. Ecpl.*, Vol. 46, pp. 99-110.

Strickland, J. D. H. & T.R. Parsons, 1972. A practical handbook of seawater analysis. *Fish. Res. Bd. Canada Bull.* Vol. 167, 310 pp.

Tauber, M. J. & C. A. Tauber, 1978. Evolution of phenological strategies in insects: a comparative approach with eco-physiological and genetic considerations, In *Evolution of Insect Migration and Diapause*, edited by H. Dingle, Sringer-Verlag, New York, pp. 53-71.

tom Dieck, I., 1991. Circannual growth rhythym and photoperiodic sorus induction in the kelp *Laminaria setchellii* (Phaeophyta). *J. Phycol.*, Vol. 27, pp. 341-350.

Underwood, A. J. & S. J. Kennelly, 1990. Ecology of marine algae on rocky shores and subtidal reefs in temperate Australia. *Hydrobiologia*, Vol. 192, pp. 3-20.

Vadas, R. L., S. Johnson & T. A. Norton, 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *Br. Phycol J.*, Vol. 27, pp. 331-351.

Venable, D. L. & L. Lawlor, 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia*, Vol. 46, pp. 272-282.

Viitasalo, M., 1992. Calanoid resting eggs in the Baltic Sea: implications for the population dynamics of *Acartia bifilosa* (Copepoda). *Mar. Biol.*, Vol. 114, pp. 397-405.

Watanabe, J. M., R. E. Phillips, N. H. Allen, & W. A. Anderson, 1992. Physiological response of the stipitate understory kelp, *Pterygophora californica* Ruprecht, to shading by the giant kelp, *Macrocystis pyrifera* C. Agardh. *J. Exp. Mar. Biol. Ecol.*, Vol. 159, pp. 237-252.

Wiencke, C. & I. tom Dieck, 1989. Temperature requirements for growth and survival of macroalgae from Antarctica and southern Chile. *Mar. Ecol. Prog. Ser.*, Vol. 59, pp. 157-170.

Wiencke, C. & I. tom Dieck, 1990. Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic Region. *Mar. Ecol. Prog. Ser.*, Vol. 54, pp. 189-197.

Wilkinson, L., 1990. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois. 750 pp.

Zimmerman, R. C. & J. N. Kremer, 1984. Episodic nutrient supply to a kelp forest ecosystem in southern California. *J. Mar. Res.*, Vol. 42, pp. 591-604.

Table 1. Sporophyte recruitment on various substrates in relation to relative availability of these substrates in Stillwater Cove. Recruits sampled in April, 1993

Substrate	% cover	% of recruits (# recruits)
nongeniculate coralline algae	16	91 (291)
geniculate coralline algae	52.5	6.5 (21)
other (sponges, sessile invertebrates, bryazoans, algae, rock)	31.5	2.5 (9)
Total	**100**	**100 (321)**

Table 2. Date of initial *Desmarestia ligulata* sporophyte appearance in Stillwater Cove (= onset of recruitment) each year (1993 - 1996). Dates were determined by the first occurrence of sporophytes in 30 haphazardly allocated quadrats within two sites. The range for 1992 was determined from observations made by Clark (1996).

Year	Date of appearance
1992	April 8 - 15
1993	April 7
1994	April 4
1995	April 17
1996	April 11

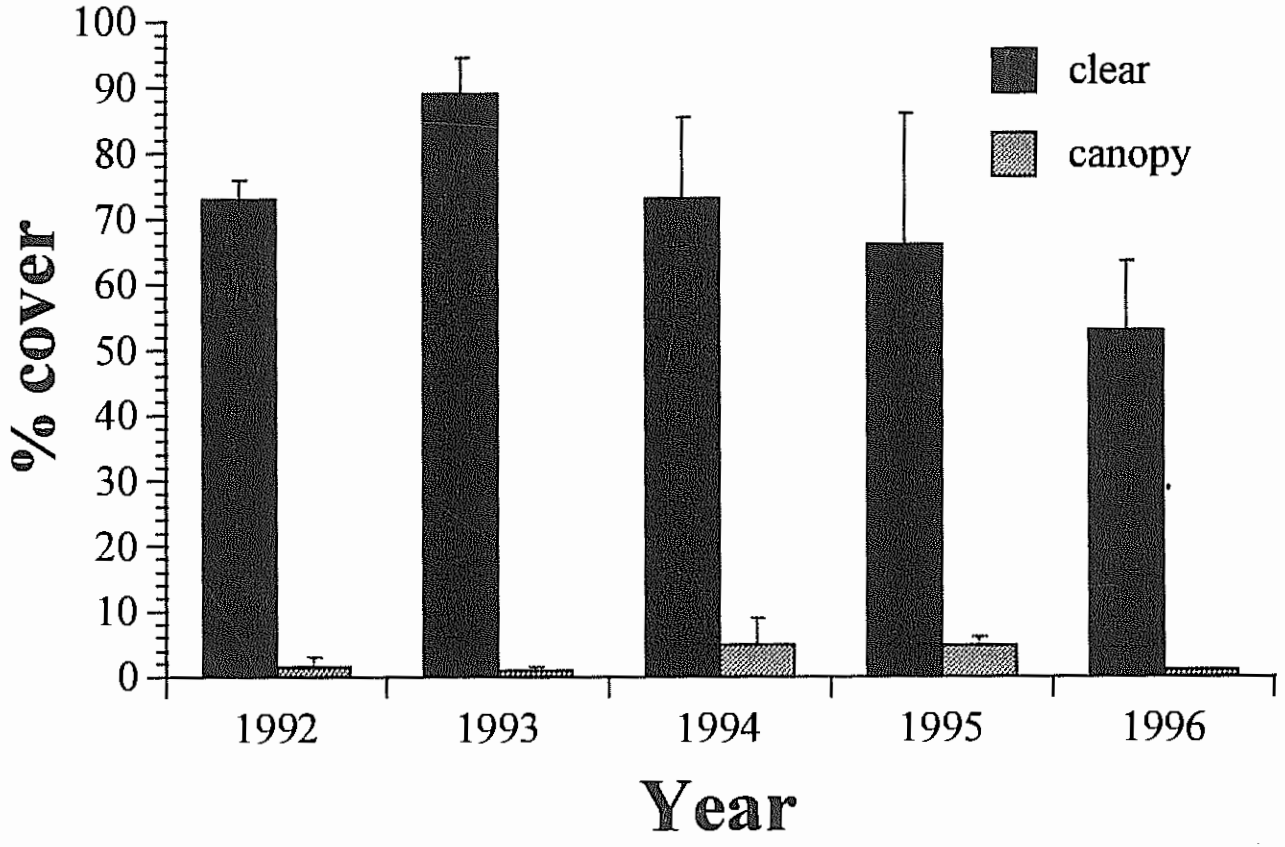


Figure 1. Maximum bottom cover of *Desmarestia ligulata* sporophytes under kelp canopies and in clearings during 1992 - 1996 (mean + standard error), n = 2.

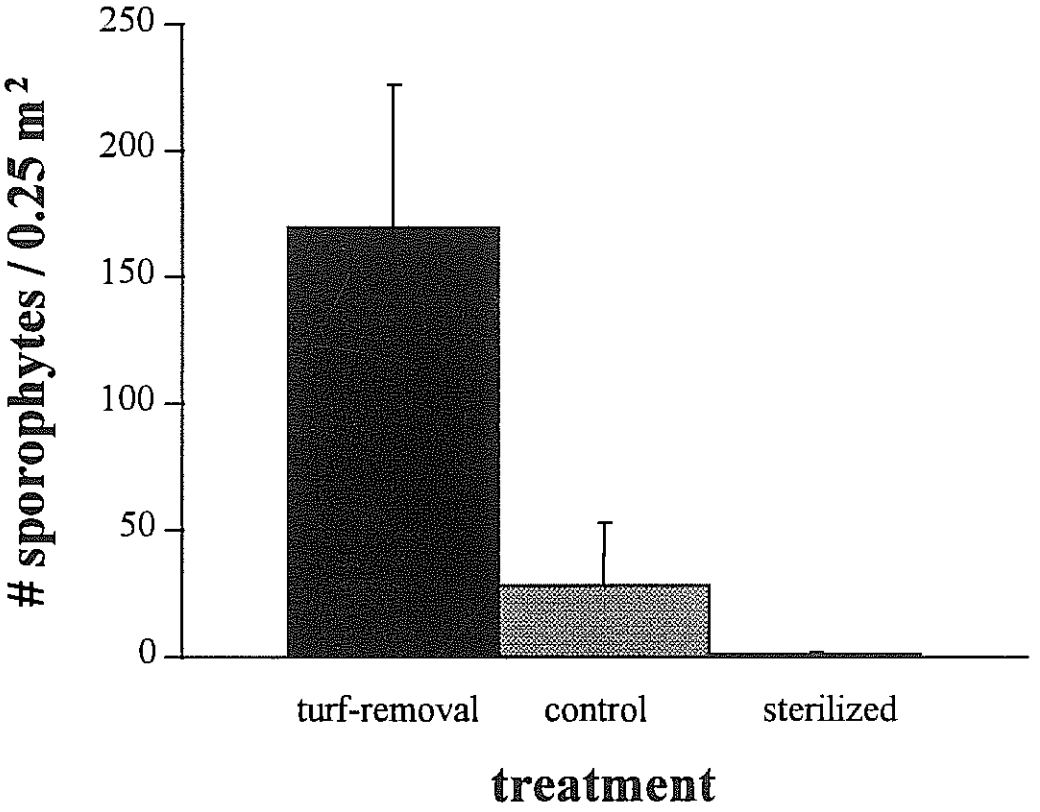


Figure 2. Maximum number of *Desmarestia ligulata* recruits occurring in sterilized, turf-removal (scraped) and control (non-scraped) plots during spring, 1993 (mean + standard error), n = 3.

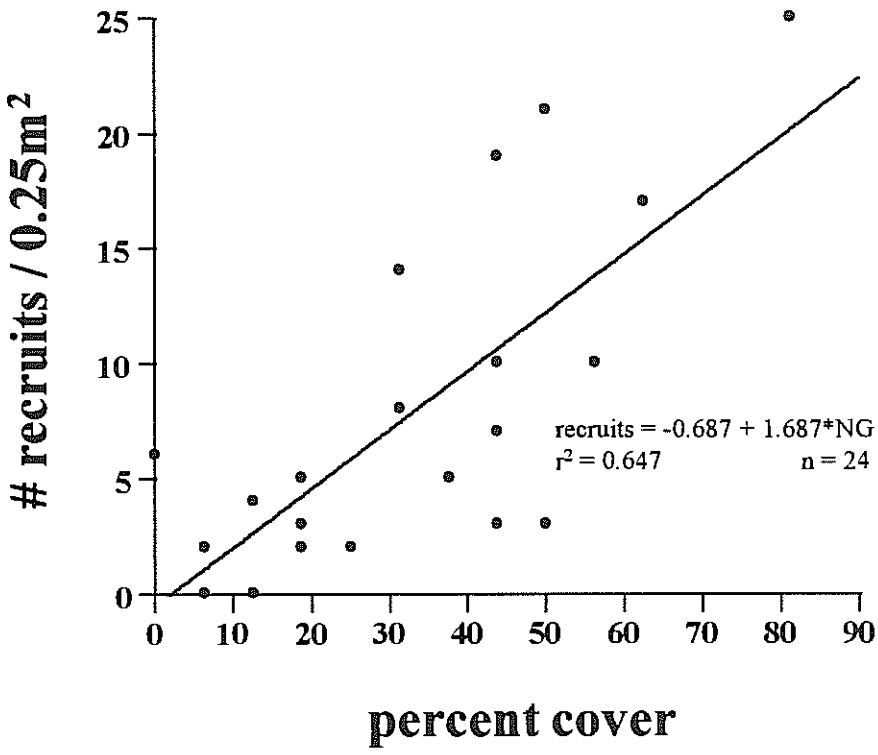


Figure 3. Relationship between *Desmarestia ligulata* sporophyte recruitment and cover of nongeniculate coralline algae within two sites in Stillwater Cove.

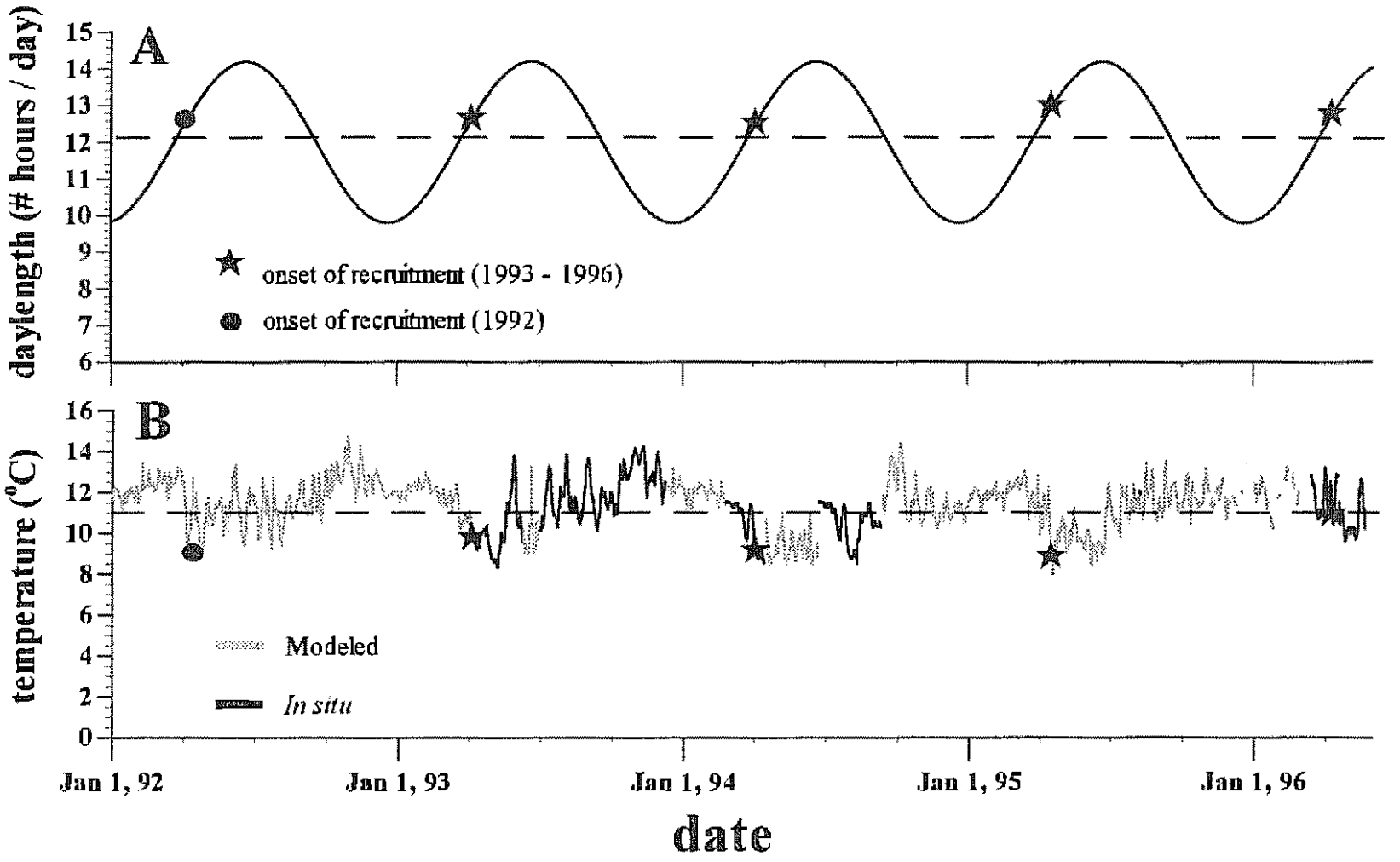


Figure 4. (A) Daylength modeled for Stillwater Cove (1992 - 1996) and its relationship to the timing of *Desmarestia ligulata* sporophyte recruitment. Hatched line denotes the mean daylength (12 hrs/day). (B) Sea temperature within Stillwater Cove [obtained from *in situ* measurements and modeled from Granite Canyon laboratories data (1992 - 1996)] and its relationship to the timing of *D. ligulata* sporophyte recruitment. Hatched line denotes the mean temperature in the cove (11.34 C).

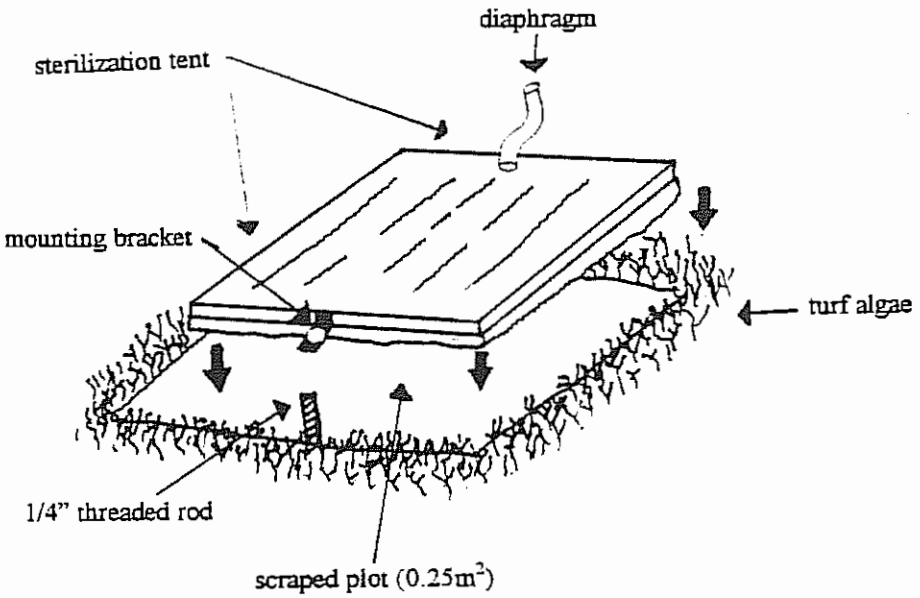


Figure 5. Sterilization tent used to remove microscopic algal thalli from the substrate

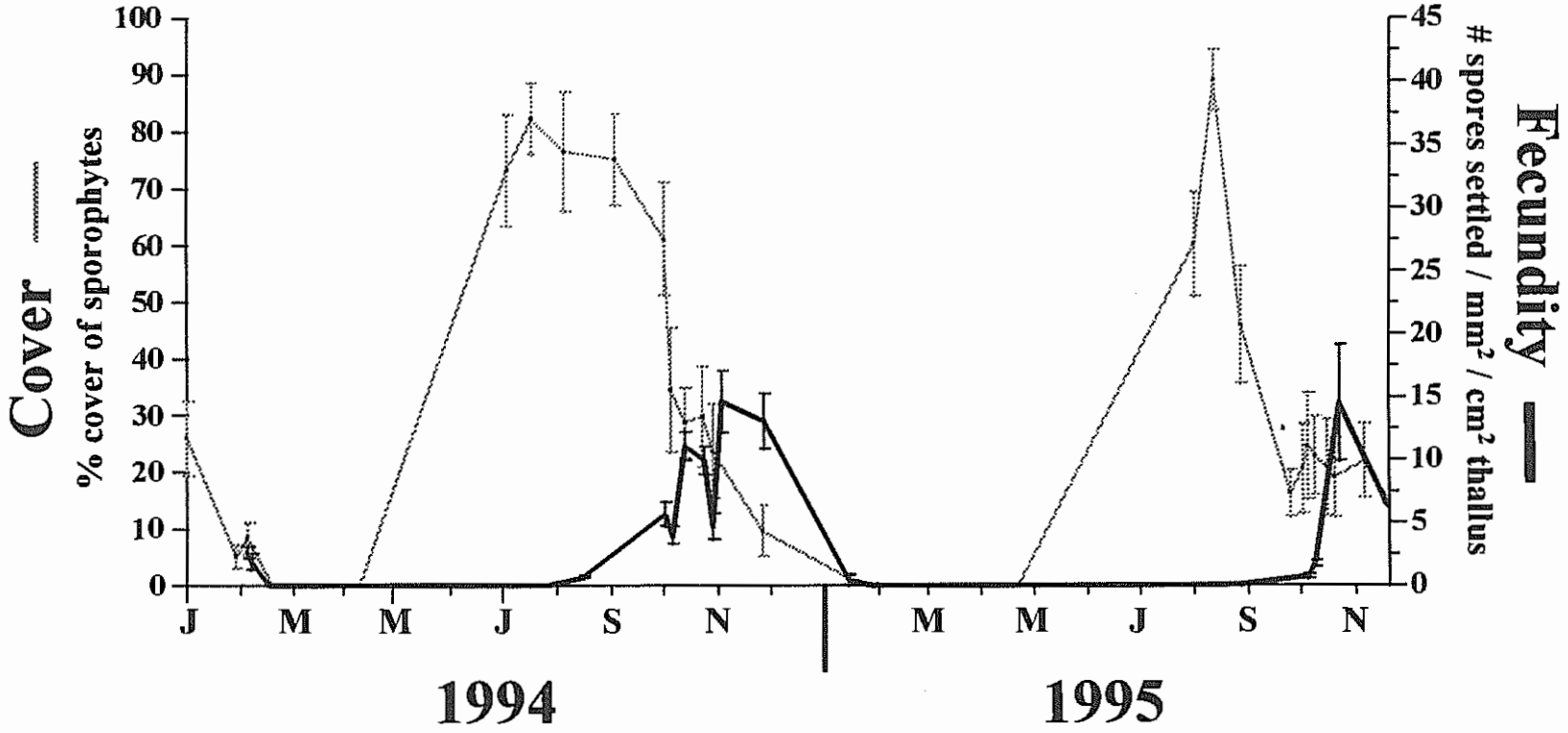
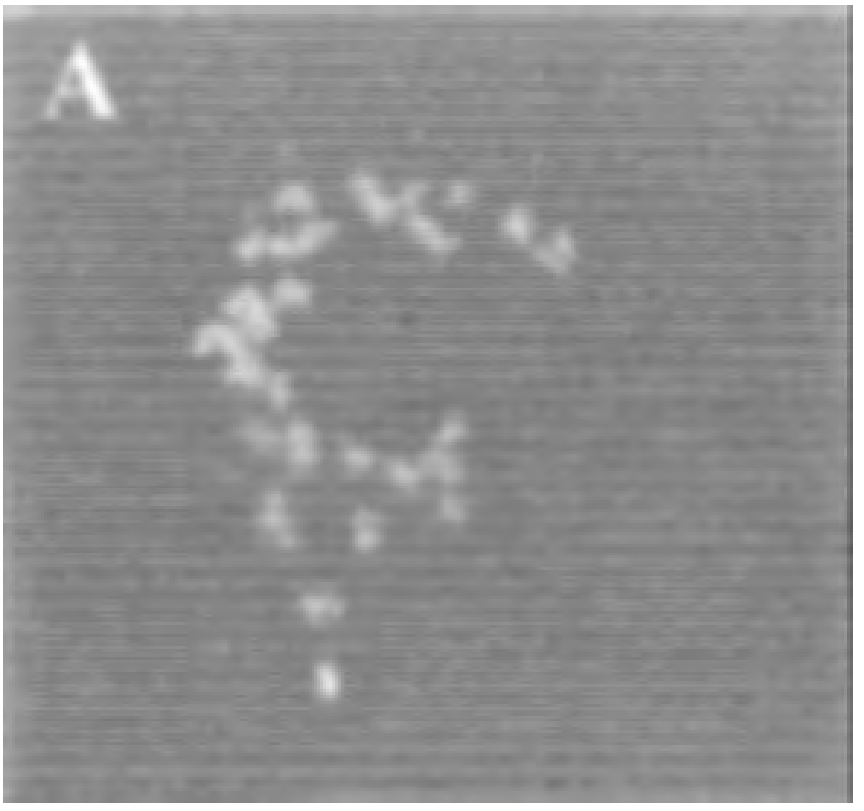
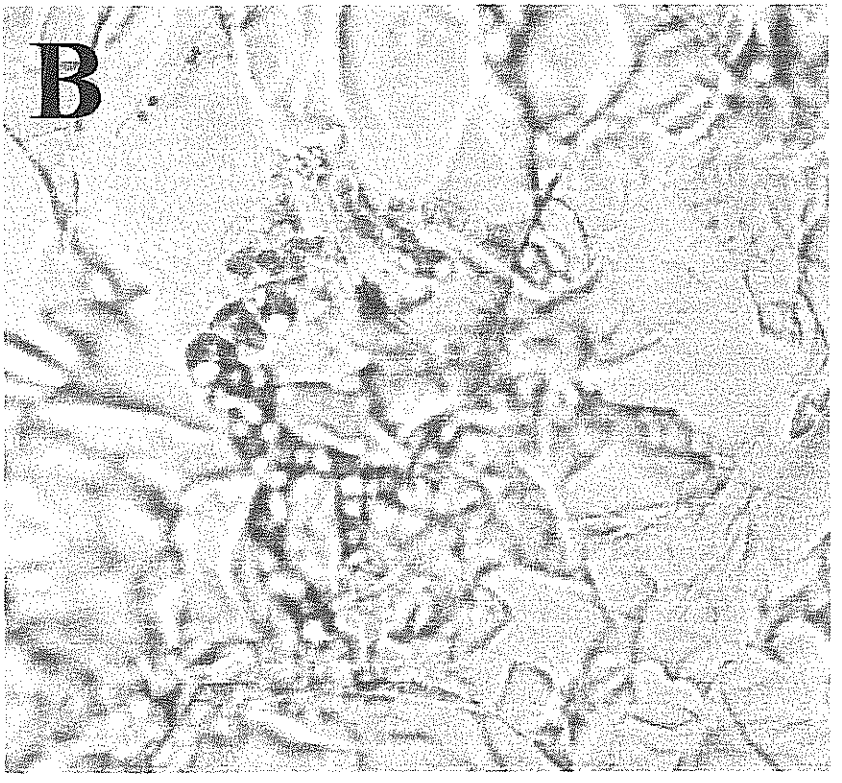


Figure 6. Bottom cover and fecundity of *Desmarestia ligulata* sporophytes in canopy-cleared area within Stillwater Cove between January, 1994 and December, 1995 (mean ± standard error), n = 10.

Figure 7 (Next page). (A) Fluorescently labeled *Desmarestia ligulata* thalli examined under UV light (magnification = 100X). Red fluorescence identifies thalli stained with *Fungi-fluor*® vital stain. (B) Stained thalli examined under white light. Identifies life-history stage as gametophyte.


A


B

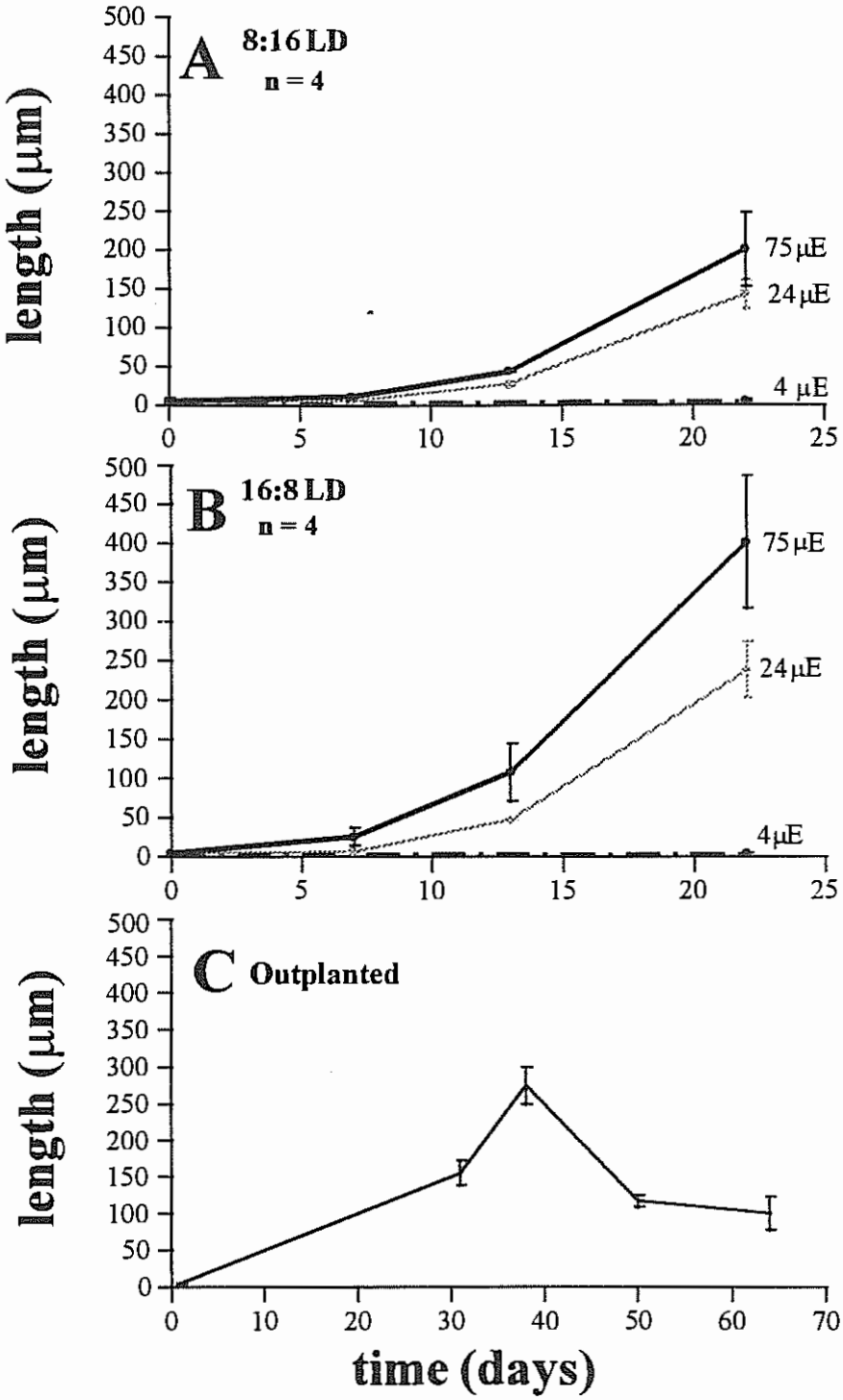


Figure 8. Growth rates of *Desmarestia ligulata* gametophytes cultured under three irradiances within summer (A) and winter (B) photoperiods. (C) Growth rates of gametophytes outplanted in winter within a canopy-cleared area (decreases in size were the result of damage from larrge winter swells that entered the cove).

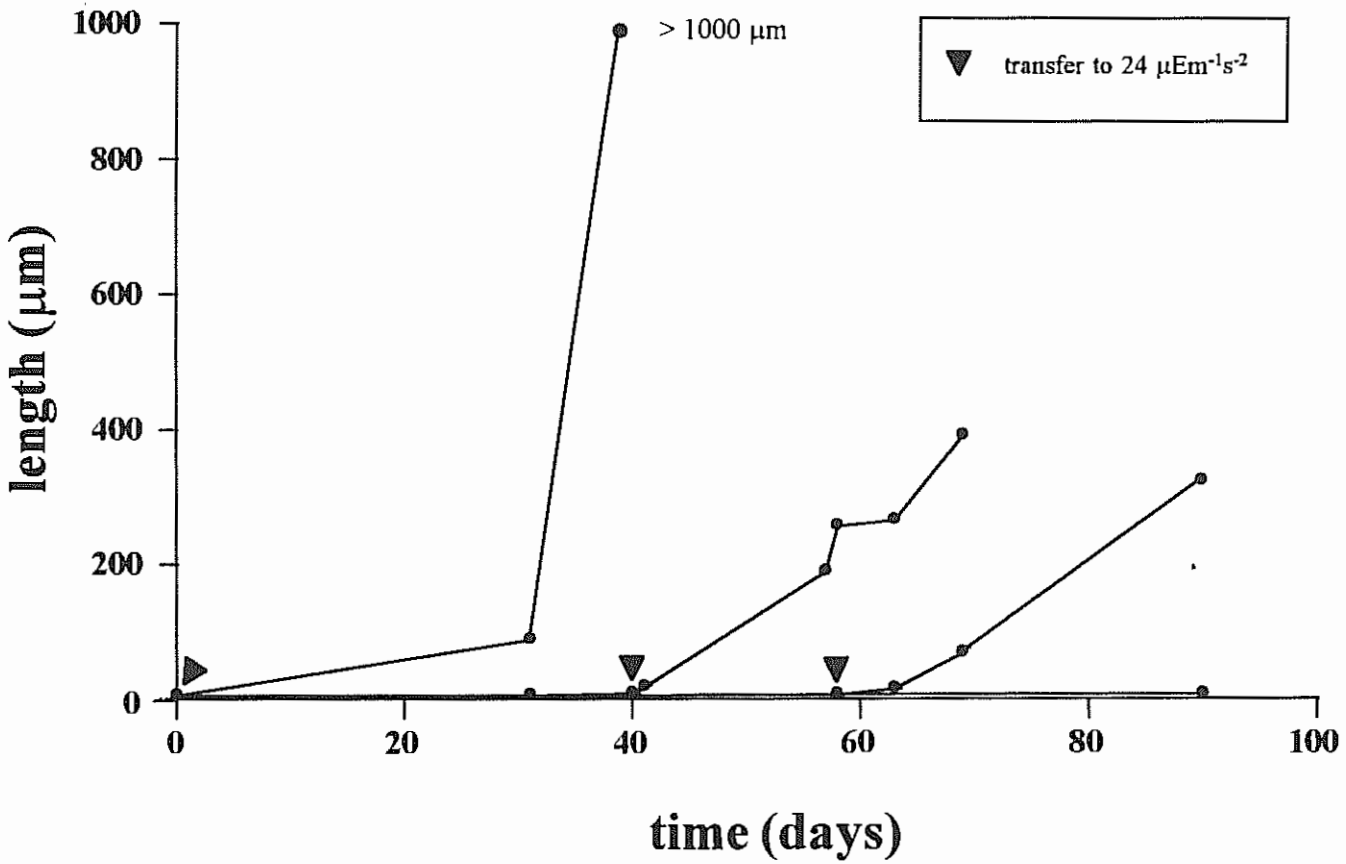


Figure 9. Mean growth rates of *Desmarestia ligulata* gametophytes cultured under low irradiance ($4\mu Em^{-2}s^{-1}$) and then transferred to higher irradiance ($24\mu Em^{-2}s^{-1}$) after 0, 40 and 62 days. Arrows indicate date of transfer to higher irradiance (each datum represents the mean of five gametophytes subsampled per culture dish). Treatment n = 1.

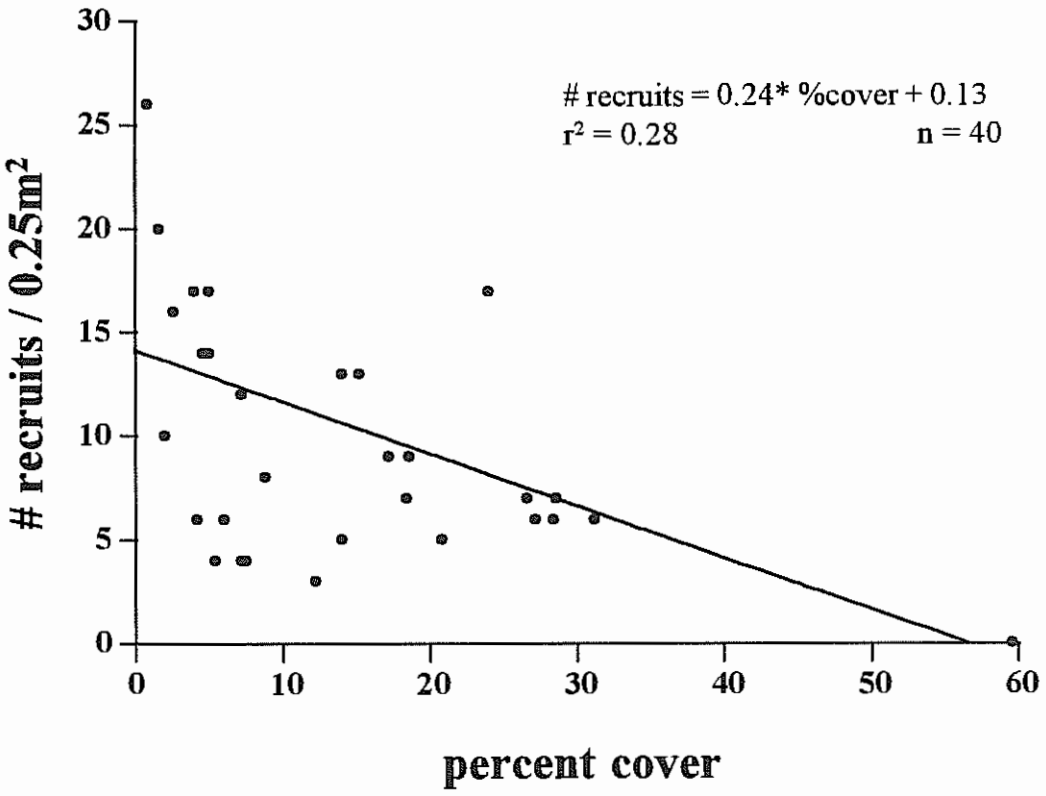


Figure 10. Relationship between *Desmarestia ligulata* sporophyte recruitment and percent bottom cover of sediment in Stillwater Cove.

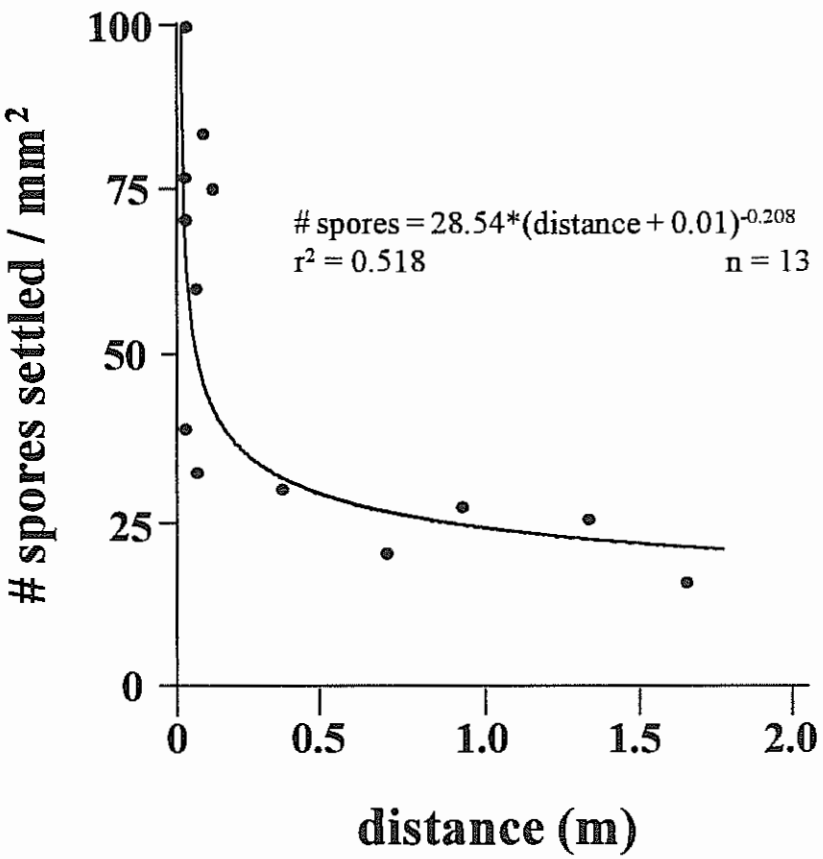


Figure 11. Relationship between settlement density of *Desmarestia ligulata* zoospores and distance from nearest sporophyte (spore source).

Appendix Table 1. Three-way nested ANOVA testing arcsin transformed sporophyte percent-cover data from two sampling methods (random vs. haphazard) on two dates.

Source	SS	DF	MS	F-ratio	p
sample date (A)	0.252	1	0.252	8.533	0.005
location {date} (B)	0.309	2	0.154	5.225	0.008
method (C)	0.005	1	0.005	0.158	0.692
date x method (AXC)	< 0.001	1	< 0.001	0.012	0.915
Error	2.187	74	0.03		

Appendix Table 2. One-way blocked ANOVA testing arcsin transformed sporophyte percent-cover data between no-canopy and control treatments among years.

Source	SS	DF	MS	F-ratio	p
canopy treatment (A)	3.232	1	3.232	89.787	< 0.001
yeart (B)	0.137	4	0.034	0.761	0.574
A x B	0.146	4	0.036	0.808	0.547
Error	0.36	10	0.036		

Appendix Table 3. (A) One-way ANOVA testing log transformed recruitment density data in turf-removal, sterilized and control plots on date of maximum sporophyte density in 1993 (April 28). (B) Bonferoni adjusted pairwise comparisons (for two comparisons) of log transformed density data among turf treatments.

A

Source	SS	DF	MS	F-ratio	p
plot treatment (A)	34.514	2	17.257	17.252	0.003
Error	6.002	6	1.000		

B

Comparison	Mean difference	p
turf-removal vs. control plots	2.527	0.021
turf-removal vs. sterilized plots	4.794	0.001

Appendix Table 4. ANCOVA testing relationship (slope) between arcsin transformed nongeniculate percent-cover data and sporophyte recruitment density at two sites.

Source	SS	DF	MS	F-ratio	p
cover (A)	656.237	1	656.237	34.938	< 0.001
site (B)	64.73	1	64.730	3.393	0.080
Error	400.63	21	19.078		

Appendix Table 5. Three-way nested ANOVA testing sporophyte density data obtained by random and haphazard sampling methods for two dates.

Source	SS	DF	MS	F-ratio	p
sample date (A)	0.200	1	0.200	0.268	0.606
location {date} (B)	4.100	2	2.050	2.748	0.071
method (C)	0.050	1	0.050	0.067	0.796
date x method (AXC)	0.450	1	0.450	0.603	0.440
Error	55.200	74	0.746		

Appendix Table 6. (A) Two-way ANOVA testing effects of irradiance and photoperiod on gametophyte growth rates. (B) Bonferoni adjusted probabilities for pairwise comparisons of different irradiances on gametophyte growth rates.

A

Source	SS	DF	MS	F-ratio	p
Irradiance (A)	356578	2	178289.025	24.04	< 0.001
Photoperiod (B)	58558.8	1	58558.76	2.869	0.106
A x B	40436	2	20218.01	2.727	0.092
Error	133497	18	7416.498		

B

Comparison	Mean difference	p
$75\mu Em^{-2}s^{-1}$ vs. $24\mu Em^{-2}s^{-1}$	110.44	0.058
$75\mu Em^{-2}s^{-1}$ vs. $4\mu Em^{-2}s^{-1}$	295.45	< 0.001
$24\mu Em^{-2}s^{-1}$ vs. $4\mu Em^{-2}s^{-1}$	185.01	0.001

Appendix Table 7. One-way ANOVA testing the relationship (slope) between arcsin transformed sand percent-cover data and sporophyte recruitment density within site 2.

Source	SS	DF	MS	F-ratio	p
regression slope	458.638	1	458.638	15.0128	< 0.001
Error	1159.74	38	30.519		

Appendix Table 8. Two-way ANOVA testing sporophyte density in *Desmarestia* - removal and unmanipulated areas at two sites between two years.

Source	SS	DF	MS	F-ratio	p
Treatment (A)	0.311	1	0.311	20.750	0.010
Year (B)	0.284	1	0.284	2.263	0.207
AxB	0.015	1	0.015	0.105	0.762
Error	0.55	4	0.138		

Appendix Table 9. One-way ANOVA testing relationship between the distance from nearest sporophyte and zoospore settlement density within site 2.

Source	SS	DF	MS	F-ratio	p
regression slope	37884.6	2	18942.281	45.392	< 0.001
Error	4596.71	11	417.883		