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THE ROLE OF ALTERNATE LIFE-HISTORY STAGES OF A MARINE MACROALGA: A SEED BANK ANALOGUE?

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Abstract. Many organisms occurring in temporally variable environments have evolved life-history traits that enable their populations to persist during unfavorable environmental conditions. Numerous terrestrial plants, insects, and marine invertebrates, for example, rely on resting stages that disperse their propagules in time. Although widely observed among many taxa, few examples exist for marine macroalgae, at least in part because of the methodology involved in studying them. Here, I determined that microscopic life stages of the annual marine macroalga *Desmarestia ligulata* overwinter during periods when the macroscopic thalli are absent, thereby allowing this species to persist in temporally variable environments. Examination of field-grown microscopic stages with fluorescence microscopy identified these stages as gametophytes. Holdfast tagging experiments determined that recruitment of the macroscopic stages was not enhanced by regrowth of perennial thalli as observed in other macroalgae, suggesting that overwintering gametophytes were the sole source of sporophyte recruitment. In contrast to true resting stages, *Desmarestia* gametophytes were not dormant, but rather were metabolically active, sensitive to small differences in environmental quality, and highly subject to physical damage. Gametophyte photosynthetic rates were greater under higher irradiance, and growth rates were greater under longer photoperiods and higher irradiance. Although their survival appeared to be reduced by grazing from large (>1 cm) invertebrates and sedimentation, gametophytes were able to survive in the field for at least 15 mo and thereby enhance sporophyte recruitment more than a year after settlement. I suggest that *Desmarestia* gametophytes be regarded as alternate life-history stages that simply maintain populations under a different set of environmental conditions than the macroscopic sporophytes do, rather than as "dormant" or "resting" stages.

Key words: annual alga; Carmel Bay, California (USA); Desmarestia; *dormancy; gametophyte; life-history stages, alternative; marine macroalga; microscopic stages; overwinter; recruitment; seed bank.*

INTRODUCTION

The ability to survive during long periods of unfavorable environmental conditions and to recover following severe disturbances is crucial to the persistence of natural populations occurring in temporally variable environments. Many species become dormant or exhibit reduced metabolic activity during unfavorable conditions and then re-establish normal metabolic activity when conditions improve (reviewed in Hinton 1968, Crowe 1971, and Hochachka and Guppy 1987). In extreme cases, where adult mortality is complete, immature life-history stages can maintain dormancy during the unfavorable periods (Venable and Lawlor 1980, Hollibaugh et al. 1981, Maier 1990, Pake and Venable 1996). In these cases, dormancy is often referred to as a "temporal dispersal strategy" and is generally considered to be a trade-off with spatial dispersal strategies (Venable and Lawlor 1980, Levin et al. 1984, Cohen and Levin 1987). When environmental quality is seasonally predictable, dormant stages may play an important role in maintaining annual life histories (Tauber and Tauber 1978, Venable and Lawlor 1980, Klinger 1984). When environmental quality is unpredictable, dormant stages may promote opportunistic life histories, allowing populations to rapidly recover following stochastic changes in environmental quality such as disturbances (Pierce and Cowling 1991, Tyler 1996). Although disturbances typically increase mortality (reviewed in Pickett and White 1985), they can also enhance reproductive success by synchronizing reproduction (Barry 1989, Reed et al. 1997), renewing limited resources (Harris et al. 1984, Sousa 1984) and removing co-occurring dominants (Levin and Paine 1974, Cowen et al. 1982, Dayton et al. 1984, Reed and Foster 1984, Edwards 1998). Therefore, by producing new adults immediately following disturbances, dormant stages may allow competitively subordinate species to coexist temporally in areas from which they would otherwise be excluded.

In many coastal marine communities, large ocean waves are the primary form of disturbance influencing species survivorship and reproduction (reviewed in

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Dayton [1985], Foster and Schiel [1985], and Schiel and Foster [1986]). Much like fires in terrestrial plant communities (e.g., Keeley 1987, Enright and Lamont 1989, Pierce and Cowling 1991, Carleton and MacLellan 1994, Schimmel and Granström 1996, Tyler 1996), large waves typically damage or remove adult macroalgae (Paine 1979, Barry 1989, Seymour et al. 1989, Graham 1997) and thereby renew limited resources such as space and bottom light (Sousa 1979, Harris et al. 1984, Reed and Foster 1984, Kennelly 1987, Dayton et al. 1992). Although macroalgae lack dormant seeds characteristic of terrestrial plants, many species survive these disturbances by exhibiting morphological variations that presumably make them more tolerant to physical damage. This may be accomplished through phenotypic plasticity in a single life-history stage (Richardson 1981, Mathieson 1982), or through heteromorphic life histories (Lubchenco and Cubit 1980, Slocum 1980). In environments characterized by long periods of unfavorable conditions, some species may rely on dormant microscopic life stages for survival (reviewed in Hoffman and Santelices [1991]). Consequently, these stages have been referred to as "banks of microscopic forms" (Chapman 1986), the functional equivalent of plant seed banks.

The shallow (< 30 m) nearshore waters in temperate and high latitudes of the Northern Hemisphere are dominated by large brown algae, primarily kelps (order Laminariales), that form dense stands on rocky substrates and that alternate between macroscopic and microscopic life-history stages (reviewed in Dayton [1985], Foster and Schiel [1985], and Schiel and Foster [1986]). It is generally assumed that the microscopic stages of at least some of these species persist during periods that are unfavorable to the larger morphologies (see Kain 1964, Dayton 1975, Lüning 1980, Anderson 1982, Foster 1982, Klinger 1984, Blanchette 1996). However, because they are small and difficult to observe in the field, the relative contribution of these stages to the persistence of the larger morphologies in seasonally variable environments has remained relatively unexplored (Santelices et al. 1995), as has their precise identity (spore, gametophyte, or embryonic sporophyte) in the field (Dayton 1985, Reed et al. 1997, Edwards 1999; but see Dube and Ball 1971, Hsiao and Druehl 1973). This identity may be important, especially for species whose various life-history stages respond differently to similar environmental conditions (Fain and Murray 1982, Hoffman et al. 1984, Anderson et al. 1990) or exhibit different competitive abilities (Reed 1990). Further, although these stages are generally referred to as being dormant, it is unclear if they are, in fact, dormant or if they remain metabolically active and therefore sensitive to changes in environmental quality.

Study organism

Desmarestia ligulata var. *ligulata* (order Desmarestiales, hereafter *Desmarestia*) is an annual subtidal alga commonly found in disturbed areas in the Northeast Pacific Ocean (Foster 1982, Reed and Foster 1984, Dayton et al. 1992, Edwards 1998). *Desmarestia* exhibits a heteromorphic life history, alternating between macroscopic diploid sporophytes and a variety of haploid and diploid microscopic stages (Nakahara 1984; Fig. 1). Sporophytes recruit in the spring (early-middle April), grow during the summer, reproduce (release zoospores) in the fall-early winter (peak zoospore release about November), and then disappear (Edwards 1996, 1998). Zoospores settle on the bottom and germinate into either male or female gametophytes. These undergo sexual reproduction to produce microscopic sporophytes that in turn grow into new macroscopic sporophytes. Upon fertilization, the eggs remain attached to the female gametophyte, effectively preventing embryo dispersal following gametophyte reproduction (Chapman and Burrows 1971). Given that *Desmarestia* sporophytes typically disappear completely from large geographic areas, it is unlikely that sporophyte recruitment occurs from zoospores that disperse from (unknown) neighboring populations, but rather that it occurs from one or more of the microscopic stages that overwintered from the previous year's population. Although it has been suggested that these stages overwinter as gametophytes (Kain 1964, Dayton 1985, Dayton et al. 1992, Reed et al. 1997), neither their identity nor their survival in the field are known. Also, while the holdfasts of other algae have been observed to persist during periods of sporophyte absence and then regrow, enhancing the next season's sporophyte recruitment (Chapman and Burrows 1971), their relative importance to *Desmarestia* is unclear. In this study I described the relative contribution of overwintering microscopic stages and of regrowth of perennial holdfasts to the recruitment of *Desmarestia* sporophytes, as well as identified the life-history stage responsible. I also determined if these microscopic stages were in fact dormant during this period, and subsequently evaluated the effects of environmental quality (irradiance and photoperiod) on their growth. Finally, I determined if these stages were able to survive in the field for more than one year, and examined the effects of invertebrate grazing and sedimentation on their survival. *Desmarestia*'s annual and opportunistic life history made it an ideal species for examining these questions in the field.

METHODS

Study site

Field research was done from January 1992 to July 1998 in Stillwater Cove, Carmel Bay, California, USA (36°34′ N, 121°56′ W). This cove opens to the south and is relatively protected from large ocean swells that are typically associated with winter storms. Its physical characteristics, flora, and fauna have been well described (Foster 1982, Reed and Foster 1984, Foster and

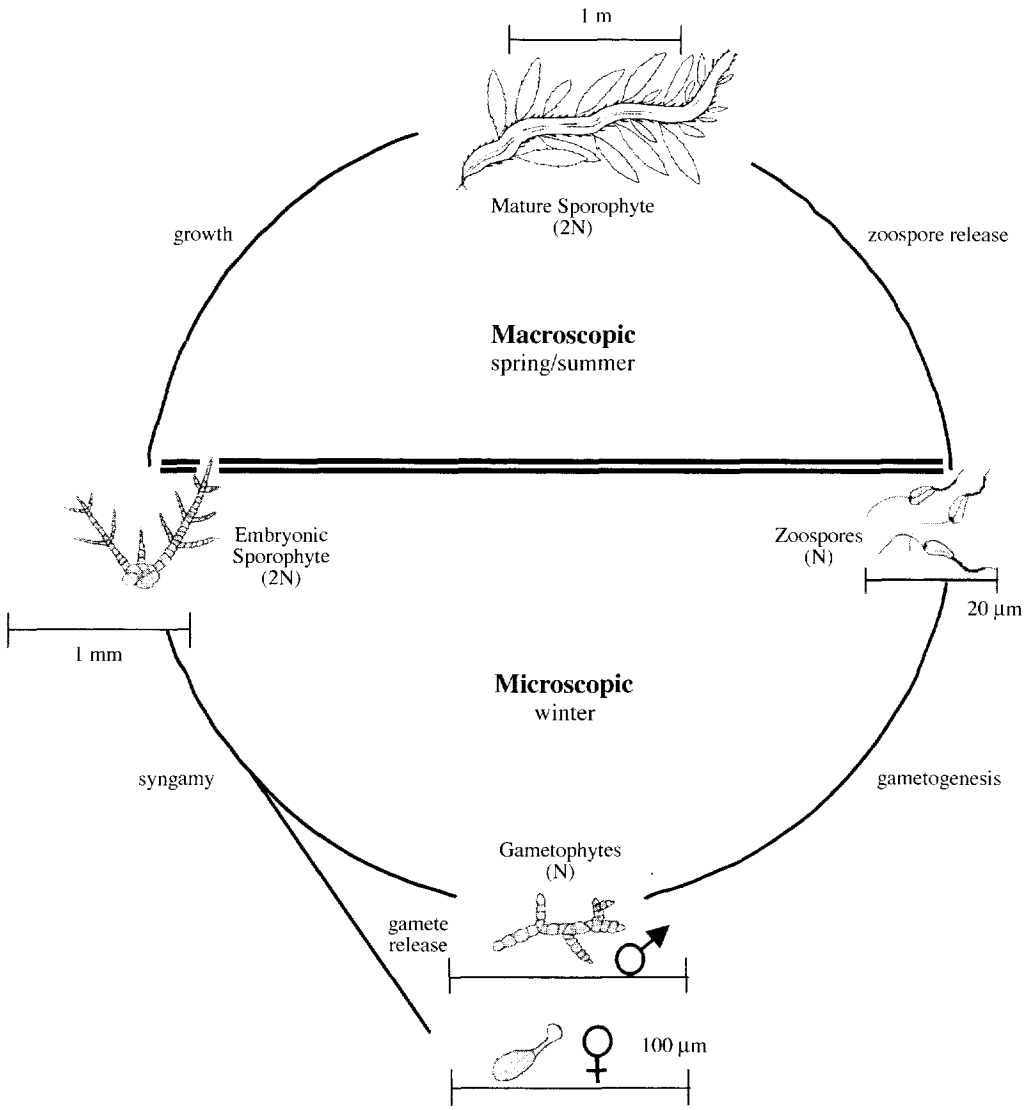

FIG. 1. *Desmarestia* life history, showing both macroscopic and microscopic stages. Scales are provided to give estimates of size, but should be interpreted with caution due to wide variability in thallus sizes for each stage. 2N is the diploid number of chromosomes, and N is the haploid number.

Schiel 1985, Edwards 1998). The study sites within the cove were two 628-m^2 semicircles where the canopy-forming kelps *Macrocystis pyrifera* and *Pterygophora californica* were experimentally excluded, and *Desmarestia* sporophytes occurred in high densities (Edwards 1998).

The contribution and quantification of the microscopic stages

To determine the relative contribution of overwintering microscopic stages vs. regrowth of perennial holdfasts to the recruitment of *Desmarestia* sporophytes, I compared sporophyte recruitment between substrates with and without microscopic stages, and estimated holdfast survival and regrowth. To do this, all microscopic algae were removed from three 0.25-m^2 plots in one of the study sites in February 1993 (after all *Desmarestia* sporophytes had disappeared from the cove). Here, all macroscopic algae were first removed from the plots by abrading the substrate with a wire brush. A 0.25-m^2 watertight tent was then placed over each plot and sealed to the substrate. One liter of household bleach was injected into each tent, and the tents were left for two days before being retrieved (see Edwards [1999] for a more detailed account of methods and their effectiveness). Also, all macroscopic algae were removed from three additional 0.25-m^2 turf-removed plots, while taking care not to damage the substrate, and three 0.25-m^2 unmanipulated control plots were established. All nine plots were then monitored weekly during the following winter and spring for sporophyte recruitment. Recruitment was ultimately com-

pared between the sterilized and turf-removed plots to assess the importance of microscopic stages, and between the turf-removed and control plots to assess the effects of the turf removal (see Edwards 1998). The low replication of this experiment ($n = 3$) resulted from logistical difficulties associated with developing methods to sterilize substrates in situ. Statistical power, however suspect, was not problematic.

Survival and regrowth of perennial *Desmarestia* thalli were estimated by tagging 20 holdfasts in the study sites in January 1993 and 25 in January 1994 by attaching plastic surveyors tape to the substrate 6 cm on either side of each individual. Holdfasts were then monitored for survival during the remainder of each winter, and for regrowth the following spring. In addition, in spring 1993, 321 newly recruited *Desmarestia* sporophytes occurring in 25 randomly placed 0.25-m^2 quadrats were closely examined to determine if they recruited from regrowth of perennial holdfasts.

The precise identification of the microscopic stages involved in overwintering (January–April) was determined by directly examining them on microscope slides at weekly intervals. To do this, *Desmarestia* zoospores were settled onto 90 frosted-glass microscope slides in January 1994 and then immersed in a 20% solution of Fungi-fluor (0.01% solution Cellufluor; Edwards 1999) to label the microscopic thalli with a an ultraviolet (UV), sensitive stain that did not affect their physiology (Cole 1964, Nakazawa et al. 1969, Hsiao and Druehl 1973). These slides were placed on three polyvinyl chloride slide racks (30 slides per rack), transported to the field in opaque plastic bags to avoid exposure to direct sunlight, and bolted to the substrate at a depth of 12 m in one of the study sites. Three slides per rack were collected each week for the next 10 wk and examined under fluorescence microscopy in the laboratory. Stained (known *Desmarestia*) thalli were easily identified when examined under UV light, and their life-history stage (spore, gametophyte, or embryonic sporophyte) determined under white light.

To determine if *Desmarestia*'s microscopic stages were dormant while they overwintered, I estimated their growth in the field, examined the effects of irradiance on photosynthesis, and assessed the effects of photoperiod and irradiance on growth in the laboratory. To estimate growth in the field, the longest axis length of five haphazardly chosen individuals occurring on each of the slides retrieved for life-history identification on days 1, 31, 38, 50, and 64 were measured with an ocular micrometer at 100×. On each date, the mean thallus size per slide, the mean thallus size per slide rack, and the overall mean thallus size for the three slide racks ($n = 3$) were determined. I then determined if photosynthesis of the microscopic stages varied under different light intensities by estimating carbon uptake under various irradiances in the laboratory. Because summer bottom irradiance under kelp canopies at 12 m in the cove varied between ~24 and ~75 μmol photons·m^{-2}·s^{-1}, and was as low as 4 μmol photons·m^{-2}·s^{-1} in areas under perennial turf algae (Edwards 1998), I assessed the metabolic activity of the microscopic stages under a variety of light intensities spanning this range. To do this, *Desmarestia* zoospores were settled onto 24 glass cover slips (~27 spores/mm^2) and incubated under short-day (8 h light/d) and low-irradiance (24 μmol photons·m^{-2}·s^{-1}) conditions for 1 wk at 10°C. All cover slips were then placed in glass test tubes with 70 mL of 0.2-μm filtered seawater, and 21 of these inoculated with 18.5 Bq of ^{14}C dissolved in 10 μL of sodium bicarbonate (pH 8.5) (Arnold and Littler 1985). The tubes were capped, transported to an outdoor incubator, and allocated to one of five irradiances (8, 20, 45, 75, and 105 μmol photons·m^{-2}·s^{-1}); irradiance levels were established by shading an ambient irradiance of 800 μmol photons·m^{-2}·s^{-1}, and water temperature was the same as ambient ocean water (~11°C). Irradiance treatments were established by covering the test tubes with various grades of wire screen, and the ambient photoperiod was ~10 h light/d. The remaining three uninoculated tubes were left in the original incubator. After 6 h, all 24 tubes were collected, their contents (water and cover slips) vacuum-filtered through Whatman GF/F glass filters (0.2-μm pore size, Whatman Incorporated, Ann Arbor, Michigan) to collect all algal thalli (suspended and settled). The cover slip and filter associated with each tube were then placed in a scintillation vial with 5 mL LSC (liquid scintillation counter) cocktail (Scintsafe, Fisher Scientific, Chicago, Illinois). Gametophyte biomass on the cover slips was estimated fluorometrically using a Turner 10-AU fluorometer (Turner Flurometer, Sunnyvale, Calfornia, USA). For each vial, radioactivity was measured in a liquid scintillation counter (Packard Tri-Carb 2000CA/LL [Packard Instrumentation, Meriden, Connecticut, USA]), the activity determined (in counters per minute) and the metabolic activity of its contents calculated as the amount of carbon fixed per gram of thallus per hour.

Since photoperiod and bottom irradiance within Stillwater cove vary seasonally and as a function of both kelp-canopy cover and turf-algal density, I measured growth of *Desmarestia* microscopic stages under different combinations of photoperiod and irradiance (under which *Desmarestia* microscopic stages were believed to persist in the field). To do this, *Desmarestia* zoospores were settled onto 24 glass microscope slides (~50 spores/mm^2) and placed in glass dishes with 200-mL nutrient-enriched seawater (70 mL Alga Grow [Carolina Biological Supply, Burlington, North Carolina, USA]/L filtered seawater). The dishes were then randomly assigned to one of six treatments defined by three irradiances (4 μmol photons·m^{-2}·s^{-1}, 24 μmol photons·m^{-2}·s^{-1} and 75 μmol photons·m^{-2}·s^{-1}) and two photoperiods (16 h light/d and 8 h light/d). Here, dishes were placed in one of two culture chambers, each with a different photoperiod (16 h light/d and 8 h light/day);

within each chamber dishes were shaded with wire screen to produce the three irradiances similar to those observed under kelp canopies in the field. Culture chambers were set at 8–9° C. The dishes were incubated for 2 mo, with the culture media changed weekly. A 0.2-mL saturated solution of GeO_2/L culture media was used during the first week only to prevent diatom contamination. Each week the slides were examined microscopically and the longest axis length of five haphazardly chosen filaments on each slide measured with an ocular micrometer at 100×. The mean thallus size per slide and the mean size per treatment were then estimated from the four dishes ($n = 4$). After 3 wk the sizes of the microscopic stages in some treatment combinations became too large to precisely measure and the experiment was terminated.

Survival of the microscopic stages

Because in situ survival of the microscopic stages could not directly be observed on natural rock substrates (Dayton 1985, Edwards 1999), I used sporophyte recruitment to estimate it (Hoffman and Santelices 1991, Santelices et al. 1995). Therefore, to determine if *Desmarestia*'s microscopic stages were able to survive in the field for >1 yr, I compared sporophyte recruitment on substrates that had microscopic stages that were more than a year old with recruitment on substrates where the microscopic stages had been removed more than a year prior. To do this, I randomly selected 28 boulders (~ 4.5 kg each) from a 15-m-deep boulder field located ~ 100 m from one of the study sites in an area where *Desmarestia* sporophytes were commonly observed following kelp canopy thinning (*personal observation*). In January 1997 fourteen of these boulders were taken back to the laboratory and placed in the sun for 2 wk to kill all living microscopic algae (Reed et al. 1997). After this time I transplanted all 28 boulders (14 "sun-dried" and 14 "control") to a 25-m-deep "holding site" located ~ 150 m from the boulder field while taking care not to expose the control boulders to direct sunlight. The holding site was chosen based on three criteria. (1) It was isolated from large populations of *Desmarestia* sporophytes and therefore should have been only weakly influenced by additional zoospore settlement (Edwards 1996). (2) Although it was within the depth range where *Desmarestia* sporophytes naturally occur (Abbott and Hollenberg 1976), a thin kelp canopy and the natural attenuation of light in the water column resulted in light levels similar to those observed under the more dense kelp canopies in the shallower (12 m) parts of the cove (*personal observation*), thus preventing sporophyte production (Foster 1982, Reed and Foster 1984, Edwards 1998); no *Desmarestia* sporophytes recruited in the holding site during the experiment. Any losses of the microscopic stages should therefore have been due to their mortality and not sporophyte production. (3) Although their relative abundance varied, the composition of co-occurring species, especially the cove's major gastropod and echinoid grazers, was similar between this site and other areas of the cove where *Desmarestia* commonly occurred. To assess survival of the microscopic stages after 3 mo in the field (i.e., one winter), I transplanted seven boulders from each treatment to one of the shallow (12 m) study sites in March 1997 and then monitored them for sporophyte recruitment. The remaining seven boulders of each treatment were left in the holding site for an additional year. To assess survival of the microscopic stages after 15 mo in the field (i.e., two winters), the remaining boulders were transferred from the holding site to the study site in March 1998 and monitored for sporophyte recruitment. Sporophyte recruitment densities were standardized among boulders by only counting sporophytes in the center 100 cm^2 of each boulder.

To examine the effects of large (>1 cm) invertebrate grazers on the survival of the microscopic stages, I compared sporophyte recruitment on substrates where grazers were excluded with those where grazers were allowed access. To do this, similar densities (~25 individuals/mm^2) of *Desmarestia* zoospores were settled onto fifteen 24-cm^2 tile slates in a large well-mixed tank. The slates were then transferred to the field in opaque plastic bags to prevent exposure to direct sunlight and bolted to the substrate in one of the study sites. The slates were randomly allocated to one of three treatments: (1) completely enclosed in wire mesh (1 cm^2) stainless-steel "cages," (2) partially enclosed on two sides and a roof by wire mesh "cage-controls," and (3) completely uncaged "controls." The slates were monitored for sporophyte recruitment during the following spring and summer.

I estimated effects of sedimentation on the survival of the microscopic stages by assessing the relationship between sediment bottom cover and sporophyte recruitment in spring 1994. To do this, sediment bottom cover was estimated using a point-contact method (see Cowen et al. 1982) and the number of *Desmarestia* sporophytes counted within each of thirty-eight 0.25-m^2 quadrats that were randomly placed within the study sites.

Statistical analysis

Statistical analyses were done using SYSTAT (Wilkinson 1990). Prior to testing, data were examined for homogeneity of variances using an F test or Cochran's C test and for normality by graphical interpretation of residuals. Appropriate transformations were applied to data not meeting these assumptions and the data reexamined. If problems could not be fixed by transformation, an alternative test was used. Power analyses were performed on nonsignificant results (Cohen 1988) using an imposed "small" effect size of a 20% deviation among treatment means (Cohen 1988, Thomas 1997). Due to the logistical difficulties associated with studying microscopic algal stages in situ, some exper-

iments had low replication, and thus low statistical power (Cohen 1988). Therefore, some statistical tests were modified (i.e., specific null and/or alternative hypotheses were evaluated) to increase the power of the tests.

Sporophyte recruitment data for experimental plots were heteroscedastic and remained so after transformation. Thus, significant treatment effects were evaluated using an extension of Bahrens-Fisher's T test for three groups (Rice and Gaines 1989). However, because of low replication ($n = 3$) and large differences among the treatment variances (several orders of magnitude), the power of this test was questionable. Therefore, an ordered heterogeneity (OH) modification, which evaluated the null hypothesis (H_o: $\mu_{\text{turf-removed}} = \mu_{\text{control}} = \mu_{\text{sterilized}}$) against the simply ordered alternative hypothesis (H_A: $\mu_{\text{turf-removed}} > \mu_{\text{control}} > \mu_{\text{sterilized}}$) was applied (Rice and Gaines 1994). This alternative hypothesis was chosen based on the findings by Reed and Foster (1984) and Edwards (1998) who showed that sporophyte recruitment was greater in areas where turf algae had been removed than in control areas. The composite test statistic (r_sP_c), which combined both magnitude and ordering measures of the data, was determined as the product of the Spearman's rank correlation coefficient (r_s) between the observed and expected rankings of the treatment means and the compliment of Bahrens-Fisher P value ($P_c = 1 - P_{\text{Bahrens-Fisher}}$). The new P value ($P_{(OH)}$) was then determined by graphical interpretation of the r_sP_c test statistic (Rice and Gaines 1994). A one-tail Bahrens-Fisher's T test was then used post hoc to evaluate the specific hypothesis: $\mu_{\text{turf-removed}} > \mu_{\text{sterilized}}$.

Data for photosynthetic rates (μg C fixed·μg chl a^{-1}·h^{-1}) were heteroscedastic, and therefore transformed ($\sqrt{x}$) prior to testing. Differences in photosynthetic rates between the microscopic stages cultured at 8 μmol photons·m^{-2}·s^{-1} and a hypothesized mean of zero (i.e., no photosynthesis) were assessed with a one-sample t test (H_o: $\mu_{8\mu\text{mol photons}} = 0$). Differences in photosynthetic rates between microscopic stages cultured at 80 μmol photons·m^{-2}·s^{-1} and microscopic stages cultured at 8 μmol photons·m^{-2}·s^{-1} were examined with a two-sample t test (H_o: $\mu_{8\mu\text{mol photons}} = \mu_{80\mu\text{mol photons}}$). To avoid among-test α-error inflation, Bonferoni-adjusted probabilities were used to evaluate significance of the two t tests. Because a single culture chamber was used to establish each photoperiod treatment, differences in growth of laboratory-cultured microscopic stages were compared among the irradiances at the end of 3 wk using a separate one-way ANOVA for each photoperiod. Differences among the three irradiance levels were then examined post hoc with Bonferoni-adjusted planned comparisons (Simes 1986). Because recruitment on control boulders was assumed to be greater than on sun-dried (see *Results: The contribution and quantification of the microscopic stages*, below; see also Reed et al. 1997), differences in sporophyte recruitment on sun-dried vs. control boulders after both 3 mo and 15 mo in the holding site were examined with separate one-tailed, two-sample t tests (H_o: $\mu_{\text{control}} > \mu_{\text{sun-dried}}$). To avoid among-test α-error inflation, Bonferoni-adjusted probabilities were used to evaluate significance of the two t tests. Notation for reporting the results of these t test details the degrees of freedom only; α-level and number of tails used to interpret each test are described in the text (see *Results: Survival of the microscopic stages*, below).

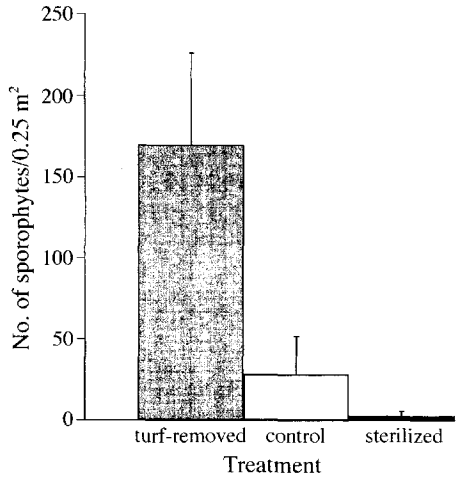

FIG. 2. Maximum number of *Desmarestia* sporophytes that recruited to sterilized, turf-removed, and control plots during spring 1993. Data are means and 1 SE; $n = 3$ plots per treatment.

The effect of grazers on sporophyte recruitment was assessed with a one-tail, two-sample t test that evaluated the a priori hypothesis $\mu_{\text{caged}} > \mu_{\text{cage-control}} = \mu_{\text{control}}$ (where cage-controls and controls were assumed to be equivalent in that they allowed access to grazers). To examine the relationship between sediment bottom cover and sporophyte recruitment, sediment-cover data were transformed (arcsine $\sqrt{x}$) and the relationship assessed with a nonlinear regression ($y = a \times x^{-b}$).

RESULTS

The contribution and quantification of the microscopic stages

Desmarestia sporophytes recruited to the cove in early April and then disappeared during the following winter each year, leaving a period of 3–4 mo of sporophyte absence (Edwards 1998). In general, sporophyte recruitment was significantly different among the sterilized (3.33 ± 3.33 recruits/plot [mean ± 1 SE]), turf-removed (169 ± 56.67 recruits/plot) and control (28.33 ± 23.30 recruits/plot) plots (Bahrens-Fisher$_{(OH)}$: $r_sP_c = 0.87$, $P < 0.02$; Fig. 2). Specifically, sporophyte recruitment was lower on substrates where the microscopic stages had been removed by sterilization than on substrates where only the turf algae had been removed (Bahrens-Fisher T test: $P = 0.045$), indicating that recruitment occurred from microscopic stages that

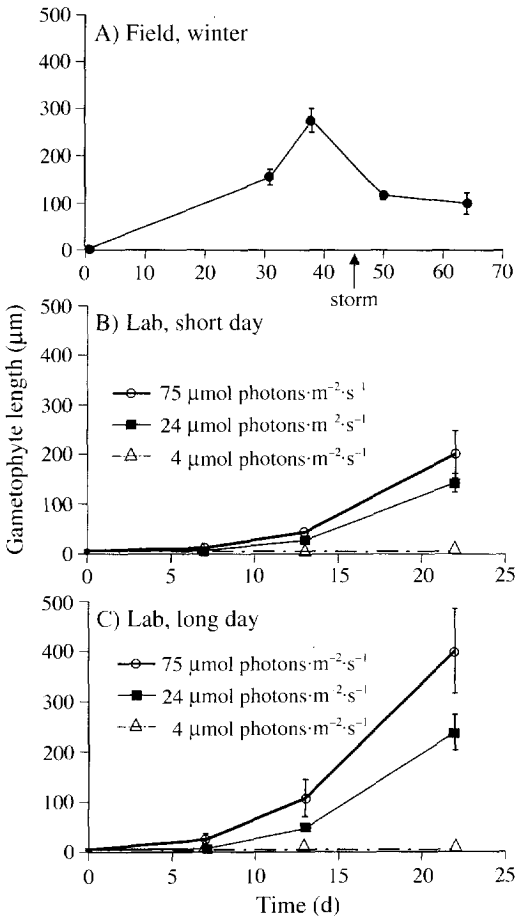

FIG. 3. Average length of *Desmarestia* gametophytes grown under different conditions. (A) *Desmarestia* growing on slides that were out-planted to the study sites during winter 1994. For each sample date, a mean thallus length was estimated for each slide from five haphazardly selected gametophytes, and the mean for each slide rack was determined from three haphazardly selected slides. Data are means ± 1 SE; n = 3 slide racks/sample date. "Storm" indicates the occurrence of large storm-driven swells that entered the cove during the study. *Desmarestia* gametophytes cultured in the laboratory under (B) short-day (8 h light/d), and (C) long-day (16 h light/d) photoperiods, and three irradiances (75 μmol photons·m^{-2}·s^{-1}, 24 μmol photons·m^{-2}·s^{-1} and 4 μmol photons·m^{-2}·s^{-1}). On each sample date, the average thallus length per dish was determined from five haphazardly selected gametophytes. Data are means ± 1 SE; n = 4 dishes/treatment combination.

were already on the substrate at the time the plots were sterilized. None of the holdfasts tagged in 1993 or 1994 survived through the following winter and no new sporophytes recruited to their same locations the following spring. Furthermore, none of the 321 sporophytes examined in 1993 recruited from regrowth of persistent holdfasts. Together, this indicated that overwintering microscopic stages were the sole source of sporophyte recruitment.

The microscopic stages that were labeled, out-planted to the field, and then collected periodically throughout the winter (January–April) were easily identified when examined using fluorescence microscopy. Subsequent examination under white light determined that these stages overwintered as gametophytes. These gametophytes grew while they overwintered (attaining lengths of almost 300 μm in 38 d), but were either reduced in size, or suffered a high mortality of larger individuals, during a period of large swell activity (Fig. 3A). Furthermore, gametophytes did not remain dormant; ^{14}C uptake demonstrated that photosynthesis varied with irradiance. Although significantly greater than zero (one-sample t test: t_2 = 1.705, P = 0.022), photosynthesis was reduced (0.87 ± 0.03 μg C fixed μg chl a^{-1}·h^{-1}) under very low light levels (8 μmol photons·m^{-2}·s^{-1}) compared to higher light levels (6.46 ± 1.23 μg C fixed μg chl a^{-1}·h^{-1} at 75 μmol photons·m^{-2}·s^{-1}) (two-sample t test: t_2 = 6.34, P = 0.013). Gametophytes grew significantly larger in higher irradiances when cultured under both short-day (ANOVA: $F_{2,9}$ = 11.23, P = 0.003) and long-day (ANOVA: $F_{2,9}$ = 14.06, P = 0.002) photoperiods. Further, gametophytes appeared to grow larger under long-day photoperiods (Fig. 3B and C). Gametophytes, however, did not grow in extremely low irradiance (4 μmol photons·m^{-2}·s^{-1}) regardless of photoperiod, but began growing immediately after being transferred to a higher light irradiance (Edwards 1996). Whether gametophytes photosynthesized at this irradiance was not examined.

Survival of the microscopic stages

Desmarestia gametophytes survived on the experimental boulders for at least 15 mo and contributed to sporophyte recruitment over multiple years (Fig. 4). Differences in sporophyte recruitment between the sun-dried and control boulders in spring 1997 (after 3 mo in the holding site) were significant (t test: t_{10} = 2.236;

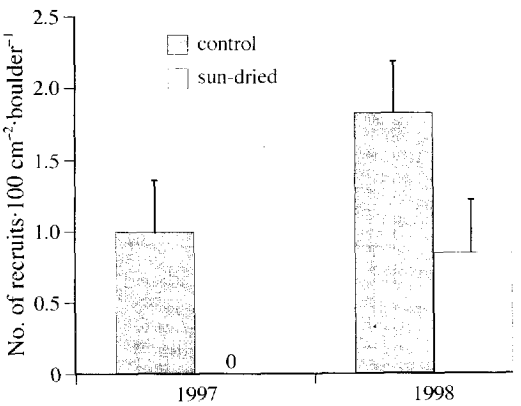

FIG. 4. Number of *Desmarestia* sporophytes that recruited within the center 100 cm^2 of sun-dried and control boulders transferred from the holding site after 3 mo (1997) and 15 mo (1998). Data are means ± 1 SE; n = 7 boulders per treatment.

Bonferoni-adjusted $P = 0.049$), supporting the results of the substrate sterilization experiment; no sporophyte recruited onto substrates where the microscopic stages were removed several months prior. Sporophyte recruitment, however, was observed on both boulder treatments in spring 1998 (after 15 mo in the holding site), suggesting that zoospore settlement had occurred in the holding site. Although differences in recruitment between the boulder treatments at this time were not significant (t test: $t_{10} = 1.336$; Bonferoni-adjusted $P = 0.108$), likely due to low statistical power (0.18) resulting from small sample sizes, the magnitude of the difference in recruitment between the boulders treatments remained constant between years (Fig. 4).

Grazing by large (> 1 cm^2) invertebrates appeared to reduce gametophyte survivorship on the tile slates. The cages were effective at excluding the cove's most abundant invertebrate grazers (i.e., the bat star *Asterina miniata*, and the gastropods *Tegula brunnea*, *T. puligo*, *Calliostoma annulatum*, *C. caniculatum*, and *Aplysia californica*) from the slates (no grazers were ever observed on them, while grazers were frequently observed in the surrounding areas and occasionally on the cage-control and control slates). Although sporophyte recruitment on caged slates was not significantly different from zero (t test: $t_3 = 1.4$, $P = 0.13$), believed to be the result of low statistical power (0.29) resulting from low replication and high among-slate variance, they were the only slates on which sporophyte recruitment was observed (4.6 ± 6.4 recruits per slate, [mean ±1 SD]); no recruitment was observed on either cage-control or control slates.

Sedimentation had a negative affect on gametophyte survival within the study sites (regression equation: Number of sporophytes = 3.76 × sediment cover$^{-0.37}$; $r^2 = 0.47$; Fig. 5A). Graphical interpretation of the residuals suggested that variances were heteroscedastic, and that sedimentation was more important (deterministic) to survival at high levels of cover (Fig. 5B). Consequently, although this regression should be interpreted with caution, it appeared that, overall, sedimentation negatively affected sporophyte recruitment, and was more deterministic at higher levels of sediment cover. At lower levels of sediment cover, then, other factors such as competition with turf algae (evidenced by the differences in recruitment between turf-removed and control plots) and differences in substrate type appeared more important (Edwards 1998). It is also important to note that even at the highest levels of sediment cover examined (32%), *Desmarestia* sporophyte recruitment still exceeded 5 sporophytes / 0.25 m^2, suggesting that, although sedimentation did have a negative effect on gametophyte survival, the levels examined were not sufficient to prevent sporophyte recruitment.

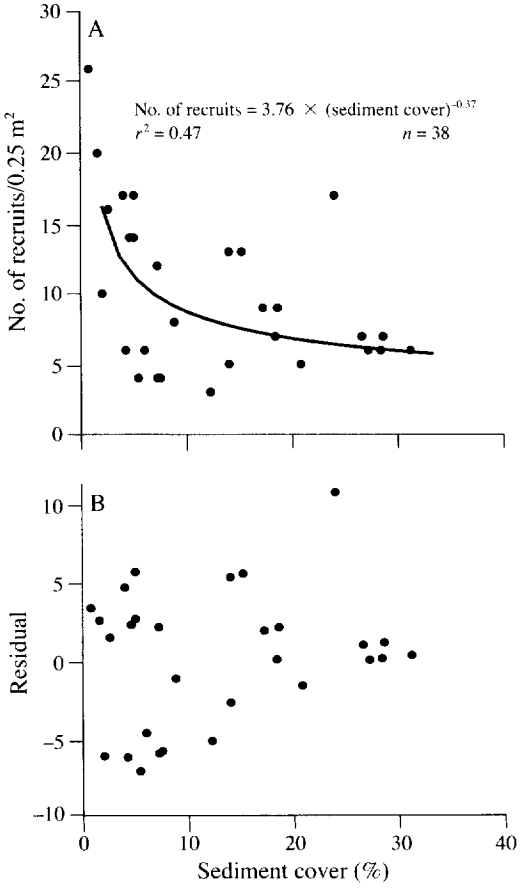

FIG. 5. Sporophyte recruitment as a function of sediment cover. (A) Nonlinear regression ($y = ax^{-b}$) of the relationship between sediment bottom cover and *Desmarestia* sporophyte recruitment (used here as an estimate of gametophyte survivorship). For each datum, sediment cover and sporophyte density were estimated within the same 0.25-m^2 quadrat; $n = 38$ quadrats. (B) Regression residuals (recruitment vs. sediment cover) showing decreasing variability with increasing levels of sediment cover.

DISCUSSION

Temporal variability in environmental quality is one of the most important factors influencing biological populations (reviewed in Pickett and White 1985). For species that are especially vulnerable to unfavorable environmental conditions, or that have relatively short-lived adults, dormancy is a common method of survival and often occurs through alternate life stages (reviewed in Hinton 1968, Crowe 1971, and Tauber and Tauber 1978). Many species of terrestrial plants, for example, rely on dormant seed banks to persist during periods of drought, cold temperatures, or low light (reviewed in Leck et al. 1989). Likewise, many insects (Tauber and Tauber 1978), copepods (Grice and Marcus 1981) and diatoms (Hollibaugh et al. 1981) become dormant during periods that are unfavorable to their adults. Much as spatial dispersal of propagules allows some species to persist in geographically heterogeneous environments (Levin et al. 1984), dormancy of propagules may act as a temporal dispersal strategy, thereby allowing populations to persist in areas where they

would otherwise be excluded. By maintaining large populations, dormant stages also promote rapid recovery following severe disturbances (Tyler 1996). Although it has been assumed that dormant stages occur in marine macroalgae (Foster 1982, Hoffman and Santelices 1991, Dayton et al. 1992, Santelices et al. 1995), there has been relatively little evidence to support this assumption (but see Santelices et al. 1995). This study found that much as seed banks promote the persistence of many annual plant species, microscopic life stages of the annual macroalga *Desmarestia* are the primary means by which its populations persist in seasonally variable environments. These microscopic stages further allowed *Desmarestia*'s sporophytes to be opportunistic, recruiting high densities following disturbance-induced kelp canopy removal (Reed and Foster 1984, Edwards 1998).

Since sporophytes were absent from the cove for at least 3 mo prior to sporophyte recruitment each year (Edwards 1996), and given that algal zoospores are typically short-lived (Nakahara 1984, Hoffman 1987; see also Santelices 1990) with their settlement competency decreasing rapidly within hours to days after release (Kain 1964, Hoffman and Camus 1989, Reed et al. 1992), sporophyte recruitment must have arisen from overwintering microscopic stages. The complete disappearance of the sporophytes tagged in 1994 and 1995 together with the close examination of newly recruited sporophytes further indicated that sporophyte recruitment did not occur from regrowth of perennial holdfasts as observed for other species of macroalgae. A few untagged sporophytes, however, did survive the winter in 1995, but these remained small and tattered and did not produce healthy sporophytes during the following spring (*personal observation*). Here, the removal of all microscopic stages from the substrate at a time when no replacement source was available greatly reduced or prevented sporophyte recruitment the following spring. Differences among the sterilized, turf-removed, and control plots (Fig. 2) demonstrated that sporophyte recruitment occurred from microscopic stages that were already on the substrate by at least February, and then persisted through the winter (approximately February–April). While recruits were abundant in all of the non-sterilized plots in 1993, they were completely absent in all but one of the sterilized plots. These few recruits, however, likely resulted from microscopic stages that survived the sterilization process and not from recently settled zoospores, as sterilizing this plot was problematic due to an inefficient watertight seal between the tent and the substrate. This indicates that not only did microscopic stages of *Desmarestia* overwinter periods of sporophyte absence, but also they were the sole source of sporophyte recruitment in the spring.

Examination of the out-planted thalli with fluorescence microscopy demonstrated unequivocally that *Desmarestia*'s microscopic stages overwintered from February to April as gametophytes. Whether or not the microscopic stages that settled earlier in the winter (i.e., around November) also overwintered as gametophytes was not determined, but given that only gametophytes were observed during this period, it is plausible that most, and perhaps all, of *Desmarestia*'s microscopic stages were gametophytes. Although this life stage was previously assumed to be the overwintering stage for *Desmarestia*, as well as a number of other macroalgae (Kain 1964, Chapman and Burrows 1971, Foster 1982, Klinger 1984, Dayton 1985, Dayton et al. 1992, Blanchette 1996, Reed et al. 1997), it had not been shown in field studies; gametophytes of several species of macroalgae have been found growing in the field (Dube and Ball 1971, Hsiao and Druehl 1973, Moe and Silva 1989), but their small size has made it difficult to determine their survival times or whether they represent overwintering stages.

Unlike the seeds of terrestrial plants (Venable and Lawlor 1980, Keeley 1987, Alvarez-Buylla and Martínez-Ramos 1990, Pake and Venable 1996), or the resting stages of marine copepods (Grice and Marcus 1981, De Stasio 1989, Maier 1990, Viitasalo 1992), diatoms (Hollibaugh et al. 1981), and insects (Tauber and Tauber 1978), laboratory studies on marine macroalgae indicate their microscopic stages remain physiologically active under light and temperature conditions that are unfavorable to the macroscopic stages (Kain 1964, Anderson and North 1969, Shreader and Moss 1975, Fain and Murray 1982, Nakahara 1984, Anderson and Bolton 1989, Santelices et al. 1995). This is true for *Desmarestia*; gametophytes were not dormant while they overwintered, but rather were metabolically active and thus sensitive to changes in environmental quality. In fact, their growth was significantly reduced at lower irradiances (Fig. 3B and C) and appeared to be reduced under shorter photoperiods. They also continued to photosynthesize even under very low (8 μmol photons·m^{-2}·s^{-1}) irradiance, although growth was not observed at 4 μmol photons·m^{-2}·s^{-1}. Remaining metabolically active, and thus able to repair damaged tissue, may be crucial to their surviving for extended periods in the field, given that gametophytes lack the protective coats characteristic of the true dormant stages of other organisms. If these gametophytes were dormant, they may not have been able to repair damaged tissue incurred during storms (Fig. 3A), and thus would have accumulated non-lethal injuries until they became lethal (Hinton 1968, Crowe 1971, Hochachka and Guppy 1987).

Although the microscopic gametophytes of most macroalgal species appear to survive in the field for only a few weeks to several months (Deysher and Dean 1986, Hoffman and Camus 1989, Reed et al. 1997), *Desmarestia* gametophytes appear able to survive in the field for at least 3 mo, and likely for 15 mo. Even though differences in sporophyte recruitment between sun-dried and control boulders was not significant after

15 mo in the holding site, the magnitude of the differences in recruitment remained constant among years. This suggests that, although sporophyte recruitment did arise from zoospores that settled during the previous winter, the gametophytes that were already on the boulders at the beginning of the experiment were able to survive for at least 15 mo and thus increase sporophyte recruitment in subsequent years. The contribution of the recently settled zoospores, then, increased sporophyte recruitment on all boulders (Fig. 4). Therefore, the importance of long-lived gametophytes may differ among areas where the sporophytes are common and subsequent zoospore settlement is high, and areas where the sporophytes are consistently rare and subsequent spore settlement is low. For example, Reed et al. (1997) observed that in a southern California kelp forest, where *Desmarestia* sporophytes were relatively common, sporophyte recruitment was primarily driven by recently settled zoospores, and that long-lived (> 1 yr) gametophytes either did not occur or were simply unimportant to sporophyte recruitment. Thus, much like a terrestrial seed bank, gametophytes may accumulate on the bottom in areas where *Desmarestia* is consistently rare or absent (such as under dense kelp canopies), and then produce sporophytes in great abundance when conditions suddenly improve (e.g., after canopy removal). This idea is supported by surveys of other areas in the cove during late summer 1998; following extensive kelp canopy removal from severe winter storms, *Desmarestia* sporophytes became extremely abundant in areas where they had been rare for several years prior (*unpublished data*). It has also been suggested that long-lived gametophytes allow species to maintain annual life histories by delaying sporophyte recruitment until favorable conditions or seasons occur (Dayton 1975).

Although this is one of only a few studies to demonstrate the importance of long-lived microscopic life-history stages to the local persistence of populations in the field, other species may also exhibit similar patterns upon further investigation. For example, although gametophytes of *Macrocystis pyrifera* have only been observed to survive in the field for a few weeks (Deysher and Dean 1986, Hoffman and Camus 1989, Reed et al. 1997), they have been observed to survive in the laboratory for several years. This indicates that they are physiologically capable of long-term survival and raises the possibility that they may have long-term survival that operates under certain environmental conditions; for example, *M. pyrifera* sporophytes can recruit in high densities into areas along Baja, Mexico, after being both completely absent for several months, as well as separated from a significant source of new zoospores by large distances (M. S. Edwards, *unpublished manuscript*). Much as for *M. pyrifera*, long-lived gametophytes were previously thought to be unimportant to the persistence of local populations of *Desmarestia*, likely due to the lack of evidence to support such a claim, resulting from a lack of appropriate methodologies for examining such stages in the field. More complete experimental investigations are required to examine properly how long the macroalgal microscopic stages of a number of species of macroalgae can survive under a variety of environmental conditions, or if they can serve as a bank of microscopic stages. Regardless, long-term survival of the microscopic stages of at least some marine macroalgae remains a viable mechanism by which populations survive during, and recover following, long periods of unfavorable environmental conditions. It therefore would be useful if future studies of marine macroalgae examined the relative contribution made by microscopic stages to the persistence of natural populations in seasonally variable environments, as well as the ecology of the microscopic stages themselves.

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