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Demography of the intertidal kelp *Alaria marginata* along the Big Sur coast

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DEMOGRAPHY OF THE INTERTIDAL KELP *ALARIA MARGINATA*
ALONG THE BIG SUR COAST

A Thesis

Presented to

the Faculty of Moss Landing Marine Laboratories

and the Department of Marine Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

By

Laurie Anne McConnico

August 2003

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ABSTRACT

DEMOGRAPHY OF THE INTERTIDAL KELP *ALARIA MARGINATA* ALONG THE BIG SUR COAST

by Laurie Anne McConnico

Though *Alaria marginata* dominates exposed rocky intertidal shores along the Big Sur coast of California, this is the first population dynamics study of the alga. Experimental clearings and controls were established to assess recruitment timing and plant survivorship. Plants were collected monthly to determine population growth and reproduction. Results indicated *Alaria* was an annual. Sporophyte recruitment occurred in early spring and maximum growth rates were during April. Sorus development began as early as March, peaked during August-October, and decreased as adult plants were tattered or ripped from substrate by winter surf. Spore release was greatest between October and January, and apparently stimulated by high water motion. Survivorship of plants beyond one year was rare. Persistence of this large, annual, intertidal kelp appears to be related to massive spore production at the onset of fall storms, persistence of microscopic stages for three months, and rapid growth and maturation of sporophytes.

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TABLE OF CONTENTS

List of Tables	viii
List of Figures	ix
Introduction	10
Methods	14
Results	20
Discussion	26
Conclusions	35
Literature Cited	38
Appendices	
A. Tables	44
B. Figure Legends	46
C. Figures	48

LIST OF TABLES

Table 1. Analysis of Variance on the effect of site (Big Creek/Gorda), treatment (Control/Cleared), and time (March/October) on density of the 2002 *Alaria* cohort.

Table 2. Percent cover ($\mu \pm \text{SE}$) of available substrate and *Alaria* recruitment ($\mu \pm \text{SE}$) to that substrate in cleared and control plots at Big Creek and Gorda during March 2002. Species with <5% cover were not included in the table, but were used in analyses.

LIST OF FIGURES

Figure 1. Illustration of *Alaria marginata* showing the vegetative blade and sporophylls with sori (adapted from O'Clair and Lindstrom 2000).

Figure 2a. Density of *Alaria* m^{-2} ($\mu\pm\text{SE}$) in experimental plots between July 2001-October 2002 at Big Creek Reserve.

Figure 2b. Density of *Alaria* m^{-2} ($\mu\pm\text{SE}$) in experimental plots between July 2001-October 2002 at Gorda.

Figure 3. Density of *Alaria* m^{-2} ($\mu\pm\text{SE}$) in plots cleared in July 2001 and partially re-cleared (0.5 m^2) in February 2002.

Figure 4. Total length of *Alaria* ($\mu\pm\text{SE}$) at Big Creek and Gorda between July 2001-November 2002.

Figure 5. Sorus area of *Alaria* ($\mu\pm\text{SE}$) at Big Creek and Gorda between July 2001-November 2002.

Figure 6. Number of spores released $\text{mm}^{-2} \text{ hr}^{-1}$ ($\mu\pm\text{SE}$) at Big Creek and Gorda between October 2001-October 2002.

Figure 7. Number of spores released per plant at Big Creek and Gorda between October 2001-October 2002.

Figure 8. Number of *Alaria* per size class ($\mu\pm\text{SE}$) at Big Creek during July 2002.

Figure 9. Proportion of fertile *Alaria* per size class ($\mu\pm\text{SE}$) at Big Creek during July 2002.

Figure 10. Density of *Alaria* m^{-2} ($\mu\pm\text{SE}$) in canopy cleared plots and controls between July 2002-October 2002.

Figure 11. Survivorship of 2001 *Alaria* cohort at Big Creek and Gorda since July 2001.

Figure 12. Survivorship of 2002 *Alaria* cohort in cleared and control plots at Big Creek and Gorda.

INTRODUCTION

Seaweeds grow, reproduce, and die; thus, persistence in marine environments is dependent on the ability to repeatedly secure and maintain space throughout their lifecycle. Some algae complete this cycle annually, while others are perennial. Population persistence and the mechanisms ensuring persistence can vary depending on the species' life history. In low or moderately disturbed environments, once perennial seaweeds colonize habitat they can potentially persist and hold space for years, often as the competitive dominant (Dayton 1975, Foster 1975a, Sousa 1979a, 1979b, 1980). Conversely, annuals are absent from the environment for a portion of each year (persisting often as microscopic alternate phases) and require some mechanism for re-establishment (Edwards 2000). In terrestrial plant communities, annuals are frequently weedy species that exploit disturbed environments by growing rapidly and saturating the area with seeds (Harper 1977). Similarly, annual marine algae are often successful in disturbed environments where growth of perennial algae is suppressed (Reed and Foster 1984), or in some cases are dependent upon disturbance events to re-establish themselves (Dayton 1973, DeVogelaere 1991).

Kelp populations in general are persistent as many grow fast (Scagel 1947, Vadas 1968, Foster 1975b, Coyer and Zaugg-Haglund 1982), have high reproductive output and can saturate the environment with spores (Scagel 1961, Anderson and North 1966, Kain 1975, Chapman 1984). Additionally, all kelps have heteromorphic alternation of generations that may facilitate survival during unfavorable or seasonally variable conditions (Clayton 1988, Santelices 1990) and may also allow for recolonization of

macroscopic plants after large-scale disturbances. Seed banks, microscopic phases including gametophytes or embryonic sporophytes, and perhaps more appropriately called spore stores, are often cited as the source of recovery (Hoffmann and Santelices 1991, Reed et al. 1997, Edwards 2000, Kinlan et al. 2003). These rapid growth and extensive reproductive capabilities may be even more essential to the persistence of annual kelps, given the importance of timing of recruitment, growth, reproduction, and survival of microscopic phases for re-establishing populations each year.

Understanding the influence of life histories on population persistence is most rigorously achieved through demographic analyses. Population dynamics of perennial kelps including the genera *Laminaria*, *Macrocystis*, and *Pterygophora* are well established (Kain 1975, Chapman 1984, De Wreede 1986, Schiel and Foster 1986, Graham et al. 1997). Thorough demographic studies of annual algae in marine environments are less common. Population dynamics have been investigated (in varying detail) for annual kelps including *Pelagophycus porra* (Coyer and Zaugg-Haglund 1982), *Nereocystis luetkeana* (Maxell and Miller 1996), *Costaria costata* (Maxell and Miller 1996), *Cymathere triplicata* (Roland 1984) and *Alaria nana* (Pfister 1992). The data indicate these seaweeds with large, annual sporophytes recruit in spring or early summer, grow rapidly, and release spores near the end of the sporophyte's life. Survivorship and longevity of microscopic stages were not investigated for any of these annuals, but population persistence is attributed to survivorship of microscopic phases during months in which sporophytes were absent.

Most of what is known about persistence of annual kelps comes from studies on *Postelsia palmaeformis*, which indicate the alga is dependent on winter disturbances to remove mussels and create bare space for colonization each year (Dayton 1973, Paine 1988, Blanchette 1996). Dayton's (1973) clearing experiments indicated that *P. palmaeformis* sporophytes can colonize cleared areas within a few weeks by developing from spore to sporophyte after mussels are removed, while Blanchette (1996) suggested that gametophytes/microscopic sporophytes (over-wintering phase not assessed) develop beneath mussel beds, germinate quickly, and develop into macroscopic sporophytes following the removal of mussels by disturbance. It is unknown whether a spore store exists beneath mussel beds, or if spores settle, germinate, and gametophytes eventually produce adult sporophytes only after the removal of mussels.

Despite attempts to understand *P. palmaeformis* persistence, no researchers have examined how the alga's demography may influence persistence. Information on the timing of recruitment and reproduction are observational (Dayton 1973). No data are available on reproductive output or their possible seasonality. There are some estimates of *P. palmaeformis* growth rates (Paine 1986). Knowledge of gametophyte habitat and longevity are also necessary to determine how and where the alga survives during winter. More thorough investigations from a demographic perspective would facilitate understanding of persistence in exposed intertidal habitats.

As in *P. palmaeformis*, seasonality of spore production and release has not been quantitatively assessed for many annual kelps. Some estimates of annual spore production based on counts of sporangia are available for *Nereocystis luetkeana* (Scagel

1961) and indicate that spores are released as abscised pieces of sorus in high densities ($\sim 3 \times 10^{12}$ per plant) toward the end of the season before sporophytes are dislodged. Estimates of spore production using similar methods are available for perennial kelps (Kain 1975, Chapman 1984, Joska and Bolton 1987). While timing of spore release may influence recruitment of perennial species, their persistence beyond one year and ability to reproduce more than once affords some reproductive flexibility. Conversely, timing of reproduction is essential for successful recruitment of annual kelps. Survival in the absence of a long-lived spore store is dependent upon spore release prior to sporophyte loss and under conditions that are favorable for the survivorship of microscopic phases contributing to the next cohort.

Alaria marginata Postels & Ruprecht (Fig. 1, adapted from O'Clair and Lindstrom 2000) is another intertidal kelp that occupies wave exposed intertidal habitats. The alga occurs in the northeast Pacific from Alaska to near Point Concepcion, CA (Widdowson 1971). It is particularly abundant on exposed mid to low rocky intertidal shores along the Big Sur coast of California, at summer densities of up to 500 m^{-2} (pers. obs.). With the exception of Yendo's (1919) monograph of the genus *Alaria* there is limited information on its growth rates and reproductive phenology; most of the available literature on *A. marginata* is taxonomic. The comprehensive taxonomic revision of the genus by Widdowson (1971) provides information on morphological features of species within the genus and their ranges. No thorough studies of the population dynamics of this alga have been conducted, and the literature is conflicting on whether *A. marginata* is

annual, perennial or biennial (Yendo 1919, Vadas 1968, Abbott and Hollenberg 1976, Kusumo and Druehl 2000, Paine 2002).

The recruitment, growth, reproduction, and survivorship of *A. marginata* (here after *Alaria*) sporophytes were investigated in this study. By following cohorts of *Alaria* in the field and examining spore release it was possible to determine if the alga is annual, how populations vary through the growing and reproductive season, and how these demographic attributes effect population persistence along the Big Sur coast. Finally, understanding *Alaria* demography is critical for mitigation and management of Cal Trans road maintenance dumping activities, which are common along the Big Sur coast of California.

METHODS

Study Sites

Field work was done at two sites along the Big Sur coast, California: Big Creek Reserve (here after Big Creek) and Gorda, between July 2001 and November 2002 (Big Creek: 36° 04.166' N, 121° 35.919' W; Gorda: 35° 51.522' N, 121° 25.522' W). Big Creek was the primary site for field work, plant collections, and lab experiments, whereas Gorda was visited less frequently and used primarily to determine how consistent patterns of recruitment, growth, reproduction, and survivorship were over broader spatial scales. Both sites are heavily exposed to waves (Gorda slightly less than Big Creek) and influenced by seasonal gravel inundation and scour. *Alaria* is the dominant alga, occupying much of the mid-low rocky intertidal at these sites, and other similarly exposed expanses of large boulders (2-4m in diameter) along this coast (pers. obs.).

Recruitment and Survivorship

In July 2001, eight 1m² and four 1m² areas with abundant *Alaria* were cleared at Big Creek and Gorda, respectively, to determine recruitment, survivorship, and the effect of clearings on these processes (by February 2002 one of the boulders on which a cleared plots was located was disturbed by winter swell and rolled outside of the *Alaria* zone making the treatment unviable at Gorda, hence sample size was reduced to n=3 at this site following the disturbance). Plots were cleared by scraping and wire brushing until all visible, erect plant material was removed. Non-geniculate coralline algae and encrusting red and brown algae were scraped and abraded, and geniculate corallines were removed to the crustose holdfast, but plots were not sterilized. Complete removal of *Alaria* holdfasts was not always possible and in some cases a thin layer of haptera persisted. However, regeneration from residual holdfast was never observed. Four 1m² control plots with *Alaria* abundance similar to cleared plots were established at both sites. Control and experimental plots were allocated randomly (but separated by at least 1m) along a 100-200 m stretch of the intertidal zone at each site, and marked with stainless steel bolts.

Plots were monitored monthly at Big Creek beginning in July 2001 for changes in density of the 2001 *Alaria* cohort (those plants present at the beginning of this study), and were sampled monthly for the density of the 2002 *Alaria* cohort once recruitment commenced. The Gorda site was sampled less frequently until monthly sampling began in February 2002, coinciding with the onset of recruitment at this site. A 2-Factor ANOVA (Site, Treatment; both fixed) was used to test for differences between mean

plant density in cleared and control plots at both sites. Recruitment data were analyzed with a 3-Factor ANOVA (Site, Treatment, Time; all fixed) for March and October sampling dates.

Three of the eight 1m² plots cleared at Big Creek in July 2001 were partially re-cleared (0.5 m²) in February 2002 at the time of recruitment. The fourth plot was not included in this experiment because winter swell rotated and scoured the ~2m diameter boulder on which the plot was located, making the treatment no longer viable. These new 0.5m² clearings were used to determine the effect of season of clearing on recruitment and the potential for spore stores (relative to the plots that were cleared once in July 2001). The extent of clearing was comparable to that described above, and *Alaria* density in these plots was determined monthly from February to October 2002. Data from this experiment were analyzed with a Blocked ANOVA (March data only), with each of the three plots blocked and treatments being the July 2001 cleared and February 2002 re-cleared plot halves.

Recruitment and Substrate

Substrate availability and the association of *Alaria* recruits with a particular substrate were assessed during March 2002 at Big Creek and Gorda to determine if juvenile sporophytes recruited to substrates in proportion to their abundance. Percent cover of sessile organisms and rock was determined using a modified point quadrat consisting of a string with six knots attached to a 1m PVC pipe (modified after Foster 1982). The 1m² plots were divided into five regions, and percentage cover was assessed under six random points in each region, for a total of 30 random points per plot. The

presence of *Alaria* recruits in a particular substrate was independently assessed for the plants closest to an additional 30 random points. Data (average percent cover for control and cleared plots at each site) were evaluated using a Chi-square analysis, where a 1:1 ratio of substrate availability to substrate with *Alaria* recruitment indicates recruitment proportional to habitat abundance.

Growth

To assess growth rates, total plant length was measured for the 20 largest plants throughout the entire sampling area at each sampling time. Two to three plants were collected just outside of each experimental plot, at the same tidal height. No plants were collected from within experimental plots. More plants were collected during the initial July 2001 sampling (n=33 at Big Creek, n=24 at Gorda), but because variance was minimal a subsequent reduction in sample size was possible. Growth estimates were based on mean length of the largest plants because absolute growth rates were not possible given the logistical difficulty of tagging plants and making regular field measurements. Plants were collected monthly at Big Creek beginning in July 2001 and less frequently at Gorda until monthly sampling began in February 2002. Two sample t-tests were used to evaluate differences in mean plant size between Big Creek and Gorda for July and August 2002 sampling dates.

Reproduction

The 20 largest plants used to determine patterns of growth were also used to assess changes in plant fertility at each site. The number of sporophylls present on each of these plants and the sorus area [$2(\text{Length} \times \text{Width})$]; sori occur on both sides of a

sporophyll] for each sporophyll was determined. Mean sorus area was used to infer variation in spore production during the year. Measures of sorus area per plant were monthly at Big Creek and less frequent at Gorda until monthly collections began in February 2002. These data were only examined for trends.

Spore release from each plant was also estimated to determine if reproductive output was seasonal and, if so, the time of year of greatest spore release. During months when spore release experiments were done, plants were collected and desiccated for ~2 hours, a period similar to what plants would be subjected to during a low tide. A small round core was then punched (3.5cm or 2cm diameter depending on sporophyll size) from the center of the most fertile blade on each plant (darkness of blades and large size was used to infer greatest fertility), placed into 20ml filtered seawater (0.2 μ m) and allowed to release spores for 1 hour (pilot studies indicated most release occurred during the first hour). Samples were preserved in 5% formalin and stored in a cool, dark place until counted.

To count spores, samples were homogenized and an aliquot from the 20ml sample was filtered onto a 0.4 μ m polycarbonate Nuclepore[®] filter. Filtered samples were then transferred to a microscope slide, mounted with immersion oil and glass coverslip, and released spores were counted using epifluorescent microscopy at 400x. Spore release estimates were obtained by haphazardly moving the sample slide around the field of view and counting the number of spores within a 10x10 grid. The number of spores per grid was recorded until ~200 spores were counted. When spore release was minimal, the number of spores in five grids was recorded and used to assess spore release for that

sample. Each sample slide was counted three times, and the mean of these counts was used in the final calculation of spore density per sample. The average number of spores per grid was then multiplied by the entire area of the filter pad and divided by the sample volume filtered. This value was multiplied by the total sample volume to determine the number of spores per 20ml sample. Counts were then converted to the total number of spores released $\text{mm}^{-2} \text{hr}^{-1}$. Finally, counts were multiplied by the mean fertile area per plant to obtain an upper estimate of total spore production per plant based on the 20 largest plants collected at each study site. These data were highly heteroscedastic, so they were analyzed separately by site among times with randomization tests equivalent to ANOVA. Randomization t-tests were used to evaluate which months had significantly greater spore release (Resampling Stats 1990).

Population Size Structure

To determine how representative collections of the 20 largest *Alaria* were of the size of the rest of the population, three additional 1m^2 areas were cleared in July 2002 at Big Creek. These plots were interspersed throughout the range of the experimental plots, at a similar tidal height, and had comparable densities of *Alaria*. Total length and fertility of all *Alaria* within these plots were assessed and used to determine the mean number of plants per m^2 per size class and proportion of fertile plants per size class.

Additionally, all *Alaria* $>1\text{m}$ were cleared from three 1m^2 plots in July 2002 to assess whether abundant, small under-story *Alaria* ($<1\text{m}$) would transition into larger size classes in the absence of larger, canopy forming *Alaria*. Change in density and size of

plants in canopy removal plots were compared with three 1m² control plots where canopy was not manipulated.

Grazer Observations

Qualitative observations on the genera of grazers and their relative abundance in control and cleared plots were made monthly at both Big Creek and Gorda.

General Statistical Methods

When parametric tests were used, data met the assumptions of normality and equal variances, or did so after transformation.

RESULTS

Recruitment Timing and Density Effects

There were no significant differences in mean plant density between sites (Big Creek/Gorda) or treatments (control/cleared plots) before manipulation in July 2001 (2-Factor ANOVA; Site, $F_{2,1} = 0.00$, $p = 0.95$; Treatment, $F_{2,1} = 0.40$, $p = 0.54$; the interaction term was barely significant, $p = 0.05$, and not of interest in this study). Most recruitment of the 2002 cohort into control plots at Big Creek occurred in February through April, peaked in March and densities decreased through the summer (Fig. 2a). There was a lag in recruitment at Gorda, with most recruits appearing in March at this site (Fig. 2b). The late winter/early spring recruitment patterns were similar in cleared plots, but the 2002 cohort in cleared plots (plants recruiting to cleared plots after July 2001) were less abundant than the 2002 cohort in control plots (plants recruiting to control plots after July 2001) for both sites at the beginning of the recruitment season in March and when sampling was terminated in October 2002 (Table 1). Once recruitment

occurred, the density of 2002 cohorts in cleared plots was consistent through October 2002 indicating that recruit mortality was minimal in cleared plots and that no new recruitment occurred later in the year. Conversely, the density of the 2002 cohorts in control plots declined rapidly after March (Big Creek) and April (Gorda) 2002 indicating that few to no new *Alaria* recruited to controls after this time and that mortality of recruits was great following the initial recruitment period (Figs. 2a & 2b).

Results from 0.5 m² clearings in February 2002 indicated that when plots were cleared might affect *Alaria* recruitment (Fig.3). There was a trend towards lesser recruitment in the February re-cleared plot halves, than in plot halves cleared in July 2001, but results were not statistically significant (Blocked ANOVA, March 2002; Block $F_{2,2}=2.91$, $p=0.26$; Treatment $F_{2,1}=12.49$, $p=0.07$). The non-significant result was influenced by relatively high recruitment in one of the February re-cleared plot halves, whereas recruitment was considerably less in the other two plots. Additionally, once individuals recruited to February re-cleared plot halves little recruitment occurred later in the year and plant densities were stable. There were declines in recruit density for plot halves cleared in July 2001 following the initial recruitment period in March 2002, and no further recruitment occurred.

Substrate and Recruitment

Based on percentage cover of available substrate versus substrate where *Alaria* recruited, *Alaria* did not recruit to substrate in proportion to availability in cleared and control plots at either, Big Creek (Cleared, $17.55 > \chi^2_{0.05, 9}=16.92$, $P=0.04$; Control, $46.67 > \chi^2_{0.05, 15}=25.00$, $P=0.00$) or Gorda (Cleared, $43.30 > \chi^2_{0.05, 11}=19.68$, $P=0.00$;

Control, $51.36 > \chi^2_{0.05, 14} = 23.69$, $P=0.00$). Average Chi squared values are reported for cleared and control plots at each site, however, values per plot were significant for all but one plot. *Alaria* recruitment was greater than expected to geniculate coralline algae in control and cleared plots at Big Creek and Gorda, and greater to residual *Alaria* holdfasts in control plots at Big Creek and Gorda. Recruitment was negatively associated with bare rock, crusts, and non-geniculate coralline algae at both sites (Table 2).

Growth

Changes in plant size based on collections of the largest plants indicated that *Alaria* sporophytes grew quickly, attaining lengths up to 5m between February and July 2002 (Fig. 4). Average growth rate through the entire growing season (February-July) for the largest plants was $\sim 0.7\text{m}$ per month. Maximum growth rate was estimated at $\sim 1.4\text{m}$ per month between March and April 2002 at Big Creek and Gorda. Total plant length at both sites peaked in late summer and declined through fall and winter as terminal blades were lost to increased surf during this time (Fig. 4). There was a trend towards larger plant size at Gorda vs Big Creek, but plant length was not significantly different in July (2 sample t-test $_{0.05, 2}$, $df=38$, $T=-1.62$, $P=0.11$). Plants were significantly larger at Gorda in August 2002 (2 sample t-test $_{0.05, 2}$, $df=38$, $T=-4.23$, $P=0.00$), indicating that whereas plants may not grow significantly larger at Gorda, they did maintain larger sizes.

Reproduction

Fertility, or mean sorus area per plant, was similar at both Big Creek and Gorda throughout the study. The amount of fertile tissue was consistent through fall for the

2001 cohort and declined rapidly to the least levels in winter 2001. Plants from the 2002 cohort initiated sorus development as early as March (following recruitment in February), increased sorus production throughout the spring as plants matured, and peaked in late summer/early fall. Mean sorus area for the 2002 cohort declined by November 2002 after the first set of winter storms (Fig. 5).

Lab experiments indicated *Alaria* spore release was significantly different throughout the year at both Big Creek and Gorda (Big Creek: randomization test $df=9$, $p<0.05$; Gorda: randomization test $df=7$, $p<0.05$). Spore release was generally minimal throughout the spring and summer at both Big Creek and Gorda. Most spore release occurred in late fall/winter between October and January (Fig. 6). During the one hour release period for Big Creek $\sim 1,800$ spores mm^{-2} were released in October 2001 and $\sim 12,000$ spores mm^{-2} were released in October 2002. Release was also great during January 2002 ($>2,100$ spores mm^{-2}) at Big Creek. Spore release during October 2002 was significantly greater when compared with each of the other months in which spore release was great (October 2001: randomization test $_{0.05,2}$, $df=30$, $p<0.05$; January 2002: randomization test $_{0.05,2}$, $df=36$, $p<0.05$; August 2002: randomization test $_{0.05,2}$, $d=37$, $p<0.05$). Spore release during October 2001 was not significantly greater than August 2002 (randomization test $_{0.05,2}$, $df=29$, $p>0.05$), but was greater in May 2002 (randomization test $_{0.05,2}$, $df=30$, $p<0.05$), a month in which spore release was more typical of the rest of the spring and summer. A significant increase in spore release was also observed at G in October 2002 ($>2,400$ spores mm^{-2}), relative to May 2002 (randomization test $_{0.05,2}$, $df=37$, $p<0.05$). The difference between October 2002 and the remaining sampling dates

at Gorda was assumed because there was a significant difference between October 2002 and May 2002, which had the second greatest mean spore release.

Mean spore release per plant based on total sorus area and rate of spore release indicated the greatest total contribution of spores occurred in October 2001 and October 2002 at Big Creek and October 2002 at Gorda (Fig. 7). This was true despite the high release of spores reported for Big Creek during January 2002. There were relatively few fertile plants remaining in January 2002, and those that were remaining had lost the majority of their sporophylls so sorus area per plant was also greatly reduced. Based on these calculations, large, fertile plants at Big Creek had the potential to release $>1 \times 10^9$ spores during late fall 2002. During this time, total spore contribution per plant at Gorda was estimated at $>1 \times 10^8$ spores. While total spore output was less at Gorda than Big Creek, the timing of maximum release was consistent at both sites.

Population Size Structure

Plant measurements from clearings in July 2002 indicated plants from the smallest size classes (1-50cm) were more abundant than the remaining size classes (>50 cm; Fig. 8). Plant abundance in size classes between 75 and 350cm was fairly evenly distributed. Few plants in these plots were >350 cm in length. The proportion of fertile plants per size class increased as plant size increased (Fig. 9). There were few to no fertile plants smaller than 50cm while almost all plants >300 cm were fertile.

Few *Alaria* less than 1m grew big enough to contribute to larger size classes after canopy clearing in July 2002, even in the absence of canopy forming plants. Instead, the number of small *Alaria* (<1 m) continued to decline throughout the summer and fall in

both control and canopy-cleared plots, never reaching large sizes (Fig. 10). Some of the plants present in canopy-cleared plots did become fertile between July and October 2002, but none of the sporophylls were as large as those on larger plants in natural stands.

Survivorship

The 2001 cohort in control plots (plants present in the control plots since July 2001) decreased drastically through fall and winter at both sites, with fewer than 1 individual m^{-2} remaining by July 2002 (Figs. 2a & 2b). Survivorship of these plants (based on averages for control plots, $n=4$ at both sites) to 1 yr was ~8% for Big Creek and ~12% for Gorda (Fig. 11), based upon the observed timing of recruitment in February 2002 (although time of recruitment was not assessed for the 2001 cohort). Survivorship decreased to an average of ~1% for both sites by May 2002, indicating that survival beyond 15 months was unlikely, and that plants from the 2001 cohort contributed relatively little to population persistence after one reproductive season.

Survivorship of the 2002 cohort in control and cleared plots decreased considerably between March and October 2002 (Fig. 12). Survivorship of the 2002 cohort (based on average values for control and cleared plots for each site) was ~40% greater in the cleared (60% survival) vs control (20% survival) plots, by October 2002. This pattern of greater survivorship for the 2002 cohort in cleared plots compared to control plots was consistent at both Big Creek and Gorda, indicating that density dependent mortality occurred at the high densities in control plots.

Grazer Observations

Grazers including the genera *Collissella* and *Lottia* were observed in control and cleared plots at both Big Creek and Gorda throughout the course of the study. On average there appeared to be no obvious differences in grazer densities between control and cleared plots, however, some cleared plots did have more grazers than others. Evidence of gastropod grazing (grazer yet to be identified) was common on sporophylls, but grazers were seldom found on the plants themselves.

The limpet *Notoacmaea insessa*, commonly observed on midribs of the kelp *Egregia menziesii*, was found grazing on *Alaria* stipes. Grazing by *N. insessa* was not frequent, but when it occurred limpets burrowed into and weakened stipes so that the entire terminal blade and sporophylls would be severed from the stipe and holdfast.

DISCUSSION

Alaria marginata has an annual cycle of recruitment, growth, reproduction and senescence. Sporophyte recruitment occurred in late winter/early spring, and sporophyte density declined through spring and summer as plants grow to adult size, become fertile, and began releasing spores. Spore release and total reproductive output were greatest during fall, and although not studied, the time between spore release and peak recruitment of visible sporophytes in the spring indicated that gametophytes must have developed and reproduced during fall and winter, with dormancy at some microscopic stage between spore and visible sporophyte. Survivorship of *Alaria* sporophytes through winter was minimal; most were lost to winter surf by February and few plants in the

remaining 2001 cohort survived to reproduce another year ($<1\text{m}^{-2}$ in controls by July 2002).

Recruitment Timing and Density Effects

Sporophyte recruitment occurred primarily in late winter/early spring, this is similar to other reports for this species (Yendo 1919, Widdowson 1971). No substantial recruitment occurred after spring although plants were fertile and releasing spores during summer and fall, indicating that recruitment may be driven by abiotic factors (i.e., temperature and/or day length) and not spore availability. Some of the spores released in spring and summer were deformed and not as fluorescent when examined at 400X as those spores released in fall, indicating that at least some of the spores released early in the season may not be viable. While possible, it seems unlikely that temperature negatively affects recruitment since *Alaria* are intertidal and subject to extreme temperature fluctuations, and low tides in late summer and early fall do not coincide with daylight hours when thermal effects would be greatest. Instead, annual recruitment of *Alaria* is most likely influenced by changes in light (solar energy) and/or day length as it is in other kelps (Druehl and Hsiao 1977, Dayton 1985, Lüning and tom Dieck 1989).

Re-clearings in February helped to identify the timing and source of sporophyte recruitment. The low abundance of fertile plants from the 2001 cohort during this time indicated recruitment into February re-cleared plots was most likely from microscopic phases already present in plots at the time of clearing, and not from spores released after the re-clearing. Recruits in re-cleared plots were found almost exclusively in pits and crevices that were difficult to clear further suggesting recruitment was from a spore store.

Of the three plot halves that were re-cleared in February, the topography of the one with considerably greater recruitment was such (i.e., it had many surface irregularities) that clearing may not have been sufficient enough to remove all spores and other plant material to the same degree as the other re-cleared plot, and may explain why recruitment was greater in this plot relative to the other two. Nevertheless, reduced recruitment in re-cleared plots relative to plots cleared once in July 2001, although not statistically significant, suggests there was a limited supply of microscopic stages that could potentially contribute to a spore store. Thus, longevity of microscopic stages may be restricted to one season.

Longevity of microscopic phases of perennial kelps is reportedly only a few weeks to months in the field (Deysher and Dean 1986, Reed et al. 1997), although survival under laboratory conditions can be much longer (Kain 1964). Under extreme El Niño conditions, microscopic stages of *Macrocystis* have recruited to areas after sporophytes were absent for months, indicating that microscopic phases can be more long lived (Dayton 1985, Ladah et al. 1999). Although not a kelp, field studies show that the gametophytes of the annual brown alga *Desmarestia ligulata* are also long lived, surviving for 3 months to >1yr (Edwards 2000). There are no *in situ* studies of the persistence of microscopic phases in annual kelps, although it is assumed such stages persist at least a few months for *Pelagophycus*, *Postelsia*, and *Nereocystis* (Coyer and Zaugg-Haglund 1982, Blanchette 1996, Maxell and Miller 1996) and up to 7 months for *Laminaria ephemera* (Klinger 1984) given the time between spore release and sporophyte recruitment. Similarly, microscopic stages are essential for *Alaria* persistence

during winter. Further investigation of a possible spore store is required to assess longevity beyond the 3 to 4 month interval in which most macroscopic sporophytes were absent from the population.

Although timing of recruitment was similar in July-cleared plots and controls, recruitment density in cleared plots was consistently less, suggesting that clearing plots had an effect on the magnitude of recruitment. Reasons for differential recruitment in cleared vs control plots were not investigated. However, observations suggest growth of typically understory perennials (most abundant were foliose reds in the genera *Prionitis*, *Grateloupia*, *Mazzaella*, *Callophyllis*, and *Bossiella*) between July 2001 and February 2002 following *Alaria* removal could have negatively affected sporophyte recruitment in cleared plots. This seems unlikely, however, as *Alaria* recruitment was greatest among geniculate corallines and this substrate was available in all cleared plots. It is also possible that an *Alaria* canopy affords gametophytes some sort of protection during early stages of development such that canopy removal has negative effects.

Grazing of microscopic stages may have also influenced plant density in cleared plots, but qualitative observations showed that grazer density was fairly consistent in both cleared and control plots. Despite similarities in grazer density in control and cleared plots it is possible that grazers had greater access to the spore store in cleared plots because of the removal of canopy-forming adults. Experimental exclusion of grazers would be needed to directly test their effects on recruitment.

What seems most probable is some positive relationship between the density and proximity of adult plants and sporophyte recruitment density. Recruits are often found in

clumps (30-60 individuals) near the base of *Alaria* holdfasts and amongst the haptera in control plots. Clusters of recruits were rarely observed in cleared plots; most occurred singly. Together, these observations suggest that as spores are released, many may settle and develop directly below adult plants. In cases when fertile plants are not in close proximity to available substrate, spore dilution effects may influence final recruitment densities (Reed et al. 1988). The position of sporophylls near the base of vegetative fronds may also contribute to reduced dispersal relative to other kelps (Dayton 1985).

Substrate and Recruitment

Disproportionately greater *Alaria* recruitment to geniculate corallines in control and cleared plots and residual *Alaria* holdfasts in control plots at Big Creek and Gorda suggested that recruitment, and possibly settlement were substrate specific. In most cases recruits were attached to spaces amongst the base of geniculate corallines and then overgrew upright fronds. Spore survival may be greater in these spaces due to reduced grazing pressure as was suggested by Camus (1994) for the kelp *Lessonia nigrescens* or protection from desiccation and/or scour. Settlement cues associated with coralline algae are also possible. The geniculate coralline turf may also offer a secure place for *Alaria* attachment. The great recruitment to interstitial spaces amongst residual *Alaria* holdfast in control plots indicates recruitment is enhanced on substrata that offer refuge or increase attachment ability as it does for the kelp *Ecklonia* (Anderson et al. 1997).

Growth

Alaria growth rates were rapid early in the spring, and plants reached maximum lengths during summer. By August, erosion of blade tips exceeded growth rates such that there was no positive increase in plant size. *Alaria* may still grow during this time, but probably cannot sustain high biomass throughout the entire year because of increased wave action later in the season. Initial decline in plant length after summer may be attributed to natural senescence, as wave action is relatively low during this time of year. The decrease in mean plant length after the summer also corresponds with an increase in sorus area per plant indicating that the plants may reallocate energy from growth to reproduction. Trade-offs between growth and reproduction are common in terrestrial plant communities (Harper 1977) and may be important in kelps (Maxell and Miller 1996), although there is evidence to suggest that the costs of reproduction in kelps is low (Dayton 1985).

Costs of reproduction were not evaluated in this study. However, Pfister (1992) examined reproductive investment in *Alaria nana* and showed that vegetative blades were important to growth of reproductive blades. Removal of vegetative blades resulted in decreased sporophyll production and quality, suggesting that reproductive blades were not self-supporting. If vegetative tissue in *Alaria marginata* is equally as important to sporophyll production, the larger size of the alga may be important for sustaining reproductive blades.

The rapid growth rate and large size *Alaria* attains may also be important for maintaining space in the intertidal zone. Annuals that persist in the same location may

need to modify the environment to persist. *Alaria* may do this by growing rapidly and physically shading other organisms, or suppressing growth of surrounding algae via whiplash. *Alaria esculenta* dominate exposed habitats along the Atlantic coast of Newfoundland and reduce the number of species that can co-occur because their thick canopy shades the substratum (Keats et al. 1985). Perhaps like *A. esculenta*, *A. marginata* canopy cover along the Big Sur coast is dense enough to decrease light availability and suppress colonization and growth of other species.

Reproduction

Variation in plant fertility throughout the study reflects the age of the plants present at the time of sampling. Fertility or sorus area per plant was least during the late winter and early spring when the largest plants were primarily survivors from the previous cohort (2001) with few to no sporophylls or were new recruits without sporophylls. Throughout the spring and summer the largest plants were comprised entirely of spring recruits. Sorus formation in this cohort (2002) began as early as one month after recruitment and continued to increase as plants developed throughout the year. Peak sorus area per plant occurred in fall 2001 and 2002 indicating that the greatest potential for reproduction was concentrated at the end of the year when plants were tattered and about to be removed by winter surf. Additionally, lack of 1 year or older plants in monthly collections after March 2002 suggests that even if plants from the previous cohort survived winter they did not grow as quickly as new recruits and contributed relatively few spores to the population in the next year.

Although some plants became fertile within one month of recruitment, spore release occurred seasonally. The greatest contribution of spores at both sites occurred in October, the time of year with greatest total fertile area for this alga and the onset of winter storms. Field observations suggest that *Alaria* spore release may be stimulated by wave action, as the pulse of spores released in October 2002 coincided with the first large winter swells. Release during winter storms when disturbance is high (i.e., increased boulder movement and sand scour) may be advantageous because overgrowth from perennial algae is minimal, and young *Alaria* sporophytes can develop without a thick over-story of adults. The timing of recruitment with disturbance events has been reported for other algae (Sousa 1979a, 1980, Reed and Foster 1984, Reed et al. 1997, Schiel and Hickford 2001), and may ensure spores are released and develop when space and light availability are maximal.

The reproductive potential of *Alaria* is enormous: each plant can release between 10^8 and 10^9 spores. Spore release per plant was slightly less than values reported for other kelps, which ranged between 10^9 and 10^{12} spores per plant annually for *Nereocystis*, *Macrocystis*, *Laminaria* spp., and *Ecklonia* (Scagel 1961, Neushul 1981, Chapman 1984, Joska and Bolton 1987). This difference in the estimated number of spores released by *Alaria* versus other kelps may, however, be related to how spore counts were estimated. For *Alaria*, total spore contributions were determined by counting the number of spores the alga actually released in a given time, while spore estimates for the other species (excluding *Macrocystis* and *Ecklonia*) were extrapolated from sporangial densities (Scagel 1961, Chapman 1984). While it is possible to estimate fertility and potential

spore production from sporangial density, it is not possible to determine when an alga actually releases spores and when gametophytes are first present in the population. Moreover, development of a sorus does not mean plants are necessarily contributing spores. Annual spore production for *Macrocystis* was based on *in situ* measures, and sporangial counts and spore release were used to estimate spore production for *Ecklonia* (Joska and Bolton 1987). Although Joska and Bolton (1987) found no differences between their two methods for estimating spore production of *Ecklonia*, data on *Alaria* suggest spore release may provide a more accurate estimate of spore production.

Survivorship

After the initial recruitment in February/March the number of plants from the 2002 cohort in control plots declined throughout the year at Big Creek and Gorda (Figs. 2a & 2b), while the 2002 cohort density was much less and consistent in cleared plots at both sites. These data indicate that juvenile sporophytes in natural stands are subject to density-dependent mortality. Major declines in sporophyte density coincided with the period of greatest change in plant length, indicating that as plants grow rapidly they interfere with survivorship of neighbors. Plant knotting and entanglement were common and could increase the drag on plants, impacting attachment strength. The canopy of larger, faster growing *Alaria* was also thick enough to reduce light available to understory plants and decrease their survival. It is not uncommon for larger plants to suppress the growth of smaller individuals at greater densities (Creed et al. 1998). Reduced plant survival may also be attributed to substrate failure or recruitment to unfavorable habitat as reported for *Pelagophycus* and *Nereocystis* (Coyer and Zaugg-Haglund 1982, Maxell

and Miller 1996), but this could not explain the differential survivorship observed in control and cleared plots.

Population Size Structure

Size frequency data suggest the largest plants in the monthly collections used for assessing growth and fertility were not representative of the entire population. In fact, plants from the largest size classes ($>3.0\text{m}$) were less abundant than those in smaller size classes ($<1.0\text{m}$) during July 2002. Despite high abundance of small *Alaria*, larger plants appeared to be the most important to the next generation, and inferring growth and reproductive output based on them was not unreasonable. It is unlikely that small plants beneath larger *Alaria* canopy grew larger and became reproductive. Canopy clearing experiments in July 2002 showed that once the *Alaria* canopy was removed, smaller understory plants were slow to transition into larger size classes and plant density decreased (Fig. 10). This was true in control plots with natural canopy cover, and plots where the canopy was removed. Since most plants in smaller size classes failed to grow and few became fertile, their importance to population persistence was negligible, further indicating the importance of large plant survivorship to population persistence.

CONCLUSIONS

The demographic patterns of *Alaria* are similar to those observed for other annual kelps. A large recruitment pulse in spring with few new individuals recruiting later is reported for *Postelsia* and *Nereocystis* (Blanchette 1996, Maxell and Miller 1996). Rapid growth rates and high reproductive output of *Alaria* sporophytes near the end of their life are also characteristic of other annuals. Unlike *Postelsia* (at least in the populations

studied), *Alaria* recruitment is not driven by seasonal removal of mussels. Persistence of *Alaria* does appear to be related to disturbance of other species that creates space.

Instead, maximal reproductive output may be timed with the onset of winter storms, and recruitment occurs during seasons of high disturbance that removes the previous *Alaria* cohort.

Given the annual life history of *Alaria*, persistence of this alga along the Big Sur coast is dependent on adult survivorship through a critical reproductive period in the fall when reproductive output is greatest. Inadequate or lack of adult survivorship to this reproductive period could, as indicated by the July 2001 clearings, have negative effects on further *Alaria* recruitment. The long-term effects of plant removal before fall spore release and the potential for populations to recover after one year of marginal recruitment are unknown. If plants were continually removed or densities of *Alaria* were consistently low during fall reproductive periods it seems unlikely that populations would persist. This is especially true if a spore store of microscopic stages is limited to one season.

The implication of this type of life history is important for *Alaria* as it occupies areas along the Big Sur coast that are subject to periodic natural landslides and disposal of landslide and roadside construction debris. While the effects of sand scour and sediment burial were not evaluated in this study, it is possible that impacts from such events could have lasting effects on *Alaria* populations. Landslides would have the greatest impacts on sporophyte recruitment since most slides occur during winter months just before peak recruitment periods. In this case, low recruitment would affect the number of plants surviving to reproduce the following year and ultimately population

persistence. Disturbances over large areas may also have long term impacts to population structure, as *Alaria* recruitment appears to occur largely within a meter of adult plants. Finally, future rocky intertidal surveys along the Big Sur coast need to consider that while *Alaria* may be the dominant species, it is not always conspicuous in mid winter.

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TABLE 1. Analysis of Variance on the effect of site (Big Creek/Gorda), treatment (Control/Cleared), and time (March/October) on density of the 2002 *Alaria* cohort.

Source	df	MS	F value	P
Site	1	0.41	0.75	0.34
Treatment	1	16.45	30.09	0.00
Time	1	7.10	12.98	0.00
Site x Treatment	1	0.54	0.99	0.33
Site x Time	1	0.01	0.02	0.90
Treatment x Time	1	1.54	2.81	0.11
Site x Treatment x Time	1	0.00	0.01	0.93
Error	22	0.55	0.55	

TABLE 2. Mean percent cover ($\pm$ SE) of available substrate (% Available) and percent *Alaria* recruitment (% *Alaria*) to that substrate in cleared and control plots at Big Creek and Gorda during February 2002. Species with <5% cover were not included in the table, but were used in analyses.

BIG CREEK

Substrate	Control		Cleared	
	% Available	% <i>Alaria</i>	% Available	% <i>Alaria</i>
Rock	24.2 (13.0)	1.7 (1.0)	24.2 (13.0)	6.7 (5.6)
Crusts	19.2 (2.8)	3.3 (2.4)	18.3 (4.0)	5.8 (3.3)
Non-geniculate Coralline	25.8 (13.1)	3.3 (1.9)	14.2 (4.2)	5.8 (2.5)
Geniculate Coralline	20.8 (6.0)	54.2 (8.5)	36.7 (12.8)	69.2 (14.7)
<i>Alaria marginata</i> Holdfast	4.2 (2.5)	21.7 (5.2)	0.0 (0.0)	0.0 (0.0)

GORDA

Substrate	Control		Cleared	
	% Available	% <i>Alaria</i>	% Available	% <i>Alaria</i>
Rock	20.0 (9.3)	1.7 (1.0)	21.1 (17.9)	1.1 (1.1)
Crusts	30.8 (15.7)	0.0 (0.0)	24.4 (14.4)	3.3 (3.3)
Non-geniculate Coralline	10.0 (4.9)	3.3 (1.4)	18.9 (6.8)	0.0 (0.0)
Geniculate Coralline	23.3 (11.1)	57.5 (8.9)	28.9 (15.7)	81.8 (14.4)
<i>Alaria marginata</i> Holdfast	4.2 (2.1)	23.3 (6.5)	1.1 (1.1)	0.0 (0.0)
<i>Mazzaella splendens</i>	5.0 (1.7)	5.0 (1.7)	3.3 (1.9)	6.7 (6.7)

FIGURE LEGENDS

Figure 1. Illustration of *Alaria marginata* showing the vegetative blade and sporophylls with sori (adapted from O'Clair and Lindstrom 2000).

Figure 2a. Density of *Alaria* m^{-2} ($\mu \pm \text{SE}$) in experimental plots between July 2001 and October 2002 at Big Creek ($n=4$ for Control 2001 Cohort and Control 2002 Cohort, $n=8$ for Pre-Cleared 2001 Cohort, and $n=8$ through January 2002, thereafter $n=4$ for Cleared 2002 Cohort).

Figure 2b. Density of *Alaria* m^{-2} ($\mu \pm \text{SE}$) in experimental plots between July 2001 and October 2002 at Gorda ($n=4$ for Control 2001 Cohort and Control 2002 Cohort, $n=4$ for Pre-Cleared 2001 Cohort and $n=3$ for Cleared 2002 Cohort).

Figure 3. Density of *Alaria* m^{-2} ($\mu \pm \text{SE}$) in 1m^2 plots cleared at Big Creek after being cleared July 2001 and partially re-cleared (0.5m^2) in February 2002 ($n=3$).

Figure 4. Length of *Alaria* ($\mu \pm \text{SE}$) at Big Creek and Gorda between July 2001 and November 2002 ($n=33$ at Big Creek and $n=24$ at Gorda, in July 2001, thereafter $n=20/\text{site}$).

Figure 5. Sorus area ($\text{mm}^2 \text{ plant}^{-1}$, $\mu \pm \text{SE}$) of *Alaria* at Big Creek and Gorda between July 2001 and November 2002 ($n=33$ at BC and $n=24$ at G, in July 2001, thereafter $n=20/\text{site}$).

Figure 6. Number of spores released $\text{mm}^{-2} \text{ hr}^{-1}$ ($\mu \pm \text{SE}$) at Big Creek and Gorda. Months without bars indicate no samples were collected ($n=12-20$ depending on sampling date).

Figure 7. Mean number of spores released per plant at Big Creek and Gorda. Calculations are based on the multiplication of data in figures 4 and 5.

Figure 8. Number of *Alaria* per size class ($\mu \pm \text{SE}$) in three 1m^2 plots at Big Creek during July 2002.

Figure 9. Proportion of fertile *Alaria* per size class ($\mu \pm \text{SE}$) in 1m^2 plots at Big Creek during July 2002 ($n=3$, except where indicated).

Figure 10. Density of *Alaria* m^{-2} ($\mu \pm \text{SE}$) in canopy-cleared and control plots between July and October 2002 ($n=3$ for all sampling dates, except for September: $n=2$ for Canopy Clearing).

Figure 11. Survivorship of 2001 *Alaria* cohort at Big Creek and Gorda since July 2001. Inset graph is a magnification of the data set between April and September 2002 (n=4 for Big Creek and Gorda).

Figure 12. Survivorship of 2002 *Alaria* cohort in cleared and control plots at Big Creek and Gorda (n=4 for controls at BC and G, n=4 and n=3 for cleared plots at BC and G, respectively).

FIG. 1.

FIG. 2a.

FIG. 2b.

FIG. 3.

FIG. 4.

FIG. 5.

FIG. 6.

FIG. 7.

FIG. 8.

FIG. 9.

FIG. 10.

FIG. 11.

FIG. 12.