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POPULATION BIOLOGY OF *UNDARIA PINNATIFIDA* IN CENTRAL CALIFORNIA

A Thesis
Presented to
The Faculty of the Department of Marine Science
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by

Diana Kohtio

May 2008

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ABSTRACT

POPULATION BIOLOGY OF *UNDARIA PINNATIFIDA* IN CENTRAL CALIFORNIA

by Diana Kohtio

This study combined monitoring and experimental techniques to examine natural population parameters and physiological response to temperature of the invasive kelp *Undaria pinnatifida* in Monterey Harbor, California. Natural population density, reproductive condition, and seawater temperature were recorded throughout a 20-month study. Recruitment was sampled in experimental sporophyte density plots throughout a 9-month experiment. Physiology experiments were conducted in two temperature treatments over a 55-day period coincident with reproduction measurements and nutrient analysis.

Natural population fluctuation and reproductive condition appeared to respond to seasonal variations in temperature range. Warm temperature treatments increased C:N and blade senescence but decreased time to reproduction and peak spore output. Sporophyte density reduced recruitment at high levels, likely resulting from intra-specific competition. Because *Undaria pinnatifida* is an opportunistic species responding to changes in an unpredictable environment it may have a distinct advantage when it comes to invasion success.

ACKNOWLEDGEMENTS

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INTRODUCTION

Non-native species pose a great threat to native communities, affecting many different aspects of community structure, diversity, and productivity (Carlton 1996, Richardson et al. 2000, Grosholz 2002). Non-native species that successfully reproduce beyond their area of introduction and become regionally abundant are termed invasive (Richardson et al. 2000, Kolar and Lodge 2001). Both direct and indirect effects of non-native species can lead to a decrease in native biodiversity, which influences an ecosystems susceptibility to further invasion by non-native species (Stachowicz et al. 1999). In seaweed systems, competition for light and space may lead to local extinction or a decline in the abundance of native species (Dewreede 1996). In some ecosystems, the invasive kelp *Undaria pinnatifida* has been shown to reduce species richness, diversity, and evenness of local seaweed assemblages (Casas et al. 2004), whereas in other systems there has been no observed effect. Rapid growth rates of up to 21 mm/day in optimal conditions (Castric-Fey et al. 1999), combined with the ability to form dense stands in its native ecosystems, give *U. pinnatifida* the potential to compete strongly with native species of kelp for light and space. The abundant and diverse kelp forests characteristic of coastal California support a suite of marine organisms and provide resources to the state economy that have been valued at $19,000 per hectare per year (Costanza et al. 1997). Shifts in community dynamics and trophic food webs can result when dominant macroalgae are replaced by non-native species (Walker and Kendrick 1998). In this respect, understanding the population dynamics of invasive populations of *U. pinnatifida* is essential in determining its ability to spread and persist.

California kelp forests are some of the most productive ecosystems in the world. Driven by the upwelling of cold nutrient rich waters, these ecosystems support numerous marine organisms (Dayton 1985, Foster and Schiel 1985), provide energy via carbon in the coastal, subtidal, pelagic, and bathypelagic food webs (Bustamante and Branch 1996, Harrold et al. 1998), and are known to have a positive effect on species diversity by providing structurally complex habitat (Graham 2004). Although kelp forests demonstrate remarkable long-term stability (Dayton et al. 1984, Dayton et al. 1992), these dynamic ecosystems experience a considerable amount of spatial and temporal variability brought on by the interplay of physical and biological processes (Dayton et al. 1999). Most notable are the effects of wave action, light, temperature and nutrients, shading, and grazing (Dayton 1985, Foster and Schiel 1985), as well as large-scale disturbances such as storms and El Niño Southern Oscillation events (Dayton and Tegner 1984, Dayton et al. 1999, Edwards and Estes 2006). In order to persist in their environment, kelps must respond to both spatial and temporal variability in the environment.

Organismal response to environmental variability can take the form of a strategy to achieve spatial dominance or variable timing of recruitment. For example, the annual kelp *Postelsia palmaeformis* exists in some of the most wave-exposed areas of the Pacific's low rocky intertidal zone and it has been suggested that such persistence is dependent on wave disturbance to create space by knocking out the competitively dominant mussel *Mytilus californicus* (Dayton 1973, Paine 1979, 1988). Similarly, population variability and persistence in the annual intertidal kelp *Alaria marginata*,

which also occupies the Pacific's wave exposed mid to low rocky intertidal zone, is strongly affected by winter storms. The greatest amount of spore release is synchronized with late fall as sporophyte mortality increases with the onset of the annual winter swell (McConnico and Foster 2005). Some algal species, such as *Desmarestia ligulata* can delay recruitment to the sporophyte stage until unfavorable environmental conditions pass (Hoffman and Santellices 1991, Edwards 2000), as the microscopic stage may represent a way to maintain space in a more durable and appropriate form (Edwards 2000, Kinlan et al. 2003).

Because environmental conditions vary throughout the year, mechanisms of natural selection may favor organisms able to perform certain activities at certain times of the year, thereby promoting the evolution of cue recognition and response in organisms. It has been suggested that the heteromorphic life cycles of Laminariales evolved so that reproduction and recruitment are cued to environmental signals (Clayton 1988). Specific cues throughout the entire Laminariales life cycle have not yet been demonstrated. However, it has been shown for many other species of algae that developmental processes such as reproduction, vegetative growth, and gametophyte dormancy are controlled by a photoperiodic response, a combination of temperature and photoperiod, and spectral quality of light (Luning 1980, Luning and tom Dieck 1989, Luning 1994). The photoperiodic reduction of growth rate and induction of reproduction of many Laminariales are under control of a circannual endogenous rhythm, finely tuned by variations in photoperiod throughout the year. In this photoperiodic response, development is delayed until day length surpasses a certain critical length for the onset of

the next developmental stage (Luning 1989, 1993). For such species, total daily dose of blue light has generally been identified as the direct mechanism underlying the photoperiodic regulation of growth rates and persistence of growth rhythms (Luning 1994).

Undaria pinnatifida, an annual species of kelp endemic to Russia, Korea, Japan, and China (Saito 1975, Oh et al. 1996) was first introduced to California in 2001, and is now established in harbors including Los Angeles, Santa Barbara, and most recently Monterey (Silva et al. 2002). Extensive studies on *U. pinnatifida* life history, growth, and seasonality have added to our understanding of how this alga behaves in culture, and in its native range (for examples see: Saito 1975, Oh and Koh 1996). However, only Thornber et al. (2004) have reported on the dynamics of California populations. In Asia, *U. pinnatifida* sporophtyes germinate in late summer through early fall and fertilization takes place during the fall. Recruits (sporophytes) appear and grow rapidly in winter and spring, release motile zoospores over summer as the thallus begins to senesce (due to a rise in summer seawater temperatures), and zoospores settle and develop into gametophytes (Tamura 1970, Hay and Luckens 1987). In the native range of *U. pinnatifida* , temperatures can vary from 2°C in January-February to 24-26°C in August (Hay and Luckens 1987). In culture, sporophyte growth has been shown to be optimal at 15°C, but will occur between 10-20°C. While optimal gametophyte growth and gamete release occurs between 8-20°C, gametophytes enter into a resting stage when temperatures exceed 24°C (Saito 1975). Able to withstand temperatures higher than most species of kelps (tom Dieck 1993), the temperature tolerant gametophyte stage appears to

allow *U. pinnatifida* to persist in its environment through warmer months. Unlike most kelps, which are cued by day length, the reliable seasonal temperature shifts in the Japan Sea appear to have caused *U. pinnatifida* to evolve temperature cues for growth and reproduction (Saito 1975, Hay and Villouta 1993, Kim et al. 1995, Stuart et al. 1999). As a result of these temperature cues, populations of *U. pinnatifida* are seasonal in their native range, and unlike all other kelps, gametophytes are present during the summer months rather than the winter months.

Undaria pinnatifida has the potential for overlapping generations when temperatures do not reach 24-30°C, the presumed temperature at which gametophytes go dormant (Hay and Villouta 1993, Thornber et al. 2004). Such is the case in New Zealand where mean seawater temperature rarely exceeds 20°C (Hay and Villouta 1993). In Monterey, California mean seawater temperature rarely exceeds 17°C, and does not vary predictably in the seasonal range known to cue *U. pinnatifida* (El Niño-Southern Oscillation events and the occurrence of internal waves may contribute to this variability). Although there has been some documentation of the presence of *U. pinnatifida* in Monterey, California since 2003 (Lonhart, unpublished data), the existence of individuals continuously present throughout the year has not been documented.

The evolution of adaptive strategies to cope with environmental conditions has been well documented in the terrestrial plant literature. Leaf abscission in perennial deciduous plants represents a strategy to conserve energy in response to seasonal or climate differences (Addicott 1982). Many species of kelp and fucoids (*Nereocystis* sp., *Fucus* sp., and *Ascophyllum* sp.) have been shown to abscise reproductive tissue in winter

as a strategy to decrease total biomass and thus lower respiratory demand (Addicott 1982). *Pterygophora californica* and *Pleurophycus gardneri* are examples of kelp that have been shown to be largely deciduous. Blades are produced in spring, undergo blade sloughing through the summer and fall, and are shed the following winter (De Wreede 1984, Germann 1989, Dominik and Zimmerman 2006). Biologists have long classified annual plant growth and reproduction as either determinate or indeterminate, based on persistence strategies in a predictable or unpredictable environment, respectively (Harper 1977). The annual kelp *Undaria pinnatifida* has been characterized as having a distinct growth period of variable length followed by a decay period typically lasting 4 months (Saito 1975, Stuart et al. 1999). Field observations of *U. pinnatifida* in Monterey Harbor also show this characteristic growth pattern. Further, observations show that the majority of individuals have already undergone a considerable amount of vegetative blade sloughing prior to reproduction (D. Kohtio, personal observation). Vegetative blade sloughing in *U. pinnatifida* may serve as an efficient mechanism for concentrating nutrients in the sporophyll for reproduction rather than the blade for growth. Understanding the dynamics of how individuals and cohorts respond physiologically (with respect to nutrient content and reproduction) to temperature variability will help our understanding of why *U. pinnatifida* persists.

The goal of this study was to understand how life history parameters and environmental conditions influence the population biology of *Undaria pinnatifida* in central California. Elucidating how certain biological and environmental signals control the physiology behind the production and release of viable spores, spore densities and

dispersal distance, density dependent relationships between subsequent generations, and allocation of nutrients in *U. pinnatifida* is essential to developing adequate management plans and for creating models to predict how environmental variability and disturbance affect its population dynamics. I conducted a series of field and laboratory experiments to assess environmental and biological triggers on population biology, reproductive condition, and physiology in *Undaria pinnatifida*. Specifically, this study looked at the effects of temperature on (1) presence/absence and (2) reproductive condition of *U. pinnatifida;* (3) the relative contribution of varying reproductive cohort densities to recruitment; and (4) nutrient allocation and reproductive response to temperature variability.

This study considered the extent to which local populations of *Undaria pinnatifida* from Monterey, California are controlled by variations in seawater temperature. Preliminary data showed that continuous (macroscopic) populations of *U. pinnatifida* do not exist on local (inference space of study) scales in the Monterey Harbor. Further, temperature data within the study site showed high frequency, high amplitude temperature fluctuations. Correspondence of *U. pinnatifida* population crashes with these temperature shifts would support the hypothesis that population variability correlates with high frequency, high amplitude changes in seawater temperature. In its native range, the predictable release of *U. pinnatifida* zoospores is optimal in seawater temperatures from 17-22°C and corresponds to senescence of the sporophyte (Tamura 1970, Saito 1975, Hay and Luckens 1987). Based on temperature ranges in previous studies (Saito 1975, Hay and Villouta 1993) reproductive individuals of *U. pinnatifida* may occur year round

(whenever sporophytes are present) in the cool waters of Monterey, suggesting that temperature may not affect reproduction in *U. pinnatifida* as it does in its native range. Reproduction of *U. pinnatifida* populations that is coincident with seasonal temperature variability or life-cycle stage would refute the hypothesis that reproductive condition occurs independent of a rise in temperature or senescense of the sporophyll. Additionally, this study set out to determine if a correlation exists between the density of reproductive adults and recruitment. The affect of density on patterns of growth and recruitment have been exhibited in certain species of kelps at both the microscopic and macroscopic levels (Reed 1990a, Reed 1990b). While a larger cohort of individuals may increase survival in terms of overcoming physical stress (Reed et al. 1997), a large cohort as compared to one individual is not necessarily more capable of re-establishing a patch (Paine 1988). I hypothesized that increased local sporophyte density increases recruitment by enhancing the available spore supply. Finally, this study considered if an increase in temperature would yield a physiological response in *U. pinnatifida* with respect to the production and release of viable spores and allocation of nutrients. Organisms able to respond physiologically to environmental variability may be more adaptable to a changing environment. I hypothesized that *U. pinnatifida* behaves responsively to seawater temperature regarding reproduction and allocation of nutrients.

MATERIALS AND METHODS

Background and study site

Undaria pinnatifida was first noted in the Monterey Harbor in August 2001. Currently, it can be found on the concrete dock pilings and 400+ slips throughout the

harbor. In September 2002, the Monterey Bay National Marine Sanctuary (MBNMS) staff, the Harbor Masters office, and City of Monterey volunteer staff began an on-going effort to remove and manage *U. pinnatifida* in the Monterey Harbor. The MBNMS designated a 113 m area of submerged concrete slips and their associated pilings on the northwest end of the H-tier in the Monterey Harbor for this study (Fig. 1), and no management efforts have taken place in this area since the start of this study in March, 2005. Cohorts of *U. pinnatifida* have been observed throughout this area since

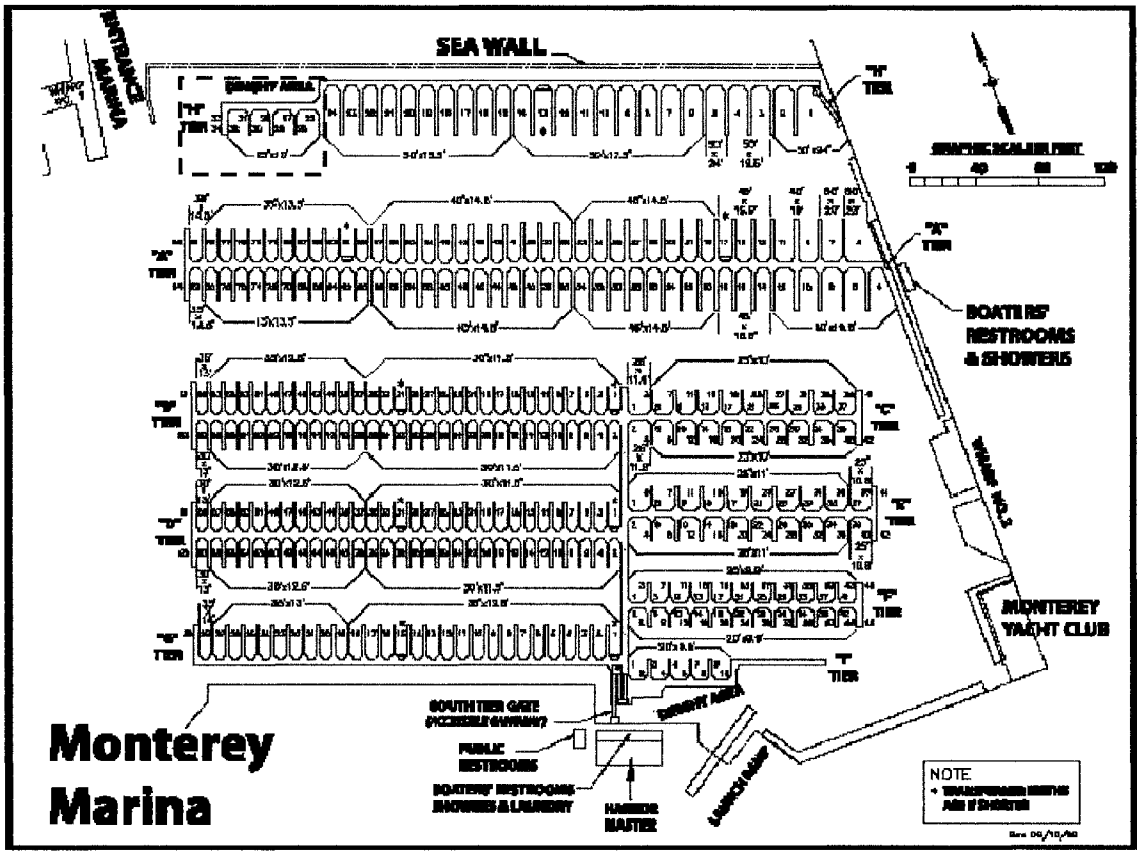


Figure 1. Study site in dashed box (upper left, 113 x 0.5 m submerged vertical dock). *Undaria pinnatifida* distributed throughout 400+ slips in marina.

September 2003(Kohtio, personal observation). The study site is located adjacent to the

marina entrance and is characterized by heavy mixing and strong tidal currents. The majority of *U. pinnatifida* in the harbor are attached to artificial substrate from the surface to the benthos (7.5 m depth average), with some individuals scattered along the benthos attached to medium-sized rocks and small boulders.

Natural population densities

To test the hypothesis that seawater temperature corresponded to variability in *Undaria pinnatifida* population dynamics, continuous seawater temperature data was collected and random quantitative surveys of the natural population were conducted. Seawater temperatures was recorded within the study site every 5 minutes from March 2005-March 2007 at a depth of 0.5 m below the surface using StowAway ® TidbiT underwater temperature loggers. Random sampling of *U. pinnatifida* to assess natural population variability took place in 15, 0.25 m^2 plots along the 113 m x 0.5 m area of submerged vertical concrete docks on the northwest end of the H-Tier in the Monterey Harbor (Fig. 1). Sampling was conducted monthly in order to observe changes in individuals with a lifespan <12 months (Thornber et al. 2004). All individuals per quadrat were counted and categorized as recruits if ≤10 cm total length, adults if >10 cm, and reproductive if individuals exhibited a reproductive morphological characteristic on their sporophylls (discussed in the following section). Data (n=29, sampling dates) were analyzed using regression to test the effect of date on density and temperature. Mean sporophyte density (dependant variable) was regressed against seawater temperature and date (independent variable). Time-lagged cross-correlations were used to analyze the relationship between seawater temperature and sporophyte density.

Additionally, to identify if an average size class prevailed on a monthly basis and/or coincided with peaks in reproductive densities, all individuals per quadrat were assigned to a size class based on size frequency histograms (recruits ≤10 cm, small 10-30 cm, medium 30-90 cm, and large ≥90cm) from March 2005 to March 2006.

Natural population reproductive condition

To test the hypotheses that reproductive condition is correlated to either a rise in temperature or senescence of the sporophyte, reproductive condition was determined for each sporophyte in the random density surveys. Data were analyzed using regression (n = 29, sampling dates) and time-lagged cross-correlations to test the effect of date (independent variable) on temperature and reproductive density (dependant variable). An individual was considered reproductive if it produced and released spores (see Reed et al. 1997). Because spores are released directly into seawater and immediately disperse it is difficult to directly measure spore release in nature (Reed et al. 1988). Reproductive sporophytes of *U. pinnatifida* in the field have been observed to develop a distinct light-colored line along the edge of the sorus (Kohtio, personal observation). Similar to the giant kelp *Macrocystis pyrifera*, this suggests competency for spore release (Neushul 1963). To determine if this distinctive lightened coloring along the edge of the sorus indicates spore release, laboratory and field studies were performed as a gross estimate for reproductive condition. In the laboratory, visual characterization of reproductive status was tested by inducing spore release from 6 mm diameter sporophyll plugs taken randomly (2 per 0.25m^2 plot) during monthly sampling (McConnico and Foster 2005). Tissue plugs were desiccated for 3 hours in cool dark conditions (Reed 1990), then

transferred to a petri dish and submerged in 40 ml filtered seawater (FSW) at 12°C with 200 μM photons $m^{-2}s^{-1}$ irradiance for 2 hours (McConnico and Foter 2005). Settled spores were used as an indication of reproductive competency and density was estimated using an inverted microscope. Physical condition of growth or senescence and thallus morphometrics of the plug donating individuals were also noted. Sporophyll plugs from 116 individuals with and without lightened edges were taken during monthly natural density plot sampling from April 2006 to March 2007. Results showed that the lightening along the sporophyll's edge corresponded with reproductive competency (induced spore release resulted in settlement) 87.93% of the time, and did not correspond with reproductive competency 12.07% of the time.

Influence of sporophyte density on reproduction and recruitment

To test the hypothesis that increased local sporophyte density increases local recruitment, adult sporophyte density was manipulated in permanent plots and monitored monthly from January 2006 to October 2006. These plots were excluded from random sampling. Sporophytes (<20 cm total length) were transplanted to the center of 10 permanent plots (each 0.5 m^2) on the south side of 10 piling. Plot density levels ranged from 0-9 sporophytes, each transplanted to separate pilings with approximately 6 m distance from one piling to the next. All four-sides of each piling were scraped and wire brushed 2 m above and below the site of transplantation with the expectation of removing any gametophytes already settled on the concrete and fouling organisms. All *Undaria pinnatifida* recruits appearing on any of the four-sided plots were counted bi-monthly, throughout the length of the experiment. Plots were cleared back to their original state of

0-9 individuals after each bi-monthly sampling session so that no new individuals appearing in the plots would become reproductive and contribute to recruitment. If individuals in the plots were dislodged, new individuals of similar reproductive status were transplanted to maintain plot densities. Reproductive status was determined by the presence of a light-colored edge on the sporophyll (see previous section). Ambient recruitment from sources beyond the experimental plots was determined from the zero sporophyte plot. Reproduction events in kelps do not have a definitive start and end point, it is generally a gradual process. Therefore, peak recruitment values were used to make comparisons amongst density treatments, as these values represented the performance at maximum recruitment. The effect of increasing density (independent variable) was regressed against peak recruitment (dependent variable) by each month throughout the life of the sporophytes. Additionally, total thallus length, sporophyll length, and sporophyll width were measured during sampling to determine if density affected growth and/or sporophyll surface area. The effects of density on growth were tested using correlation analysis. The relationship between sporophyll surface area and length and width measurements of the sporophyll was determined in a separate laboratory study using sporophylls from 20 randomly collected *U. pinnatifida* individuals, these results were necessary to use in other methods. Sporophyll volumes were determined using displacement of water, and surface areas were determined via image analysis (ImageJ 1.39, Rasband WS) of scanned sporophylls. There was a strong correlation between *U. pinnatifida* sporophyll volume and surface area (Pearsons correlation; $r = 0.981$, $P<0.001$, $df = 19$) (Fig. 2), and simple surface area calculations (length*width)

accurately estimated scanned sporophyll surface areas (regression; surface area = 4.8373length*width-108.61, $R^2 = 0.8172$, $P<0.01$, df = 19) (Fig. 3).

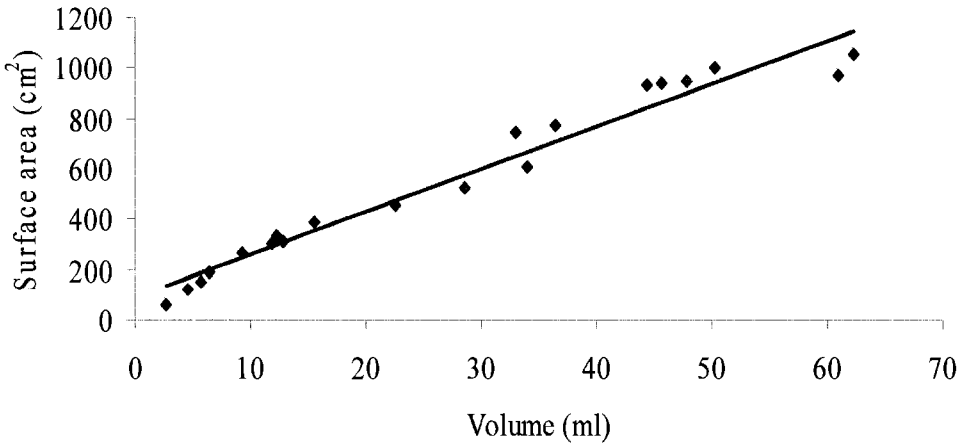


Figure 2. Sporophyll total surface area and volume of 20 randomly collected *Undaria pinnatifida* sporophytes of varying sizes and reproductive status.

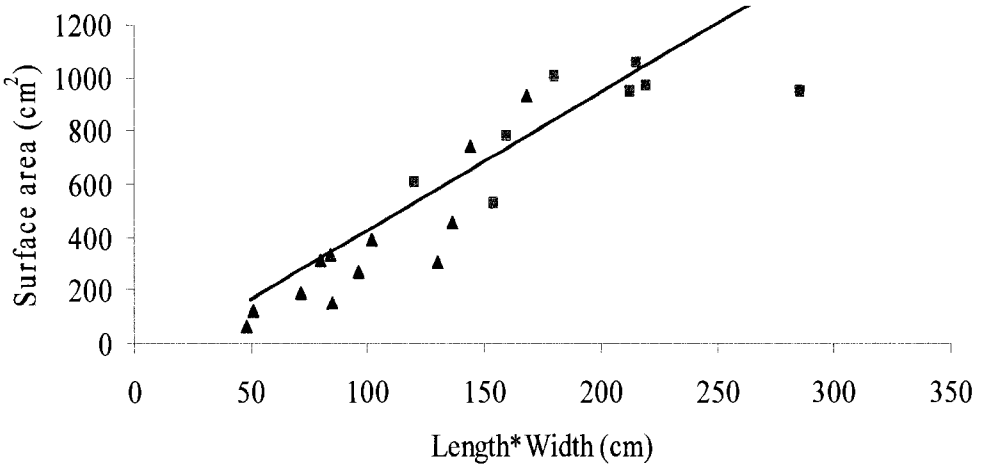


Figure 3. Relationship between sporophyll length*width and total surface area of 20 randomly collected *Undaria pinnatifida* sporophytes of varying sizes and reproductive status (regression; surface area = 4.8373length*width -108.61, $R^2 = 0.8172$, P = <0.01, df = 19). Squares (■) indicate reproductive individuals (induced spore release resulted in settlement), as distinguished from non-reproductive individuals diamonds (▲), induced spore release did not result in settlement).

Sporophyll surface area relationships (Fig. 3) indicate minimum surface areas of 526 cm^2 before sporophylls became reproductive (induced spore release resulted in settled spores).

Physiological response to temperature

To test the hypothesis that *Undaria pinnatifida* responds physiologically to variability in temperature, individuals were transplanted to an outdoor culture system with warm and cold seawater temperature treatments and monitored for their allocation of nutrients (carbon and nitrogen) and reproductive output. This experiment was held outdoors in 10 50-gallon tanks from the 20th April – 17th June, 2007 and sampled every 3 days for an anticipated quick physiological response. Two temperature treatments averaging 11.36°C (± SD 1.41) and 18.09°C (± SD 2.32) were replicated five times each and randomly distributed among the 10 tanks. All tanks contained aluminum coiling and continuously flowing seawater. In cold tanks, seawater was cooled using a closed circuit system of chiller-cooled fresh water running through aluminum coils. Warm tanks were heated using aquarium heaters. Kelp with newly formed sori on the sporophylls were transplanted from the field and acclimated for three days in cold tanks. On the 23rd of April individuals were sampled for initial carbon and nitrogen content, determined non-reproductive through laboratory spore release methods previously described, and three individuals were randomly placed into each of the 10 tanks. Sampling for treatment affects began on the 26th of April and was conducted every three days following. Replicated individuals were maintained without replacement. Sampling consisted of total length measurements and a 6-mm diameter plug taken from a similar area on the blade and sporophyll of each individual for carbon and nitrogen analysis. Residual carbon on

the filters (25-mm glassfiber Whatman GF/F) was removed by placing the filters on tinfoil and charring them in an oven at 500°F for 8 hours. The wet sporophyll and blade plugs were then placed on clean filters in petri dishes and dried at 60°F for 24 hours. Once dried, the plugs were analyzed using a CHN combustion analyzer (440 CHN – O/S Elemental Analyzer) to determine carbon and nitrogen content. Data were analyzed using ANOVA with C and N measurements as the response variables and temperature (i.e. warm vs. cold tank) as the treatment factor. Analyses were conducted on the 23rd of April and then again on the 2nd of May (the last date when both treatments were represented by equal sample size) to test for differences in C and N amongst treatments. Due to sampling limitations, nutrients were measured in micrograms on a per area basis. In order to report nutrient levels as percentages, a plug weight validation was performed. In both blades and sporophylls, there was a positive linear relationship between plug diameter and plug weight (regression; $R^2 = 0.9843$, $P<0.001$, df = 11) and (regression; $R^2 = 0.9798$, $P<0.001$, df = 11). Consequently, a 6-mm sized plug was chosen for sampling convenience and plug diameter was used to determine plug weight in CHN analysis. A second 6-mm diameter plug was taken from the sporophyll of each individual for spore release experiments. Sporophyll plugs were transported back to the laboratory and stored in cool dark conditions for three hours. Sporophyll plugs were then transferred to a petri dish containing 40 mL filtered seawater and incubated at 12°C, 200-μM photons m^{-2} l^{-1} irradiance, with a 12:12 photoperiod (McConnico and Foster 2005). Germination of settled spores (determined by presence of germ tube) was used as an indicator of reproductive output (Reed et al. 1996) and after 48 hours germination was sampled using

an inverted microscope to view 15 randomly placed ocular quadrats for each sporophyll plug. Data were analyzed using ANOVA with germination density as the response variable and temperature (i.e. warm vs. cold tank) as the treatment factor. Analyses were conducted on data collected three days following transfer into the temperature treatments (23rd of April) and on the last date when both treatments were represented by equal sample size (12th of May) to test for differences in reproductive output amongst treatments.

RESULTS

Natural population densities and reproductive condition

Population density of *Undaria pinnatifida* (adults and juveniles) in the study site showed temporal variability through time (Fig. 4). Analysis of time-lagged cross-correlations between sporophyte density and temperature revealed a significant

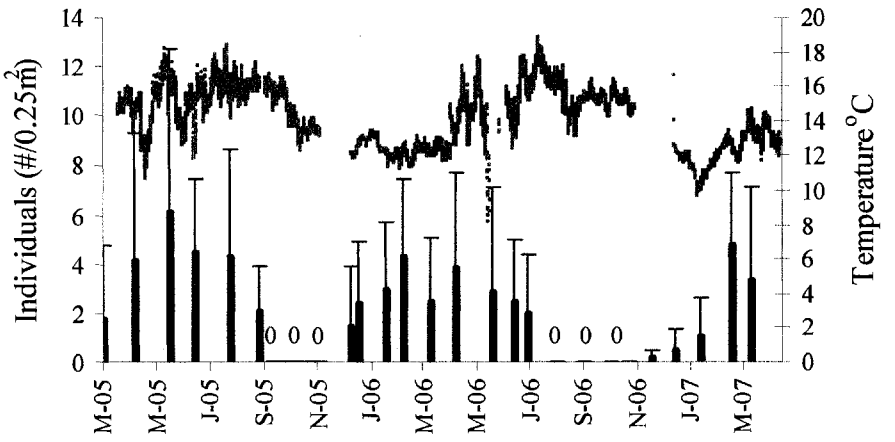


Figure 4. Temporal variability in densities of *Undaria pinnatifida* sporophytes (adults and juveniles) sampled monthly in Monterey Harbor (n=15 samples per date, mean ± SD displayed), plotted with seawater temperature. Zeroes indicate dates when sporophytes were not observed in the study site.

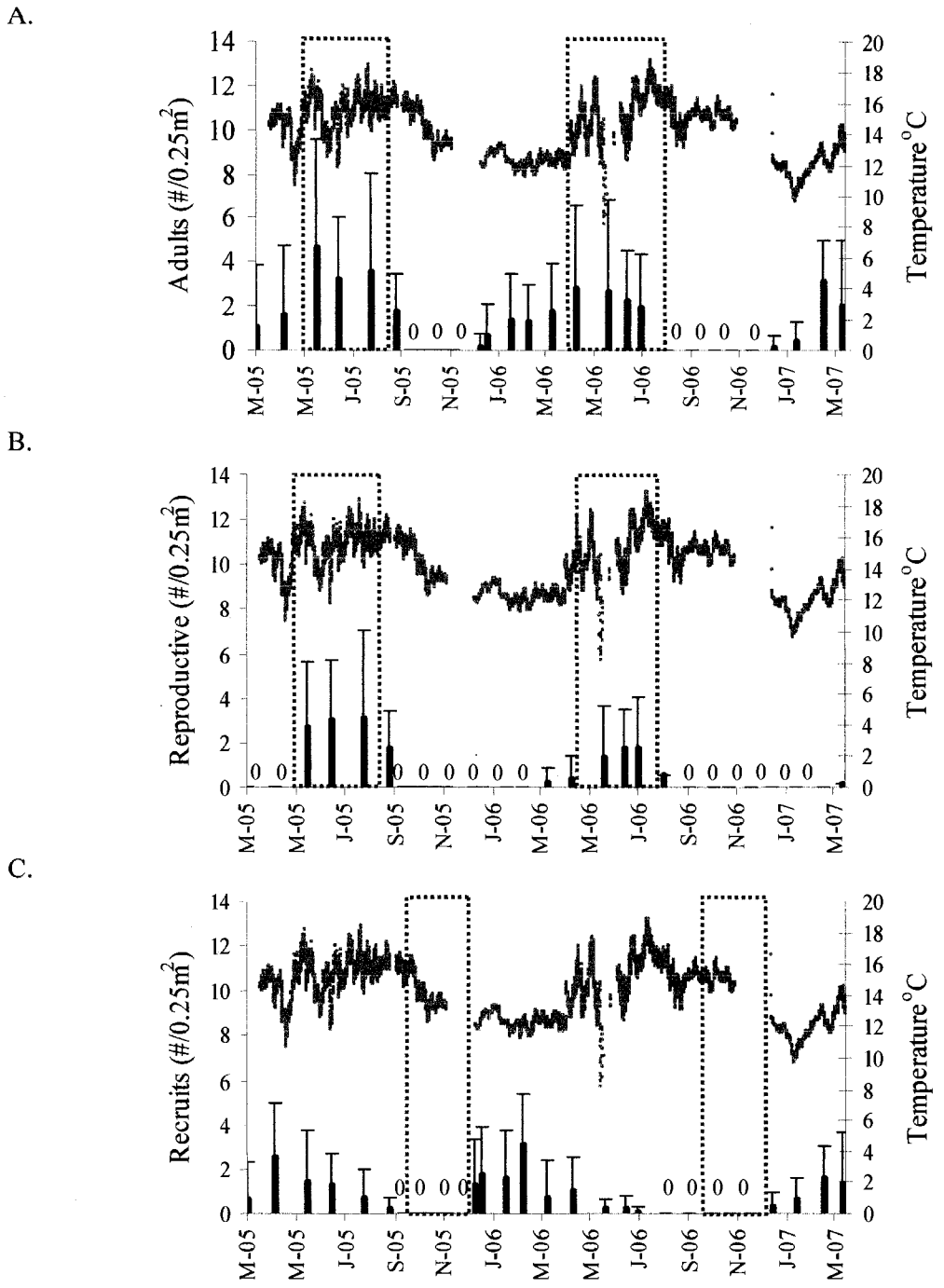


Figure 5. Temporal variability in densities of *Undaria pinnatifida* sampled monthly in natural Monterey Harbor population (n = 15 per date, data = mean ± SD), plotted with seawater temperature (A) Adult sporophytes and (B) Reproductive sporophytes, considered reproductive if induced spore release resulted in settlement: Dashed line indicates warming periods lasting approximately 3 months where temperatures exceeded 16°C. (C) Recruit sporophytes: Dashes line indicates a 3 month cooling period when temperatures dropped below 16°C.

negative correlation (within 95% confidence intervals for correlation) between adult densities and ocean temperatures from 2-3 months prior. Densities in the study plots peaked in May 2005 and again in February 2006; no individuals were found September to November 2005 and August to October 2006. Adult density patterns lagged warming periods by approximately 3 months, which ran from May to August 2005 and mid April to mid August 2006 (Fig. 5a). During warming periods, temperatures exceeded 16-17°C, an increase of 3-4° above the annual mean of 14°C. Approximately three months following the onset of warming *U. pinnatifida* densities began to decline. Densities of reproductive individuals were positively correlated with periods of warming in August of 2005 and July of 2006, and were absent from September to February 2005 and 2006 (Fig. 5b). A recruitment pulse (individuals <10 cm total length) occurred 3 months following a seawater temperature drop below 16°C (Fig. 5c). Time-lagged cross-correlations revealed a significant negative correlation of recruit densities with ocean temperatures 1-2 months prior. Recruits were absent September to November 2005 and August to October 2006. These population cycles existed despite the fact that peak temperatures never exceeded 18.5°C, the temperature threshold for continuous populations in New Zealand (Hay and Villouta 1993).

Size structure of the natural population also fluctuated with density changes. The density of small individuals decreased from May 2005 to June 2005 as the size structure shifted to larger individuals through growth. The size structure switched again between June and July 2005 as the density of large individuals decreased and small individuals increased (Fig. 6). This switch represented blade sloughing from previously large

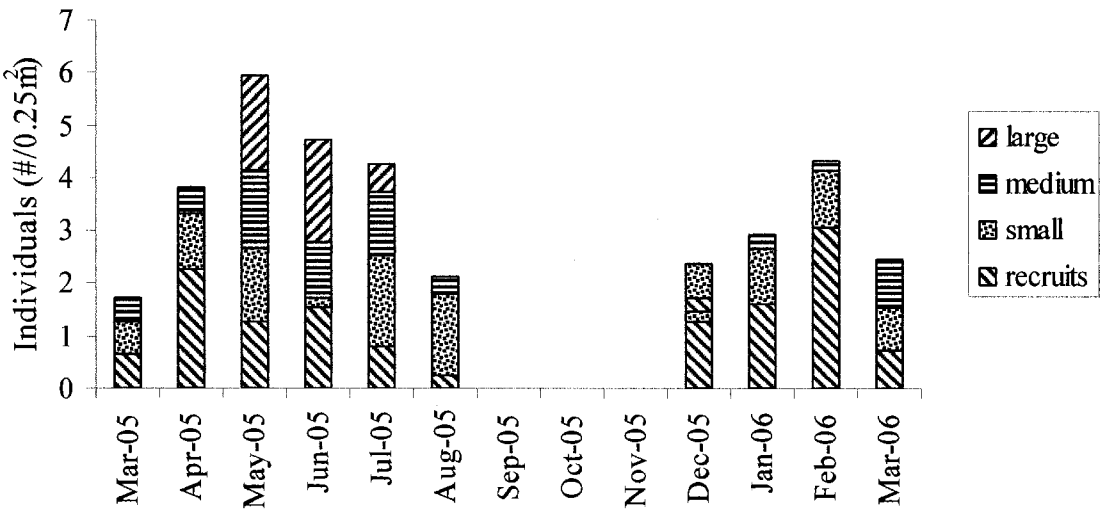


Figure 6. Size frequency distribution of *Undaria pinnatifida* sporophytes sampled monthly in 15 random quadrats (mean ± SE) over 113x0.5 m study area.

individuals rather than an increase in the number of new recruits (Kohtio, personal observation) and corresponded with peaks in reproductive densities (Fig. 5b)

Influence of sporophyte density on reproduction and recruitment

There was a positive linear relationship between the density of individuals in experimental modules and the timing of peak sorus density (regression: $R^2 = 0.63$, $P = 0.018$, df = 7), where lower density plots reached peak sorus density earlier than higher density plots (Fig. 7). There was a marginally non-significant negative relationship ($0.05<P<0.10$) between the density of adult reproductive *U. pinnatifida* and peak recruitment (regression: $R^2 = 0.4133$, $P = 0.08$, df = 7), where recruitment decreased as sporophyte density/0.25m^2 increased (Fig. 8). Within the experimental plots, density did not affect total length of individual sporophytes (regression: $R^2 = 0.026$, $P = 0.67$, df = 7).

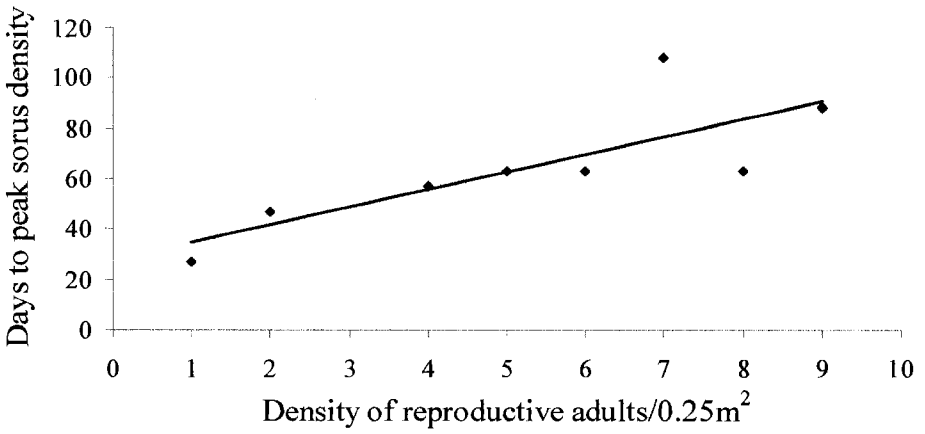


Figure 7. Effect of density of reproductive adults on time to peak sorus density in experimental plots (regression: peak sorus = 6.9369+28081*density, $R^2 = 0.63$, P = 0.018, df = 7).

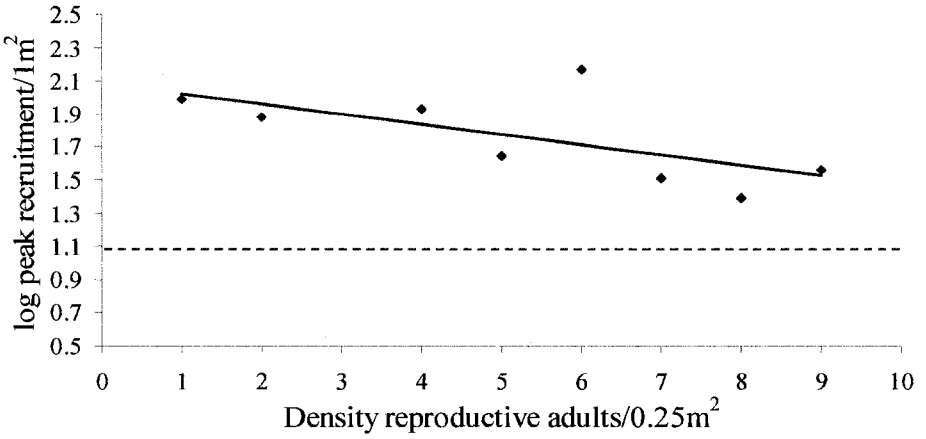


Figure 8. Effect of density of reproductive adult *Undaria pinnatifida* on subsequent recruitment in experimental plots (regression; recruitment = -0.0621density + 2.0849, $R^2 = 0.4133$, P = 0.08, df = 8). Dashed line represents density of peak recruitment in treatment plots with zero individuals (i.e., background recruitment). Peak recruitment represents recruit density per plot on the sampling date with the highest recruitment.

Sporophytes transplanted into experimental modules (transplanted at <20 cm total length) took a minimum of 37 days to reach reproductive competency (evidenced by the lightened margin). Recruitment began 47 days after transplantation in plots 1, 2, 5, 6, and 9 and 57 days after transplantation in plots 4, 7, and 8 (Fig. 9). Timing of peak

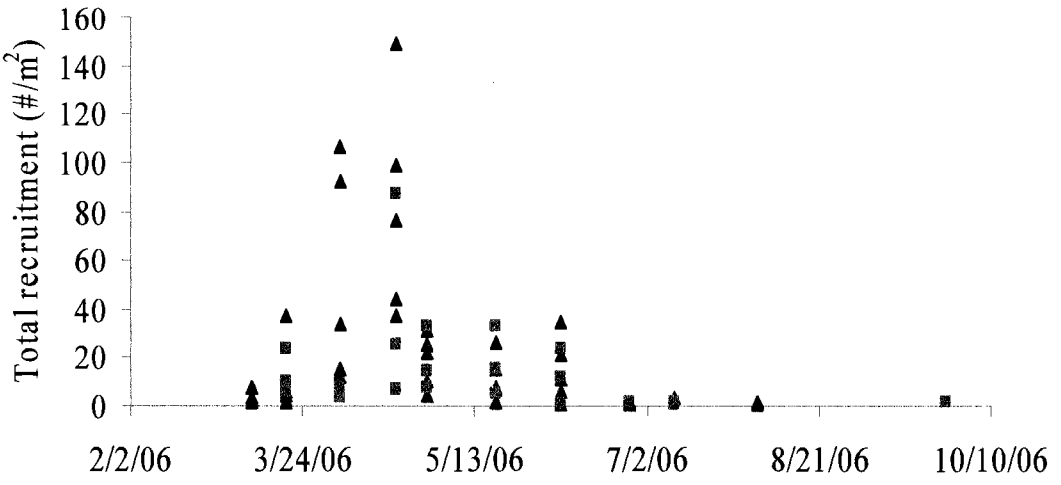


Figure 9. Date and magnitude of all recruitment events in experimental plots over a 9-month period (bi-weekly sampling). Recruitment began 47 days post transplantation in plots 1, 2, 5, 6, 9 (▲); and 57 days post transplantation in plots 4, 7, 8 (■).

recruitment was similar amongst all plots: with the exception of plots with densities of 0 and 7, all plots experienced peak recruitment on April 20th, 2006, three months after transplantation. Plot 7 experienced peak recruitment on May 19th, 2006. Recruitment in zero-density plots represented background (water column) recruitment, not from transplanted individuals. Recruitment (integrated over the last 14 days) in these plots was variable (Fig. 9) but low relative to plots containing low (1-2 individuals), medium (4-6), and high (7-9) sporophyte densities (Fig. 8). There was a marginally non-significant negative linear relationship between total sorus surface area/0.25m^2 (area estimated from sporophyll length and width measurements) and peak recruitment in the experimental plots (regression: $R^2 = 0.480$, $P<0.057$, df = 7). High-density plots, which contained the most reproductive surface area, had the lowest peak recruitment values (Fig. 10).

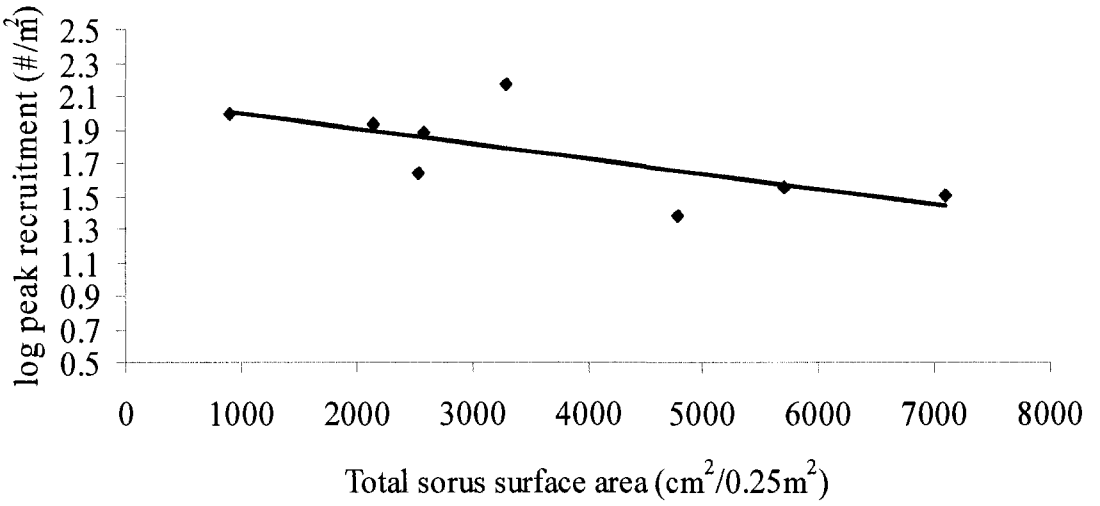


Figure 10. Effect of density of reproductive adult *Undaria pinnatifida* on the density of sorus area per plot in experimental plots (regression; peak recruitment = -9E-05 density sorus area + 2.0917, $R^2 = 0.4803$, P = 0.057, df = 7). Peak recruitment represents recruit density per plot on the sampling date with the highest recruitment.

Physiological response to temperature

Nutrient response. The mean percentage of carbon, nitrogen, and C:N in the blades and sporophylls of *Undaria pinnatifida* differed amongst warm and cold treatments (Figs. 11-13). Initial nutrient content was significantly different between tissue types (blade vs. sporophyll), but did not differ significantly among treatments (Tables 1-6). Nutrient content remained significantly different amongst tissue types, however, both tissue types responded in a similar manner to treatments (i.e. non-significant interaction term). There was a significant final nutrient difference among treatments for nitrogen and C:N (Table 4, 6). Carbon was generally conserved in *U. pinnatifida* tissue. There was a marginally non-significant effect of treatment on percent tissue carbon at the end of the sampling period (Table 2) where values dropped from 1.757 to 1.458% total wet weight of the initial sample over the course of the experiment.

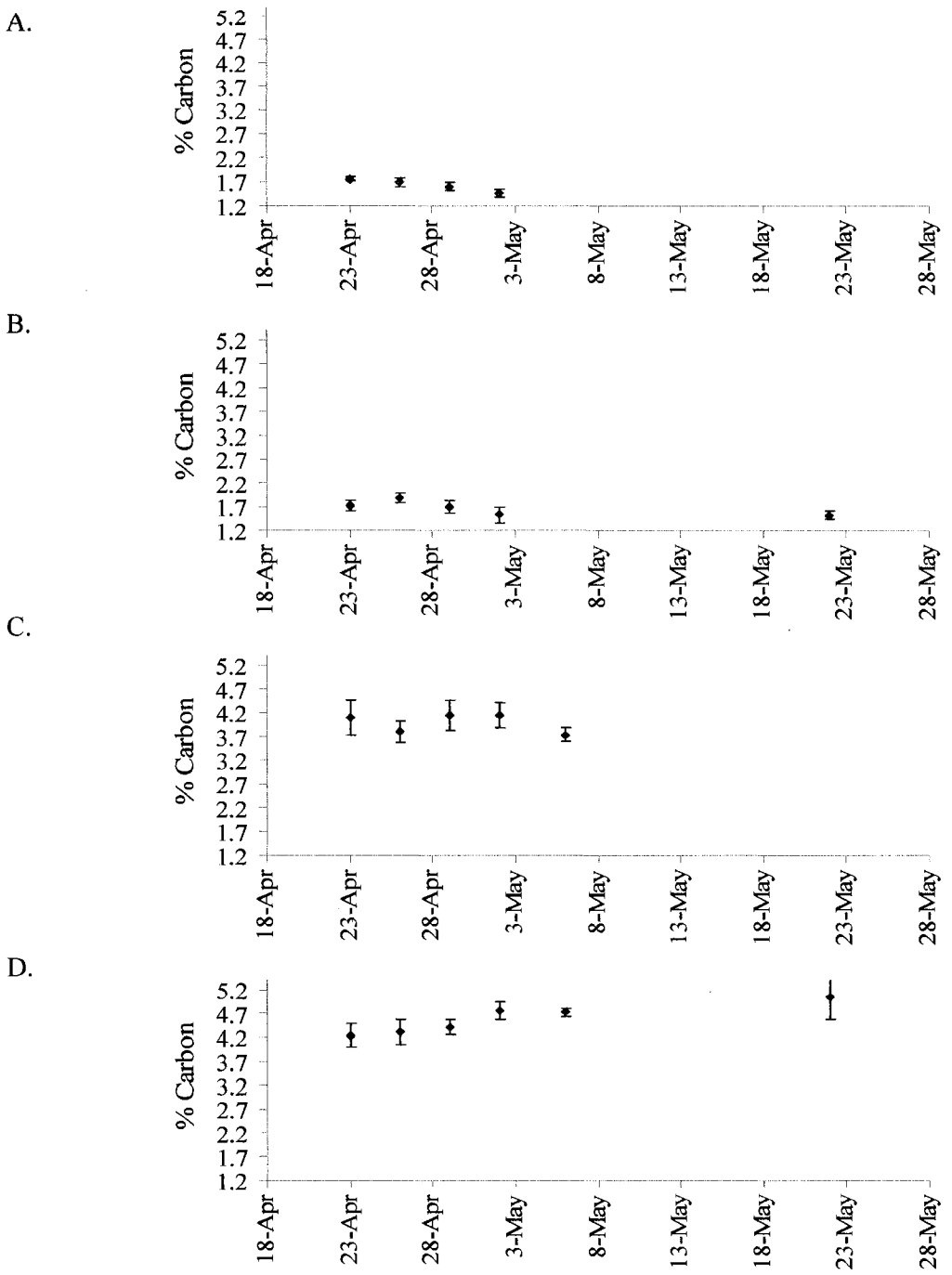


Figure 11. Carbon content of adult *Undaria pinnatifida* during temperature experiments; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate). Carbon value represents % carbon of the total wet weight of the sample in (A) blades in warm treatment, (B) blades in cold treatment, (C) sporophylls in warm treatment, (D) sporophylls in cold treatment.

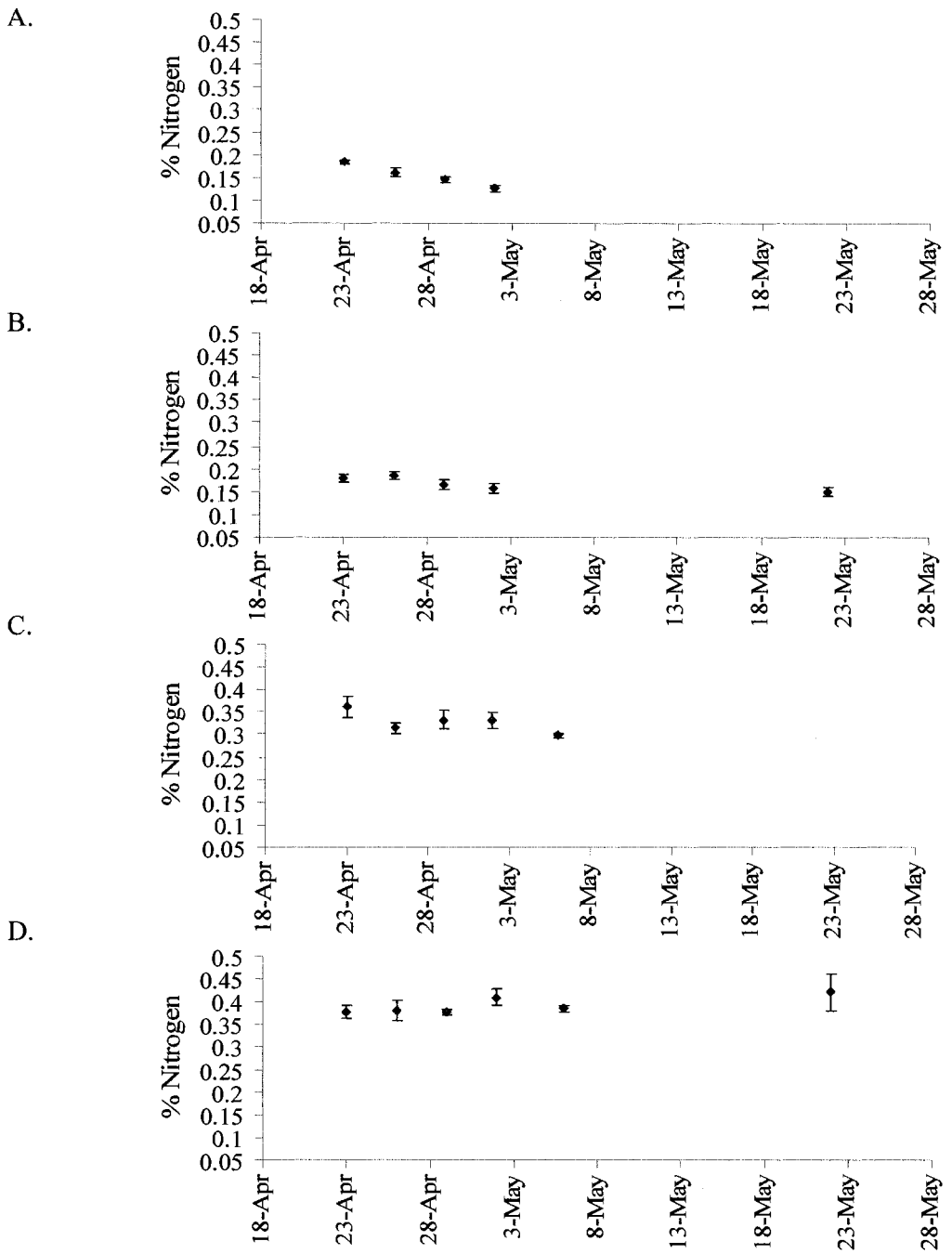


Figure 12. Nitrogen content of adult *Undaria pinnnatifida* during temperature experiments; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate). Nitrogen value represents % nitrogen of the total wet weight of the sample in (A) blades in warm treatment, (B) blades in cold treatment, (C) sporophylls in warm treatment, (D) sporophylls in cold treatment.

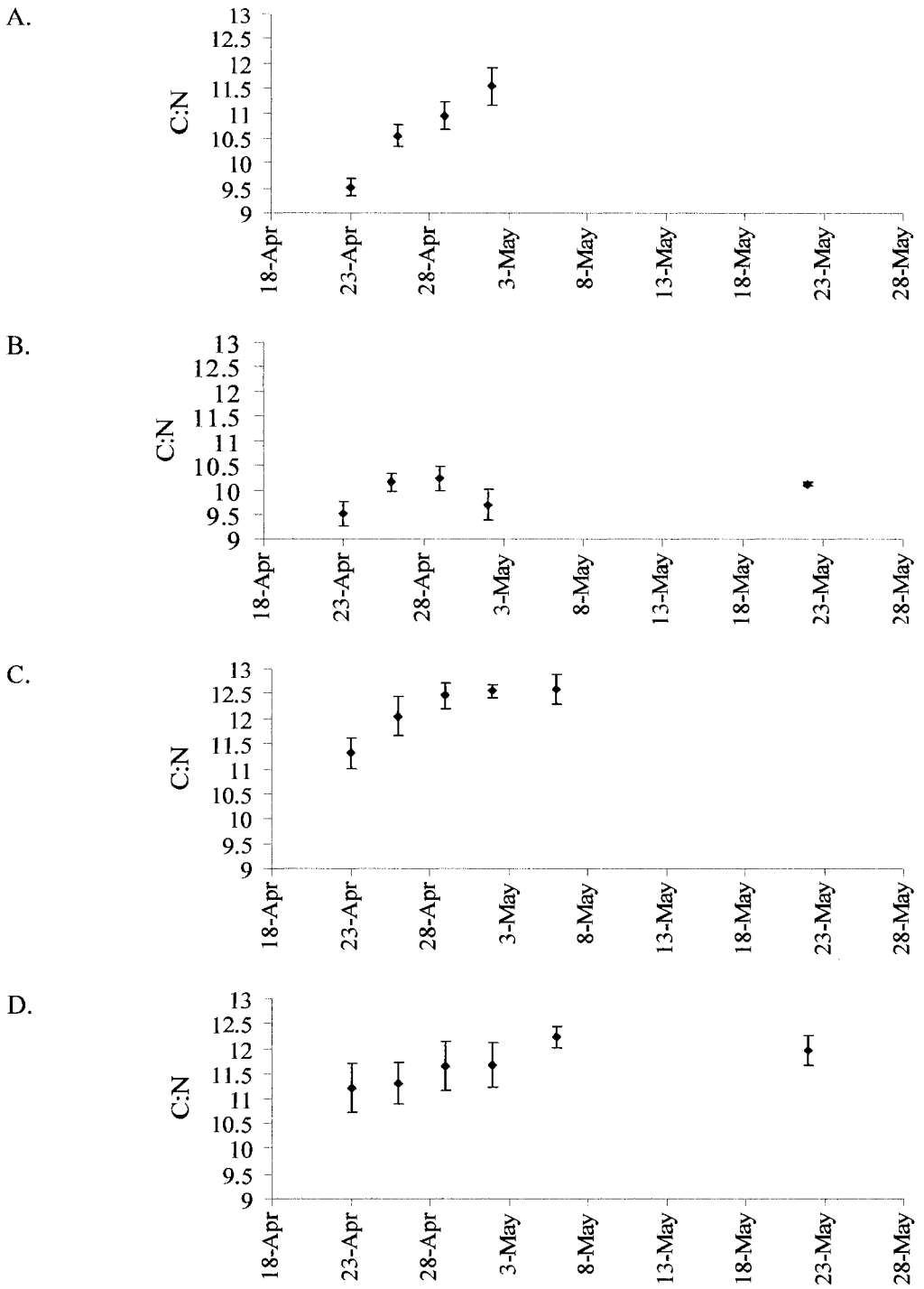


Figure 13. C:N content of adult *Undaria pinnatifida* during temperature experiments; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate). C:N value represents C:N of the total wet weight of the sample in (A) blades in warm treatment, (B) blades in cold treatment, (C) sporophylls in warm treatment, (D) sporophylls in cold treatment.

Table 1. ANOVA on the effects of temperature (warm/cold) on tissue type (blade/sporophyll) initial % carbon in *Undaria pinnatifida*.

Source	df	MS	F value	P
Tissue type	1	29.680	111.446	<0.001
Temperature	1	0.012	0.046	0.833
Tissue x Temperature	1	0.035	0.130	0.723
Error	16	0.266		

Table 2. ANOVA on the effects of temperature (warm/cold) on tissue type (blade/sporophyll) final % carbon in *Undaria pinnatifida*.

Source	df	MS	F value	P
Tissue type	1	43.974	265.921	<0.001
Temperature	1	0.593	3.586	0.076
Tissue x Temperature	1	0.352	2.130	0.164
Error	16	2.646		

Table 3. ANOVA on the effects of temperature (warm/cold) on tissue type (blade/sporophyll) initial % nitrogen in *Undaria pinnatifida*.

Source	df	MS	F value	P
Tissue type	1	0.175	169.675	<0.001
Temperature	1	0.000	0.231	0.637
Tissue x Temperature	1	0.001	0.555	0.467
Error	16	0.001		

Table 4. ANOVA on the effects of temperature (warm/cold) on tissue type (blade/sporophyll) final % nitrogen in *Undaria pinnatifida*.

Source	df	MS	F value	P
Tissue type	1	0.261	257.666	<0.001
Temperature	1	0.015	14.766	0.001
Tissue x Temperature	1	0.003	2.914	0.107
Error	16	0.001		

Table 5. ANOVA on the effects of temperature (warm/cold) on tissue type (blade/sporophyll) initial C:N in *Undaria pinnatifida*.

Source	df	MS	F value	P
Tissue type	1	15.199	28.552	<0.001
Temperature	1	0.014	0.027	0.871
Tissue x Temperature	1	0.016	0.030	0.866
Error	16	0.532		

Table 6. ANOVA on the effects of temperature (warm/cold) on tissue type (blade/sporophyll) final C:N in *Undaria pinnatifida*.

Source	df	MS	F value	P
Tissue type	1	11.180	19.753	<0.001
Temperature	1	9.301	16.434	0.001
Tissue x Temperature	1	1.163	2.055	0.171
Error	16	0.566		

Carbon content of blades in warm treatments were reduced to lower values than in cold treatments. In cold treatments, the carbon content of blades fluctuated throughout the experiment, increasing from 1.724 to 1.893% total wet weight in the first 3 days, than decreasing to 1.536% over the next 7 days. In contrast, the carbon content of sporophylls in warm treatments initially decreased from 4.110 to 3.798% total wet weight over the first 3 days but then increased to 4.15% for the remainder of the experiment. In cold treatments sporophyll carbon content steadily increased throughout the sampling period from 4.243 to 4.767% total wet weight.

Nitrogen in *U. pinnatifida* tissue was expended at a faster rate and with less variance among samples than carbon. There was a significant effect of treatment on tissue % nitrogen at the end of the sampling period (Table 4). Nitrogen content of blades in the warm treatment decreased steadily from 0.184 to 0.126% total wet weight of the sample, 2.5-times faster than the cold treatment. While nitrogen content of blades in the cold treatment also decreased, it was conserved over a longer period and decreased at a less substantial rate from 0.180 to 0.157% total wet weight of the sample. Nitrogen content of sporophylls in the warm treatment decreased from 0.360 to 0.330% total wet weight of the sample. Conversely, nitrogen content of sporophylls in the cold treatment increased from 0.378 to 0.409% total wet weight of the sample.

C:N ratios in *U. pinnatifida* appear to be driven by tissue nitrogen depletion. There was a significant effect of treatment on tissue C:N at the end of the sampling period (Table 6). C:N of blades in the warm treatment increased steadily throughout the experiment from 9.524 to 11.544, while C:N ratios of blades in the cold treatment

fluctuated between 9.526 and 10.236. Sporophyll C:N increased in the warm treatments from 11.323 to 12.557 and increased in the cold treatments from 11.213 to 11.675. However, C:N increases were 8-times greater after 3 days in temperature treatments for sporophylls in warm vs. cold treatments (C:N increase of 0.727 vs. 0.090, respectively) and reached a higher ratio at the end of the sampling period.

Reproductive response. The timing and density of the reproductive response (germination density) differed in the warm and cold treatments. Sporophytes in warm temperature treatments experienced decreased timing to reproduction, and total propagule output. Sporophytes in cold treatments experienced delayed timing to reproduction and higher total propagule output compared to sporophytes in warm treatments (Fig. 14).

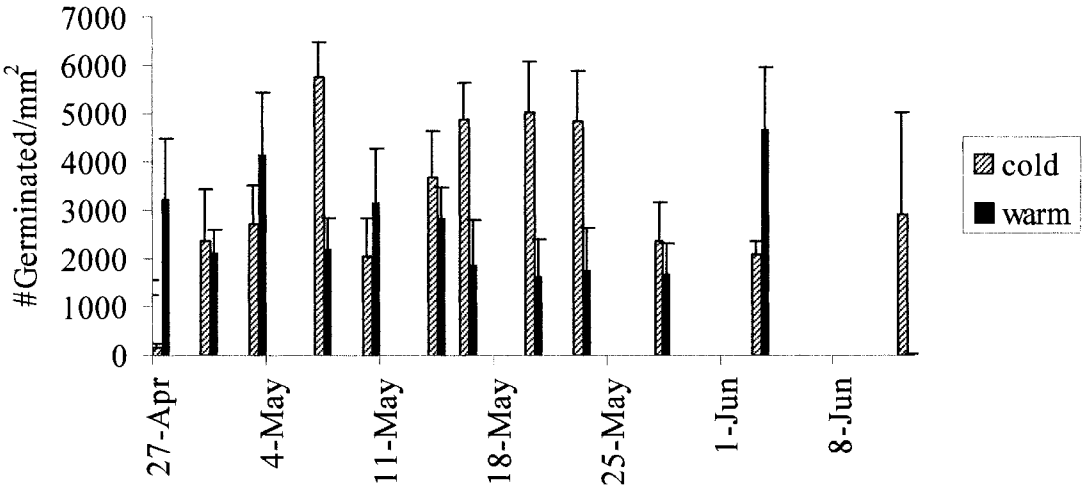


Figure 14. Density of germinated spores during temperature experiment; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate).

There was a significant effect of temperature on germination density on the first (April 27, 2007) and last (May 16, 2007) sampling dates (Tables 7-8). Although there was a non-significant Pearson's correlation, mean reproductive response was compared to mean

Table 7. ANOVA on the effects of temperature (warm/cold) on initial germination in *Undaria pinnatifida.*

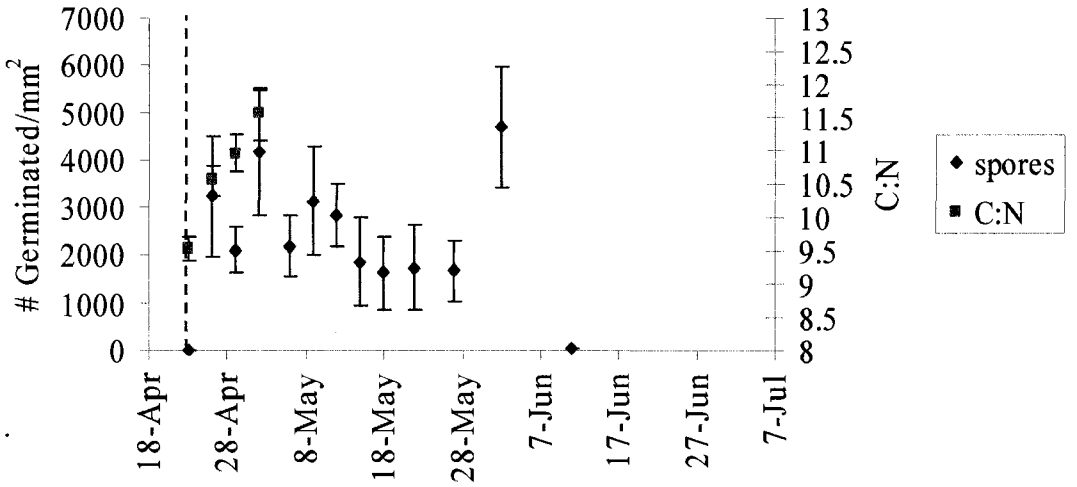
Source	df	MS	F Value	P
Temperature	1	2.371	5.984	0.040
Error	8	3961756.063		

Table 8. ANOVA on the effects of temperature (warm/cold) on final germination in *Undaria pinnatifida.*

Source	df	MS	F Value	P
Temperature	1	2.271	6.209	0.037
Error	8	3657516.188		

C:N in blades (Fig.15 a-b) and sporophylls (Fig. 16 a-b). Over the 10-day period in which nutrient and reproductive responses were compared, germinated spores in warm treatments occurred at an elevated density and earlier date than cold treatments. This was coincident with a sharper and more steadily increasing C:N in blades and sporophylls in the warm treatments as opposed to the cold treatments (Figs. 15, 16). This was most evident after 3 days in warm treatments where a rise in C:N from 11.323 to 12.050 paralleled a germination density increase from 0 to 3236/mm^2, whereas cold treatments rose in C:N from 11.213 to 11.303 and paralleled a germination density increase from 0 to 157/mm^2. Despite a fluctuation of total length in all individuals throughout the length of the experiment, the relationship between change in total length and germination in *U. pinnatifida* was not significant (Fig. 17 a-b).

A.



B.

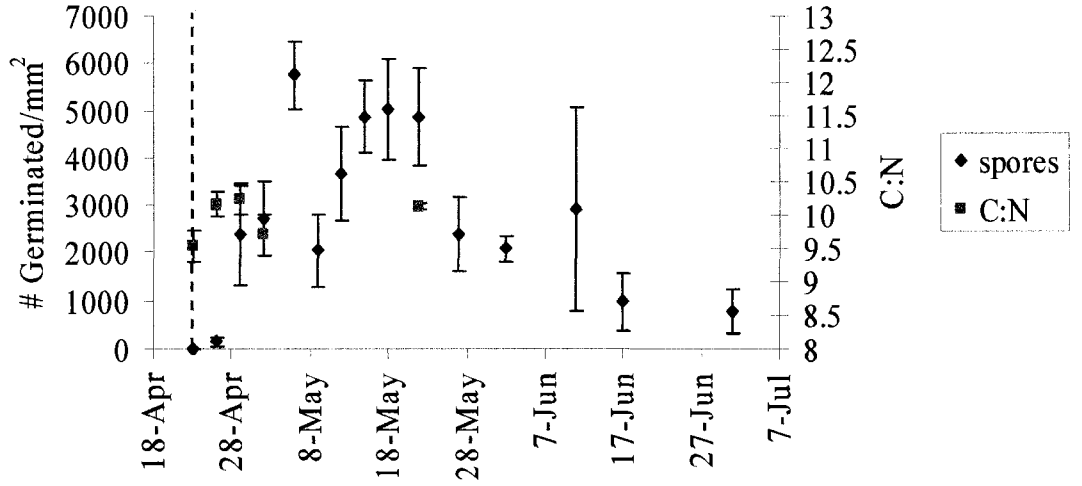
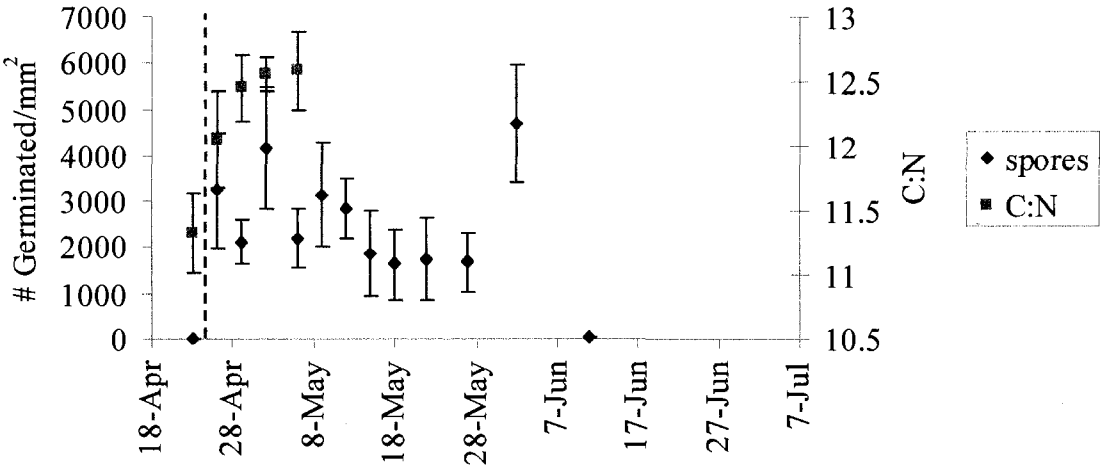


Figure 15. Density of germinated spores and corresponding blade C:N during temperature experiment; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate) in (A) warm treatment and (B) cold treatment. Date of transfer to temperature treatments is indicated by dashed line.

A.



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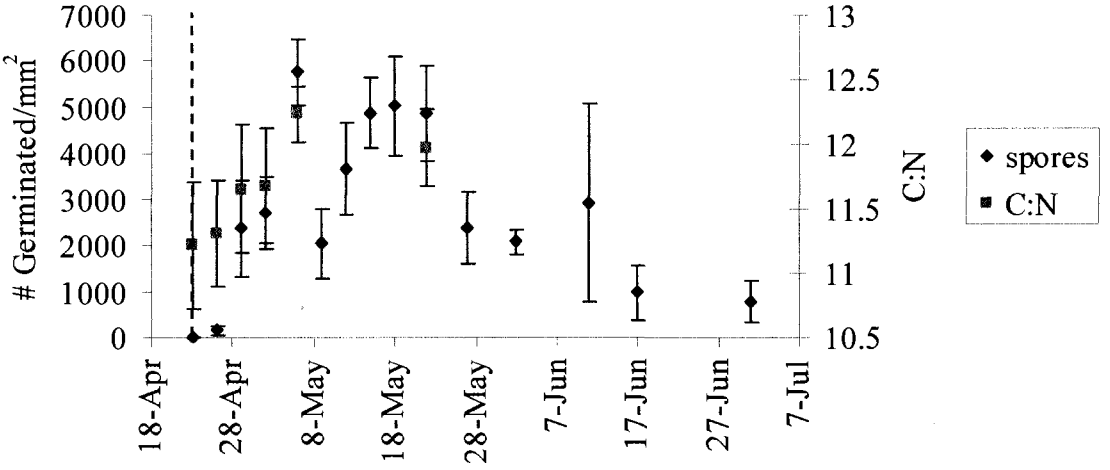
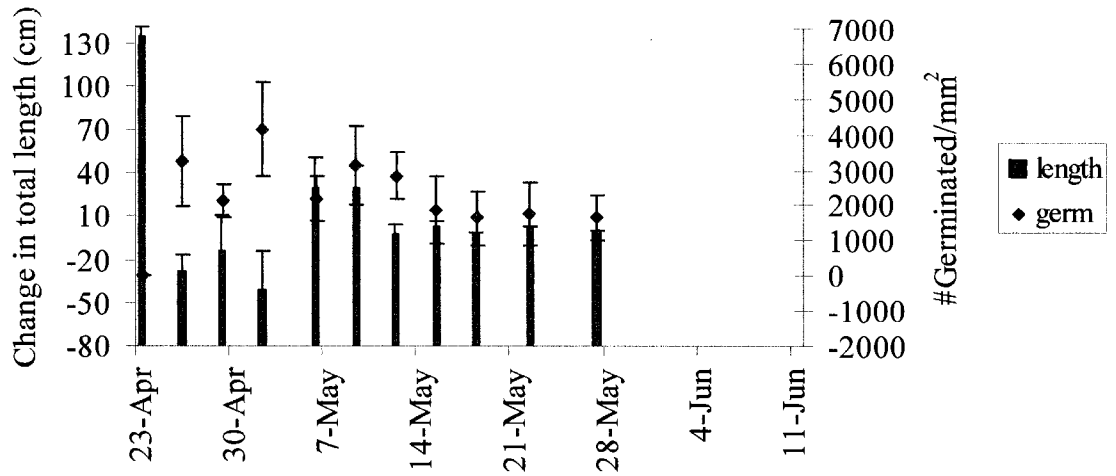


Figure 16. Density of germinated spores and corresponding sporophyll C:N, during temperature experiment; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate) in (A) warm treatment and (B) cold treatment. Date of transfer to temperature treatments is indicated by dashed line.

A.



B.

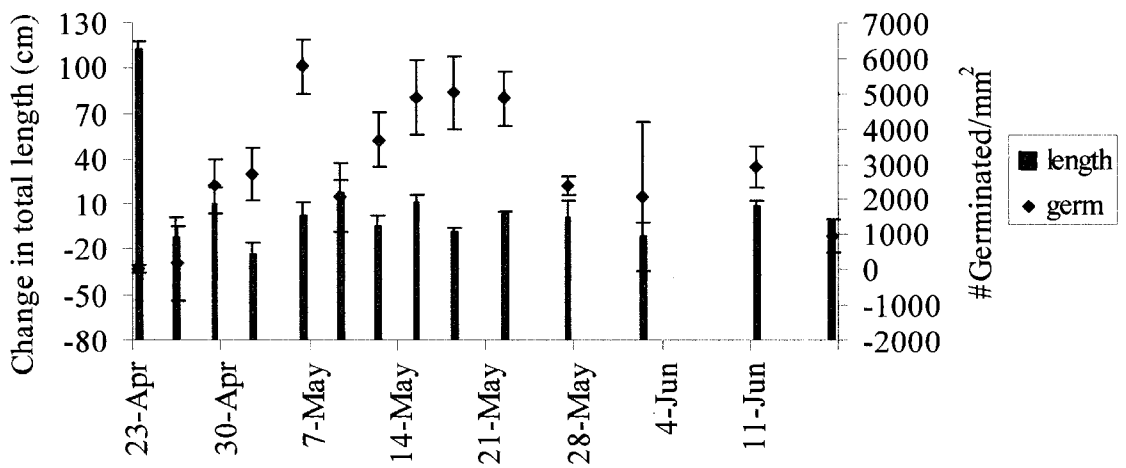


Figure 17. Density of germinated spores and corresponding sporophyte total length, during temperature experiment; data are means (± SE), n = 5 for each treatment (3 sporophytes pooled per replicate), in (A) warm treatment (Pearsons correlation; r = -0.452, df = 9, P = 0.190) and (B) cold treatment (Pearsons correlation; r = 0.193, df = 12, P = 0.528). Individuals were transferred to treatments on 4/23/07.

Discussion

Natural population densities and reproductive condition

Previous laboratory studies have shown that *Undaria pinnatifida* growth and reproduction can respond to day length cues (Pang and Luning 2004). The results of past

(Thornber et al. 2003) and current field studies in California indicate that growth and reproductive response in *U. pinnatifida* strongly correspond to temperature. Species persistence is largely determined by response to environmental cues and reproductive strategy as these factors can shape a species population size structure and how adaptable it is to change.

Undaria pinnatifida was responsive to temperature variability in Monterey Harbor. In its native range, *Undaria* experiences temperatures above 20°C, causing a decrease in zoospore growth, development, and longevity. In some areas of New Zealand it has been suggested that because temperatures never reach 20°C there is no inhibition of zoospores and gametophytes so that sporophyte populations are continuously present (Hay and Villouta 1993). Central California is a cold temperate region and even in the Monterey Harbor temperatures never exceed 18.5°C during the two years of this study. However, despite the presence of continuous cold seawater temperatures in Monterey Harbor, which is consistent with the appearance of sporophytes in its native range, *U. pinnatifida* was not present year-round within the study site. Macroscopic sporophyte populations of *U. pinnatifida* in the study site were present from early winter through late summer and absent in the fall with some annual variation (± a couple of months) and corresponded with distinct temperature patterns. *U. pinnatifida* in Monterey appears to respond to seasonal variations in temperature range rather than a specific temperature threshold. High-amplitude, high-frequency temperature fluctuations of 3-4°C during warm periods, coupled with a yearly range of 11-18.5°C, appear to be enough to induce cycling between presence and absence of macroscopic sporophytes. This cycle of

presence-absence differs from the Santa Barbara population where temperature differences caused two distinct cohorts to form per year and were associated with a noticeable difference in sporophyte density between cohorts (Thornber et al. 2004). These differences may be accounted for by the larger annual range and temperature maximum (21°C) in Santa Barbara.

Many populations of annual species have an age-frequency distribution that is uniform, with particular life stages dominating during certain seasons of the year. In some respects the same also holds true for *Undaria pinnatifida*. Recruitment of *U. pinnatifida* peaks in early winter as macroscopic sporophytes reappeared approximately 3 months after temperatures dropped below 16°C. At this time, the mean density of recruits (per $0.25m^2$) may be six-fold higher than adults. As mean adult density reached an annual peak in early summer, adults became reproductive and concomitantly mean recruit density declined. The onset of fall and a 4°C seasonal rise in temperature was followed by a decline in adult densities 3 months later. However, there was a period from roughly March through September, 2005 when overlapping cohorts of *U. pinnatifida* existed in the harbor. Therefore, there were likely microscopic stages already present, analogous to a seed bank, with variable ages due to multiple cohorts. This may be advantageous to an opportunistic species in an unpredictable environment, because gametophyte replenishing may extend the window of opportunity for responding to cues at virtually any time of the year. Recruits appearing in the winter took approximately 2.5 months to grow, develop sori, and release spores that could successfully germinate. This study found that successful germination coincided with a distinct morphological feature

(a lightened line at the edge of the sporophyll paired with dark sori) 87.93% of the time, indicating that the appearance of sori does not signify reproductive competency. Spore release and settlement from experimental sporophyll plugs was not successful in individuals that did not contain this morphological feature, even when sorus was present. However, this study found no correlation between germination density and season. Once the first reproductive adults appeared in spring at the study site, reproductive individuals remained in the area until the fall die-off, with comparable germination densities from monthly spore plugs. Unlike perennial species, where spore release is continuous and adapted to seasonal environmental variability (Reed et al., 1996) and coincides with a reliable annual event (McConnico and Foster, 2005), annual species such as *U. pinnatifida* may be more opportunistic and able to quickly respond to changing environmental conditions.

Similar to other parts of the world, physical condition of *Undaria pinnatifida* declines during the summer as the blade deteriorates. Physical condition of the sporophyte population parallels the annual die-off in Monterey. Sloughing of the vegetative blade has been observed to occur just prior to peak reproductive periods, which is followed by a population crash (Fig. 6). In New Zealand, where environmental conditions are moderate, *U. pinnatifida* is continuously present throughout the year with multiple overlapping cohorts.

Because *Undaria pinnatifida* in many ways fits the description of an opportunistic species it should exhibit reproductive plasticity. In protected areas of southern Chile, annual populations of the giant kelp *Macrocystis pyrifera* grew and produced sporophylls

earlier and produced more spores (per standardized area of fertile tissue) than perennial populations (Buschman et al. 2004). However, this study did not find any correlation between germination density and surface area of *U. pinnatifida* sporophylls, although such a comparison should be made with New Zealand populations.

Consequences of sporophyte density to reproduction and recruitment

Many environmental and biological factors interact on the microscopic level from the time a spore is released and settles through the appearance of a macroscopic sporophyte. Recruitment is an important process in determining population dynamics and subsequent community-level structure and function. Previous studies have shown that sporophyte generations are largely determined by recruitment success (Chapman 1984, Reed 1990, Graham et al. 1997). Similarly, sporophytes set the stage for recruitment by supplying spores and influencing the site of settlement as spores typically settle within a range of adults. This study looked at recruitment under varying sporophyte densities of *Undaria pinnatifida*. Experimental manipulations of *U. pinnatifida* denisty demonstrated that short dispersal distances may limit spreading capability while environmental signals and interactions within cohorts may influence population persistence. This suggests that dispersal distance may structure populations spatially, while oceanographic conditions and intra-specific competition structure populations through time.

Dispersal capabilities contribute to local persistence and strongly influence spatial and temporal variation of populations (Paine 1988). Most kelp species are thought to have limited dispersal (Santelices 1990), in part because gametophyte fertilization occurs

after spore dispersal and requires high settlement densities (Reed et al. 1991). However, certain species of kelps can extend this range through fragmentation of reproductive tissue (Forrest et al. 2000), the synchronous release of propagules during conditions that increase advection (Reed et al. 1997), or by bearing spores and germlings that can remain competent in the plankton for extended periods of time (Reed et al. 1992). The majority of *U. pinnatifida* recruitment (63%) occurred within 0-0.5 m of the transplanted plots while the remaining 37% occurred within 0.5-1 m of the plots. This trend occurred irrespective of plot density, suggesting *U. pinnatifida* in Monterey is a short-distance disperser. It is likely that if it were not for multiple sources of introduction *U. pinnatifida* would have slow spreading rates. These results compliment previous work (Forrest et al. 2000), which concluded, through artificial spore release, that fixed stands of *U. pinnatifida* contribute the greatest amount of spores within 10 m of themselves. Minimum spore settlement densities for successful recruitment have been found for some species of kelps (Reed et al. 1991). Assuming similar requirements for *U. pinnatifida*, it is likely that the strong mixing of the tidally influenced Monterey Harbor dampens dispersal distance capabilities by spreading the available spore supply thinner.

Intra-specific competition is also a major factor affecting the maximum population level supported by the community. As expected, the effects of intra-specific competition were density-dependent. Plot density had a significant effect on timing of peak sorus density (Fig. 7): adults in lower density plots reached peak sorus density at an earlier date than adults in higher density plots. Reproductive tissue and sorus area for

individuals of the perennial kelp *Pterygophora californica* is higher in low density stands than high density plots (Reed 1990).

This density-dependent response by individuals in higher density plots may be a trade-off between initially concentrating energy into rapid growth rather than reproduction. The effect of *Undaria pinnatifida* adult density on subsequent recruitment was marginally non-significant (Fig. 8). Densities >7 plants/0.25m^2 decreased total recruitment by about half (Fig. 8). Although it was not quantified, shading increased as sporophyte density increased and may have negatively affected recruitment success. Further, because the density of recruits decreased as total sorus area within an experimental plot increased (Fig. 10) it is possible that higher density plots reached their recruit limitation prior to peak plot sorus density. This suggests that relatively few individuals are needed to sustain the population in Monterey Harbor.

Undaria pinnatifida populations in Monterey Harbor may also be responding to an environmental cue. Throughout the 9 months of field observations, all experimental plots had a distinct recruitment pulse lasting several weeks and peak recruitment occurred on the same date in most plots (Fig. 9). If spore supply was limiting recruitment, one would expect recruits to peak at different times. Further, sampling in natural density plots revealed that mean germination density amongst the population did not vary through time, because of overlapping cohorts. It is likely that timing of recruitment of *U. pinnatifida* in Monterey was signaled by an environmental cue rather than a biological control.

Microscopic stages of kelps are vulnerable and experience high mortality (Chapman 1984, Dysher and Dean 1986, Reed et al. 1988). The results of this study suggest that the *Undaria pinnatifida* population in Monterey Harbor is not limited by spore supply or the ability of the supplied spores to germinate, rather they are likely controlled by post-settlement events.

Physiological response to temperature

Using environmental cues to trigger biological responses may be an adaptive strategy for opportunistic species, but these same cues may serve as disadvantageous controls of population dynamics. For example, there was a considerable effect of increased temperature on reproduction in *Undaria pinnatifida*. In general, individuals subjected to elevated seawater temperatures showed decreased nutrient content, decreased overall reproductive output, increased time to reproduction, shorter life-span, and more rapid onset of senescence when compared to their cold-water counterparts. Previous studies have shown the importance of nitrogen to seasonality in kelp (Jackson 1977). Results indicate that elevated seawater temperatures may reduces the nitrogen uptake capacity and interactions between vegetative and reproductive tissue in *U. pinnatifida*, facilitating the trade-off between vegetative and reproductive tissue and contributing to population cycling during times of warming.

Comparisons between blade and sporophyll tissues revealed that percentages of carbon and nitrogen were consistently higher in the sporophylls, roughly 2.5 and 2 times greater, respectively. Unlike blade tissue, sporophyll tissue is both photosynthetic (Oh and Koh, 1996) and packed with reproductive material. It is possible that site-specific,

and differential use and production of nutrients occurs between the blade and sporophyll in *Undaria pinnatifida*. However, previous studies have shown that *U. pinnatifida* translocates nutrients from the tip of the blade to the basal growing region in an obvious source-sink relationship (Chaoyuan and Jianxin 2004). It is likely that the sporophyll, which is basally located, benefits from this movement of nutrients from the blade. The results of this study showed some evidence for this type of nutrient transport. Carbon was generally conserved and treatment effects were marginally non-significant. However, there was a general decrease of blade carbon in cold treatments concurrent with an overall rise of carbon in cold treatment sporophylls that did not occur in warm water treatments. Nitrogen was expended at a faster rate than carbon and the effect of temperature treatment on % tissue nitrogen was significant. Blade nitrogen in warm treatments decreased at a faster and more substantial overall rate than in cold treatments. This paralleled an overall decrease in warm treatment sporophyll nitrogen, while cold treatment sporophyll nitrogen increased.

Reproductive success differed significantly between temperature treatments. Initial reproductive response (germination of settled spores) was quicker in warm treatments (3 vs. 6 days) (Fig. 14), and mirrored the increase in warm treatment blade and sporophyll tissue C:N for that period (Figs. 15-16), indicating that a rapid decrease in nitrogen was coupled with a reproductive response. However, germination success reached higher densities and persisted longer in cold-water treatments. Previous studies have found an effect of vegetative tissue on reproductive tissue quality, quantity, and nutrient levels (Reed 1987, Pfister 1992), linking blade tissue to reproduction in certain

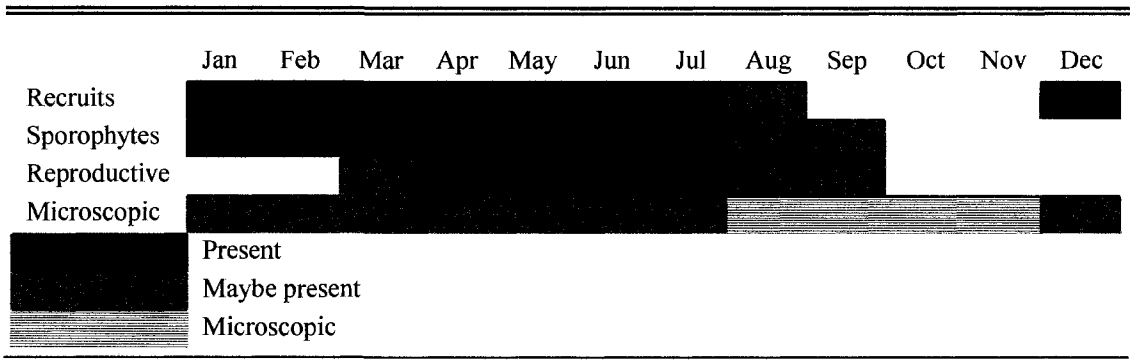
kelps. This study did not detect any significant correlation between sporophyte length and germination density (Fig. 17). Blade loss was evident in both warm and cold treatments and some of the initial loss may be an artifact of transplantation. One month into the experiment the majority of individuals in cold treatments were observed to have retained a healthy scaled down version of a blade. Conversely, the majority of individuals in the warm treatment lost their blade. Pfister (1992) suggested that for the kelp *Alaria nana* photosynthesis in the sporophylls is not as efficient as in the frond. Contributions of the scaled down blade may have worked to increase density and duration of spore release in the cold treatment, and may represent a long-term reproductive response in favorable conditions. In the warm treatments, complete loss of the vegetative blade may result as a response to a temperature cue and allocation of nutrients to the reproductive tissue and may represent a more short-term reproductive strategy in unfavorable conditions. This hypothesis would benefit from further studies looking at the movement (rather than content) of nutrients through the thallus under varying temperature treatments and physical conditions of the sporophyte.

Despite the differences in timing and quantity of reproductive response between cold- and warm-water treatments, germination density results indicated that viable spores capable of settling and germinating were released in pulses through time regardless of treatment type (Fig 14). These results corresponded well with results from natural population density sampling for reproductive individuals and suggest that there is an available and capable spore source throughout most of *Undaria pinnatifida's* life cycle.

CONCLUSION

Undaria pinnatifida within the study site in Monterey, California has an annual cycle of recruitment, growth, reproduction, and senescense (Table 9). Recruitment

Table 9. Demographic life history model of *Undaria pinnatifida* in Monterey Harbor.



occurs in early winter and continues through mid summer, peaking in late winter/early spring. Reproductive sporophytes are typically only present through spring and summer, peaking in summer at the end of their life cycle. No individuals were present in the study site during the fall, suggesting the importance of microscopic stages in driving winter recruitment. Despite the presence of a temperature range analogous to one that allows continuous populations to flourish in areas of New Zealand, populations of *U. pinnatifida* in Monterey, California are driven by seawater temperature and exhibit annual cycles of recruitment and senescence similar to populations in Asia and Southern California. Differences between New Zealand and California population dynamics may be attributed to California's single-event introduction and resulting low genetic diversity as oppose to New Zealand populations (Voisin et al. 2005).

to California's single-event introduction and resulting low genetic diversity as oppose to New Zealand populations (Voisin et al. 2005).

Many species of kelp exist as microscopic gametophytes through the winter, macroscopic sporophytes in the summer, and experience peak growth in spring. The demographics of the introduced kelp *Undaria pinnatifida* within the study site in Monterey, California are opposite to those observed for most species of kelp. The gametophyte stage of *U. pinnatifida* persists over the summer rather than the winter months in its native range, with recruitment occurring from early winter through mid summer, peaking in winter. Sporophytes are present through this same period but peak in density in early summer. Reproductive individuals are present from spring through summer but peak in mid summer. Similar to populations in its native range, *U. pinnatifida* in Monterey Harbor appears to be cued by temperature variability. Populations experience peak densities of reproductive individuals in mid-summer as yearly mean seawater temperatures peak at 18.5°C, sporophyte densities begin to decline approximately three months following a 3-4°C rise in mean seawater temperature, and recruitment occurs three months following a temperature drop below 16°C. This study has shown that *U. pinnatifida* is capable of responding to seasonal variation in temperature with high-amplitude, high-frequency temperature fluctuations of 3-4°C during warm periods with a relatively small range of 11-18.5°C, rather than a specific temperature threshold, as previously thought. Physical condition of the sporophyte parallels annual population cycling. Individuals achieve maximum total length prior to

the onset of high summer temperatures and begin sloughing of the vegetative blade during mid-summer, which parallels peaks in reproductive densities.

The effects of *Undaria pinnatifida* sporophyte density on recruitment shed light onto its persistence and spreading capabilities. Results showed evidence of density-dependent intra-specific competition, as increasing sporophyte density affected timing to peak plot reproductive capacity and recruitment density. Likely explanations of decreased reproductive capacity in higher density plots include energetic investment in growth (rather than reproduction) and intra-specific shading. However, results indicated that few individuals were actually necessary for sustaining populations, as higher density plots reached their carrying capacity of settlement prior to peak sorus plot density. One biological factor slowing the spread of *U. pinnatifida* may be dispersal distance. Results indicated that *U. pinnatifida* in Monterey harbor was a relatively short distance disperser, with the majority of recruits appearing within 0.5 m of transplanted plots regardless of plot density. It is therefore likely that the spread of *U. pinnatifida* outside of the Monterey Harbor may be facilitated by multiple introductions.

Based on the physiological response of *Undaria pinnatifida* to temperature experiments, individuals in cold water responding to increasing water temperature should experience increased senescence, decreased % nitrogen, increased time to reproduction, and decreased propagule release. There was a significant effect of water temperature on nutrient content, nutrient allocation and reproductive response, even in temperatures below those known to cue such responses in *U. pinnatifida*. It is likely that reproductive tissue benefits in some way from the movement of nutrients from the blade. Previous

studies have shown that *U. pinnatifida* exhibits translocation from the tip of the blade to the growing region in a source sink relationship (Chaoyuan and Jianxin 2004), and I have personally observed sloughing of the vegetative blade prior to peak reproduction, suggesting movement of nutrients into reproductive tissue. Population cycling during times of warming may be accounted for by reduced nitrogen uptake capacity and interactions between vegetative and reproductive tissue.

Overall results of this study indicate that *Undaria pinnatifida* is not continuously present within the study site in Monterey Harbor and population cycling responds to temperature cues. Year-round recruitment of *U. pinnatifida* does not appear to be limited by spore supply. Results from natural population sampling indicated that there was an available spore source throughout most of the time when sporophytes were present. Laboratory results also indicated that sporophytes showed spore release pulses throughout their life cycle rather than one spore release event. However, field experimentation looking at recruitment showed that despite sporophyte density, there was only one peak period of recruitment, even though a sufficient amount of spores were likely present. These results imply density-dependant recruitment inhibition. Further, many processes influence survival from the time of spore release to the presence of a macroscopic recruit, and temperature may have a stronger control on post-spore release dynamics.

Undaria pinnatifida is an opportunistic species' that has evolved an adaptive response to changes in an unpredictable environment. These adaptations may lend a distinct advantage when it comes to invasion success. Growth of *Undaria pinnatifida* in

the open coast has been reported worldwide. However, successful establishment outside of the Monterey Harbor and competition with native species of California kelp would likely benefit from the presence of populations that are continuously present throughout the year.

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