

Population ecology of the invasive kelp *Undaria pinnatifida* in California: environmental and biological controls on demography

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ABSTRACT: We combined field monitoring and laboratory experiments to examine the population ecology of both the microscopic and macroscopic stages of a new invasion of *Undaria pinnatifida* in California. Over the course of 1 yr, we observed 2 distinct recruitment pulses of individuals in the Santa Barbara harbor; the appearance of these pulses was strongly correlated with a 4°C drop in ocean temperature approximately 2 mo prior to recruitment. Cultures of zoospores and successive microscopic stages revealed thermal tolerances consistent with field recruitment data; individuals grown at 13°C had significantly higher survivorship than individuals grown at higher temperatures (harbor temperatures annually ranged from 12 to 21°C). The 2 cohorts also differed greatly in individual size, growth rate, and survival to maturity. Grazing by herbivores, predominately the native kelp crab *Pugettia producta*, effectively prevented nearly all individuals in the second cohort from reaching reproductive maturity. Grazer control was effective despite far higher rates of recruitment during the second recruitment pulse. Our results highlight the potential for extreme variability in *U. pinnatifida* demography mediated by local oceanographic and biotic factors. Understanding controls on *U. pinnatifida* demography helps to explain variation in the spread and impact of this invader worldwide, and allows better prediction of when and where *U. pinnatifida* may continue its invasion along the west coast of North America.

KEY WORDS: Invasive species · *Undaria pinnatifida* · Macroalgae · Kelp · Sporophyte · Gametophyte · Life cycle · California · Herbivory · *Pugettia producta*

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INTRODUCTION

The introduction of new species is a major threat to coastal ecosystems worldwide. Although the majority of introduced marine species fail to establish or spread widely (Ruiz et al. 1999), those that succeed often have significant effects on native population, community and ecosystem dynamics (Byers 2000, Grosholz 2002, Levin et al. 2002, Lohrer & Whitlatch 2002). Thus, there is significant interest in predicting which invaders are likely to spread rapidly and alter native communities, as well as which native communities are likely to be most susceptible to invasion (Carlton 1996, Ruiz et al.

2000, Stachowicz et al. 2002a). Specific attributes of species and the invaded habitat often confound generalization in invasion biology. However, some species have invaded a number of different regions, providing replication that may increase our predictive ability (Grosholz & Ruiz 1996). If multiple invasions of the same species into different habitats have the same outcome, our confidence in predicting the outcome of future invasions should increase.

Some studies of 'repeat invaders' have found similar demography, ecology, and impacts on native communities across locales. For example, the green crab *Carcinus maenas* has both consistent dietary prefer-

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ences and large ecological impacts (similar to native European populations) when it invades protected embayments in eastern North America, western North America, and South Africa (Grosholz & Ruiz 1996). Gut contents of *C. maenas* from all of these areas reveal comparable relative abundance of major prey types, and *C. maenas* has had similar impacts on other crabs, mollusks, and echinoderms (Grosholz & Ruiz 1996). Studies of the zebra mussel *Dreissena polymorpha* have shown that this species dramatically decreases phytoplankton abundance and increases water clarity in independent invasions (Reeders et al. 1989, Leach 1993). Demography may be more variable among locations (Shanks et al. 2003), but in many cases this variation is at least partially predictable from local environmental and ecological factors. For example, the expansion of *D. polymorpha* through navigable, commercial waterways is faster than into isolated lakes (Padilla et al. 1996).

Another worldwide invader that has recently received increasing attention is the Asian kelp *Undaria pinnatifida* (Harv.) Sur. In its native range, *U. pinnatifida* is found along the coasts of southeastern Russia, Japan, China, and Korea (Saito 1975, Kim & Lee 1995, Kitayama et al. 1995). *U. pinnatifida*, like all kelps, has a biphasic life cycle, with microscopic (haploid) gametophytes and macroscopic (diploid) sporophytes. In its native range, macroscopic recruits (sporophytes) appear during winter months, mature during the spring, and senesce during the summer, as water temperatures increase (Saito 1975). Mature sporophytes release motile zoospores, which settle and develop into dioecious microscopic gametophytes (Oh & Koh 1996). In the presence of high summer water temperatures, *U. pinnatifida* gametophytes lie dormant (Saito 1975), and thus unlike all other kelps, the gametophyte stage of this species persists over the summer, rather than the winter months. Gametophyte development occurs once water temperatures drop below ~20°C, which occurs during late summer/early fall in the native range of *U. pinnatifida* (Saito 1975, Ohno & Matsuoka 1993). Mature gametophytes undergo sexual reproduction to produce embryonic sporophytes that subsequently develop into macroscopic individuals.

This unique life history pattern (easily transportable microscopic stages present when water temperature is warmest and pleasure boat traffic is greatest) might be an important reason why *Undaria pinnatifida* is the only kelp reported in the literature to be invasive (Ruiz et al. 2000). Since 1970, *U. pinnatifida* has become widely established in temperate coastal areas, including the coasts of France, England, Argentina, New Zealand, and Argentina (Perez et al. 1981, Hay 1990, Fletcher & Manfredi 1995, Casas & Piriz 1996, Campbell & Burrige 1998). Like native *U. pinnatifida* popu-

lations, most invasive populations follow a seasonal cycle and have discrete annual generations (Floc'h et al. 1996, Campbell & Burrige 1998); however, some New Zealand populations exhibit overlapping generations and sporophytes can be found year-round (Hay & Villouta 1993). In these populations, *U. pinnatifida* competes with native macroalgal assemblages throughout the year, making its impact potentially more severe. Differences in seasonality among locales are presumed to result from differences in ocean temperature cues, which are important regulators of demography in the native habitat of *U. pinnatifida* (Saito 1975). However, with the exception of the present study, this hypothesis has not yet been experimentally tested in invasive populations.

Whether generations are overlapping or discrete, and whether the life history is strictly annual or not should have important consequences for the success of *Undaria pinnatifida*, its impact on native seaweeds, and its effect on marine community structure. For example, if macroscopic stages only appear in winter when few natives are active, *U. pinnatifida* might compete little (or less) with native annual species (Valentine & Johnson 2003); whereas if generations are overlapping, the potential for negative effects on natives is much greater. Thus, here we: (1) describe life history patterns in the field, (2) elucidate the environmental trigger(s) underlying these patterns using both field (correlational) and lab (experimental) approaches, and (3) assess the potential of interactions with native herbivores to control *U. pinnatifida* establishment and spread. To determine if there are predictable, temporal patterns of recruitment, we monitored a recently established California population of the invasive kelp *U. pinnatifida* (see 'Materials and methods'). We studied temperature thresholds for the development of microscopic gametophytes and sporophytes in the field and in the laboratory. Finally, we tracked the growth and maturation of individuals in the field, and we observed a potentially strong effect of a native herbivorous crab on the *U. pinnatifida* population.

MATERIALS AND METHODS

Study species. Starting in 2000, *Undaria pinnatifida* became established at several locations along the west coast of North America (Silva et al. 2002), where it lives primarily in wave-protected, shallow marine habitats. It can grow on both natural and artificial substrates and is frequently cultured for market as wakame (Saito 1975). *U. pinnatifida* can be spread via 2 different classes of mechanisms—localized dispersal of microscopic zoospores, or broader dispersal of microscopic and/or macroscopic stages attached to boat hulls and

other manmade substrates (Hay 1990, Forrest et al. 2000). Currently, North American populations are found as far south as Ensenada, Mexico and as far north as Monterey, California, USA (Silva et al. 2002). Population sizes at both edges of this range are increasing over time, and most populations (except one at Catalina Island) are found attached to floating docks in harbors, which typically have few other macroalgal species present (K. A. Miller, M. Graham, S. Lonhart, pers. comm.).

We studied the dynamics of *Undaria pinnatifida* in the field in the Santa Barbara harbor (Marina One, Q visiting slip docks). A large, reproductive population was observed at this location living on manmade floating docks (approx. 30 m²), relatively close to the harbor mouth, in April/May 2001 (and subsequently removed in an eradication attempt). When we initiated our studies in July 2001 (see below), all macroscopic sporophytes were absent from the study site and it was assumed that dormant microscopic stages were present on the dock. We monitored offspring of this initial generation from July 2001 to June 2002. When reproductive macroscopic sporophytes reappeared, we used individuals from this population and also from the Monterey harbor for zoospore cultivation studies (see 'Laboratory culture experiments') to compare the reproductive biology of populations between sites with different thermal regimes. No other kelp species were observed at the study site, which facilitated identification of small recruits.

Field studies. To determine the macroscopic population dynamics of *Undaria pinnatifida* in Santa Barbara, California, we tracked the appearance of recruits, subsequent growth rates, reproductive timing, and eventual mortality of *U. pinnatifida* individuals. We recorded the date of appearance, location, and size (length and width) of individual recruits (macroscopic sporophytes, approx. 2 cm in length) from July 2001 to June 2002. As soon as recruits were at least 4 cm long, we loosely tied individual tags (FTF-69 Fingerling, Floy Tag) around the base of each stipe. Size measurements of all tagged individuals were made on a weekly basis; the total length, stipe length, blade width, sporophyll length and width, and the occurrence of blade senescence and/or grazing damage were recorded for each individual. Sporophyll volume was calculated from the length and width, assuming an ellipsoid shape (consistent with sporophyll morphology; the sporophyll is generally large with respect to total plant size, and it consists of very dense, ruffled tissue). Because vegetative blades of *U. pinnatifida* can erode at the distal margins as basal growth occurs, we also monitored lengthwise growth of individuals by punching small holes in blade midribs and recording the length of new tissue growth weekly (Stuart et al. 1999) for all individuals that grew

large enough to be tagged. Grazer damage in this paper is used to refer to distinct bites and tears not attributable to sloughing of tissue along the margins of the blade, stipe, and sporophyll (when present). All data were analyzed with JMP statistical software v 4.0.4 (SAS Institute) unless otherwise noted.

Temperature loggers (Stowaway TidbiT, Onset Computer) were installed at 0.3 and 1 m depth on August 6, 2001, and recorded water temperature hourly. To examine ocean temperature prior to this date, we obtained an hourly time series of temperature at 1 m depth at the Ellwood, California pier (approximately 15 km from the Santa Barbara harbor) that overlapped the duration of our study completely, and extended to April 1, 2001 (C. Cudaback unpubl. data). We generated a hindcast temperature time series for the Santa Barbara harbor from auto- and cross-correlations of daily-averaged Ellwood and Santa Barbara data (Deutch & Journal 1998). This resulted in a 1 m depth temperature time series for the Santa Barbara harbor extending from April 1, 2001 to June 30, 2002. To assess the relationship between water temperature and *Undaria pinnatifida* recruitment, we examined time-lagged cross-correlations between these 2 variables (Chatfield 1993). These analyses were conducted using Geostatistical Software Library (GSLIB) 2.0 (Deutch & Journal 1998) and Matlab Version 6 release 12 (The Mathworks).

Laboratory culture experiments. Field observations suggested that the emergence of latent microscopic stages occurred with decreasing water temperatures (and has also been demonstrated by Saito 1975, who found a delay in gametophytic development at higher water temperatures). To experimentally assess the effect of temperature on the growth of microscopic stages of *Undaria pinnatifida*, we followed their development under 3 temperature regimes (13, 17 and 21°C) from zoospore settlement, through gametophytic development, fertilization, and the appearance of multicellular sporophytes (>37 d). To determine whether populations within California might vary their life history in response to local oceanographic conditions, we performed these experiments on populations from warmer southern waters (Santa Barbara) and colder northern waters (Monterey). The 2 sites are separated by approximately 420 km and 3°C in mean annual surface temperature (NOAA Satellite Information, available at www.nodc.noaa.gov/dsdt/cwtg/spac.html). Experimental temperatures were selected to reflect the range of ambient temperatures found in the Santa Barbara harbor (13, 17, and 21°C). While individuals in the Monterey harbor would rarely experience temperatures greater than or equal to 17°C, these temperatures are regularly experienced within the species' native range (Saito 1975).

Reproductive sporophylls were collected from each population in April 2002. Zoospore release for each population was induced by first placing sporophylls in cool, damp, and dark conditions for several hours and then transferring to filtered seawater (Saito 1975). Once release of motile zoospores had occurred, the zoospores were added to large shallow tanks (hereafter referred to as settlement tanks, 0.5 m × 2 m × 15 cm depth) to yield a final suspension of 10^3 to 10^4 zoospores ml⁻¹. Settlement tanks were lined with small (4 × 2.5 cm) glass slides. One zoospore settlement tank had an ambient water temperature of 17°C (Santa Barbara), whereas the other tank was set to 13°C (Monterey), reflecting average water temperatures for the 2 regions. Ambient irradiance was 87 to 145 $\mu\text{E m}^{-2} \text{s}^{-1}$, provided by full spectrum (GE Chroma 50) and cool white (Sylvania) fluorescent bulbs on a 12:12 h photoperiod. Germanium dioxide treatments of 0.15 mg l⁻¹ were conducted weekly for diatom control for the duration of the experiment (Markham & Hagmeier 1982).

Glass slides were removed from the settlement tanks at both 3 and 8 d after zoospore release and moved to containers with filtered seawater maintained at 13, 17, or 21°C. Three days post zoospore release, the zoospores settled and germinated; 8 d post release, they became gametophytes (C.S. Thornber & M.H. Graham pers. obs.). These 2 experiments therefore tested the effects of temperature on (1) all developmental processes after spore settlement (3 d transfers), and (2) all developmental processes after gametophyte formation (8 d transfers). On Day 3, 45 slides were moved from each of the Monterey and Santa Barbara settlement tanks. Of these 45, 3 slides were placed in each of 15 containers, and 5 of these containers were placed at each of the 3 water temperatures. On Day 8, 90 slides were moved from each settling tank and placed in 10 containers with 3 slides apiece, for each of the 3 water temperatures.

We counted the density of female gametophytes and sporophytes on slides each week (due to their morphology, female kelp gametophytes can be identified and counted with much more accuracy than male gametophytes). One slide per container was removed, stained with a dilute solution of Rose Bengal, placed on a compound microscope at 400×, and 10 replicate fields of view ($6.806 \times 10^{-3} \text{ mm}^2$ each) on each slide were counted with the aid of a reticle. After a slide was counted, it was thrown away. Slides were counted on Days 3, 8, 16, 23, 30, and 37. On Day 37, due to decreasing densities and increasing sporophyte size, the total number of sporophytes on a 324 mm² area (the area of a standard coverslip) of each slide was also counted.

The final densities of sporophytes (Day 37) were analyzed via 1-way ANOVA for differences among the

3 temperature treatments. Replicates were individual slides, since 1 large area per slide was counted. Due to the different initial temperature at zoospore release and settlement (Days 0 to 3), the Monterey and Santa Barbara populations were analyzed separately.

Weekly densities of female gametophytes at different temperatures were analyzed via 2-way nested ANOVAs, because several slides were counted from the same containers over the course of several weeks. Gametophyte density counts in individual fields of view served as replicates (10 per slide), with containers (slides) nested within temperature treatments. The Container(Temperature) × Day mean square was used as the denominator for treatment *F*-ratios. Data were examined for normality and homogeneity of variances and transformed where appropriate prior to analysis.

Laboratory grazing experiments. In the course of our study, we frequently observed grazing by the common kelp crab *Pugettia producta* on macroscopic sporophytes. Although this indicated the potential for control of *Undaria pinnatifida* by native herbivores, to assess how these grazers might affect the abundance of *U. pinnatifida* in the field it is important to know the palatability of *U. pinnatifida* relative to native seaweeds with which it might eventually co-occur. Juvenile *P. producta* (carapace width approx. 20 to 30 mm) and mature individuals of *U. pinnatifida* were collected from floating docks in the Santa Barbara harbor in April of 2002. Because a previous gut content analysis study demonstrated that *P. producta* consumes *Macrocystis pyrifera* almost exclusively (Hines 1982), we collected vegetative blades of *M. pyrifera* from nearby kelp forests along the Santa Barbara coast to serve as a comparison for relative palatability.

We conducted 2 separate grazer feeding preference assays: (1) *Macrocystis pyrifera* vs *Undaria pinnatifida* blades, and (2) *U. pinnatifida* blades vs sporophylls. In each assay, pieces of tissue approximately 3 × 3 cm were cut, spun in a salad spinner to remove excess moisture, and massed to the nearest 0.001 g. Two pieces of algae (one of each type) were added to each plastic container (14 cm diameter, 15 cm height), along with one *Pugettia producta*. Thirteen replicates were used for the first assay, and 16 for the second. Identical numbers of control containers (with algae but without crabs) were also created. Crabs were removed when each had eaten approximately 1/3 of the total mass of algae; in all cases this occurred within 24 h. All pieces of algae were removed from each container, spun in a salad spinner, and re-massed. The tissue mass removed by *P. producta* was then calculated. Controls did not exhibit significant changes in mass and will not be discussed further.

RESULTS

Field studies: recruitment

Undaria pinnatifida recruited to the Santa Barbara harbor in 2 discrete pulses over the course of 1 yr. The 2 cohorts differed markedly from each other in terms of number of recruits and pulse length. The first recruitment pulse was small ($n = 40$ individuals) and lasted for slightly over 1 mo (August 3 to September 13, 2001); the second pulse was much larger ($n = 305$ individuals) and lasted for 4 mo (January 17 to May 19, 2002; Fig. 1). In all cases, recruit density was 3 m^{-2} or lower. Recruits were found growing attached directly to the concrete floating docks, as well as to mussels (*Mytilus* spp.), solitary ascidians (mainly *Styela* spp.), holdfasts of *U. pinnatifida* from the previous cohort, and monofilament tag lines used to identify individuals of *U. pinnatifida* from the previous cohort.

The 2 recruitment pulses occurred during different mean harbor temperatures; the smaller fall pulse occurred when temperatures ranged from 17 to 21°C (mean \pm SD = $18.6 \pm 0.1^\circ\text{C}$), and the larger winter pulse occurred when temperatures ranged from 12 to 17°C (mean \pm SD = $14.1 \pm 0.1^\circ\text{C}$; Fig. 1). However, the microscopic stages of *Undaria pinnatifida* (zoospores, gametophytes, and embryonic sporophytes) that settled on the floating docks also experienced a range of ocean temperatures prior to becoming large enough to appear as recruits. Fig. 1 shows water temperature at 1 m depth in the Santa Barbara harbor (solid line) from

April 1, 2001, to June 30, 2002 (dotted lines indicate 95% confidence interval for extrapolated portion of time series, see 'Materials and methods'). Approximately 60 d prior to each recruitment pulse, there was a large drop (-4°C , to below 15°C) in ocean temperature (Fig. 1).

An analysis of time-lagged cross-correlations between ocean temperature and recruitment revealed significant negative correlation of recruitment with ocean temperature from 0 to 8 wk prior, with the strongest correlation between 6 to 8 wk prior (Fig. 2A). Cold temperatures (below $\sim 15^\circ\text{C}$) appear to stimulate the development of microscopic gametophytes and/or sporophytes into recruits (macroscopic sporophytes). Both large recruitment pulses occurred approximately 8 wk after periods when average water temperatures fell below 15°C (Fig. 2B). Also, more recruits were observed during the winter, when the water temperature was lower for a longer period of time (Fig. 1).

Laboratory culture experiments

Temperature had a significant effect on survivorship of the microscopic gametophytes and young sporophytes of *Undaria pinnatifida*; cultures raised at higher temperatures had lower densities of sporophytes throughout the duration of the experiment. This was true for both Monterey and Santa Barbara populations. Thirty-seven days following zoospore release, sporophytes from Monterey, California, raised at 13°C were

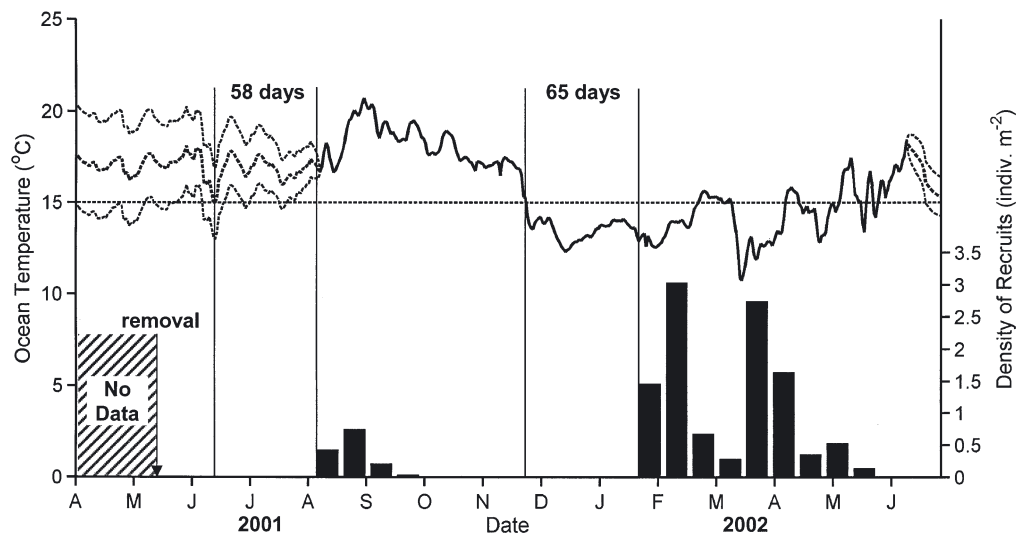


Fig. 1. *Undaria pinnatifida*. Ocean temperature (solid line) and recruitment of individuals (bars) in the Santa Barbara, California harbor. Temperature data are daily means at 1 m depth from loggers in the harbor (August 2001 to June 2002). Temperature prior to August 2001 was estimated using correlations with loggers located at Ellwood pier, approximately 15 km distant (dashed lines indicate 95% confidence limits for this estimation, see 'Materials and methods'). Dashed horizontal line indicates 15°C (see 'Results'). Solid vertical reference lines indicate the lag between periods when temperature dropped below 15°C and the first observation of recruitment. Recruit surveys were conducted on a weekly basis from July 2001 to June 2002; the data are presented here as biweekly sums for clarity

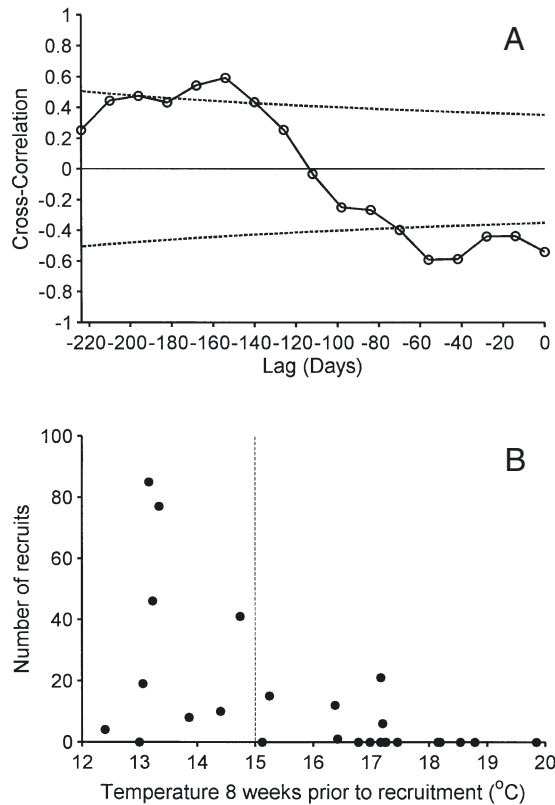


Fig. 2. *Undaria pinnatifida*. Relationship between ocean temperature and appearance of recruits. (A) Time-lagged cross-correlation between recruit density and ocean temperature. Dashed lines indicate 95% significance threshold for correlations, solid horizontal reference line denotes zero correlation. (B) Relationship between ocean temperature 8 wk prior to recruitment and the number of recruits that appeared. Dashed line denotes the 15°C temperature level. All relatively large recruitment events occurred ~8 wk following periods when average temperature was 15°C or lower

3 times as dense as those raised at 21°C; densities in the 17°C treatment were intermediate (Fig. 3A; 1-way ANOVA, $F_{2,12} = 6.33$, $p = 0.013$). Tukey-Kramer HSD tests revealed that the 13 and 21°C treatments were significantly ($p < 0.05$) different from each other, while neither differed from the 17°C treatment (Fig. 3A).

For individuals from Santa Barbara populations, the density of sporophytes at 13°C was an order of magnitude higher than densities in 17 and 21°C treatments (Fig. 3B; 1-way ANOVA, $F_{2,12} = 4.639$, $p = 0.032$). Tukey-Kramer HSD tests found that the 13 and 21°C treatments differed significantly ($p < 0.05$) from each other, but neither differed from the 17°C treatment (Fig. 3B). Thus, warm water temperature clearly inhibits development and survivorship of the microscopic stages of *Undaria pinnatifida*. This is consistent with the cross-correlation of recruitment vs temperature (Fig. 2) found in the field.

For individuals from Monterey, the decrease in density of microscopic stages occurred during development of mature gametophytes, particularly between Days 16 and 23. Fig. 4A shows the density of female gametophytes from slides moved into temperature treatments at Day 3; temperature treatments were differentiated by Day 8 and differences increased weekly. Gametophyte densities varied significantly among temperatures and sampling dates, with no significant interaction (2-way ANOVA, Table 1). The significant nesting effect (Table 1) indicates that there was also significant variation in gametophyte density among containers within individual temperature treatments over time.

A decrease in density between Days 16 and 23 was also found for slides moved into temperature treatments at Day 8 (Fig. 4B); at Day 23 there was a 3-fold higher female gametophyte density in the 13 versus 17 and 21°C treatments. Two-way ANOVA revealed significant differences among temperatures and sampling dates (Table 1). As for slides moved at Day 3, there were significant differences among containers within treatments (Table 1, $p < 0.0001$). Thus, higher temperatures negatively affected the density of Monterey gametophytes, and these differences emerged early in gametophyte development.

Similar early decreases in gametophyte density at higher temperatures were found for individuals from the Santa Barbara population, for slides moved at Days 3 and 8 (data not shown).

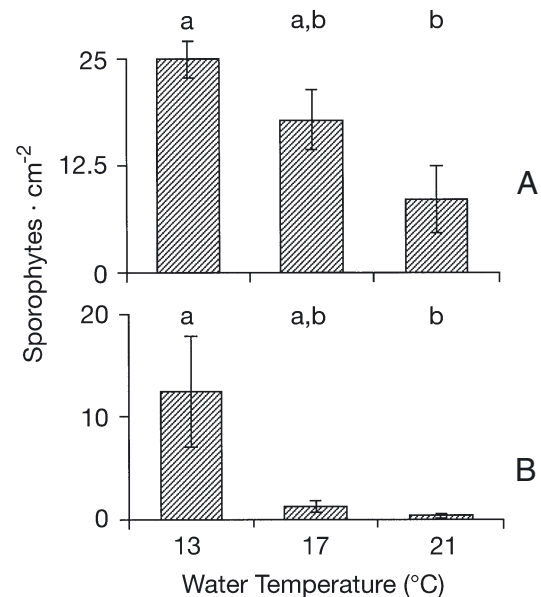


Fig. 3. *Undaria pinnatifida*. Density of microscopic sporophytes grown in laboratory culture under different temperature conditions (13, 17, and 21°C) after 37 d. Data are mean densities of sporophytes \pm 1 SE ($n = 5$ replicate slides), with a, b showing results of Tukey-Kramer HSD *a posteriori* tests. Cultures from (A) Monterey, California, and (B) Santa Barbara, California

Field studies: thallus and sporophyll size, grazer damage

The fall cohort had a larger mean blade size and sporophyll volume than the winter cohort, probably because the winter cohort had a much greater intensity and frequency of grazer damage than the fall (Fig. 5). The mean length of fall individuals was significantly greater than the mean length of winter individuals at each biweekly interval ($p < 0.01$, $t > 2.5$, $df = 42$ to 121 , Fig. 5A), with the exception of the date when recruits of each cohort first appeared. Similarly, a much greater proportion of individuals in the fall cohort than the winter cohort became reproductive (15/40 vs 1/305), and sporophyll volume was 3 times greater in the fall (mean \pm SD = 47 ± 6 cm³) than the winter (14 cm³), despite colder overall temperatures in the winter (Fig. 5B).

Table 1. *Undaria pinnatifida*. Results of 2-way nested ANOVA for Monterey female gametophyte density among dates and temperatures. On successive (weekly) sampling dates, 1 slide was removed from each of 5 containers, from each of 3 temperature treatments (13, 17, and 21°C). Ten replicate areas (6.806×10^{-3} mm²) were counted per container (see 'Materials and methods'). Results are for slides moved at (a) 3 d and (b) 8 d

Source	df (Num, Den)	SS	F	p
(a) 3 d				
Temp	2, 12	81.364	4.067	0.0448
Container (Temp)	12, 19	5.125	0.043	1.000
Day	2, 19	546.127	27.30	<0.0001
Day \times Temp	4, 19	4.759	0.119	0.9741
Container(Temp) \times Day	19, 360	4905.175	25.809	<0.0001
(b) 8 d				
Temp	2, 22	35.857	2.116	0.0150
Container (Temp)	27, 22	10.279	0.109	1.000
Day	3, 22	3001.452	285.488	<0.0001
Day \times Temp	6, 22	51.380	2.443	0.0580
Container(Temp) \times Day	22, 519	452.021	5.863	<0.0001

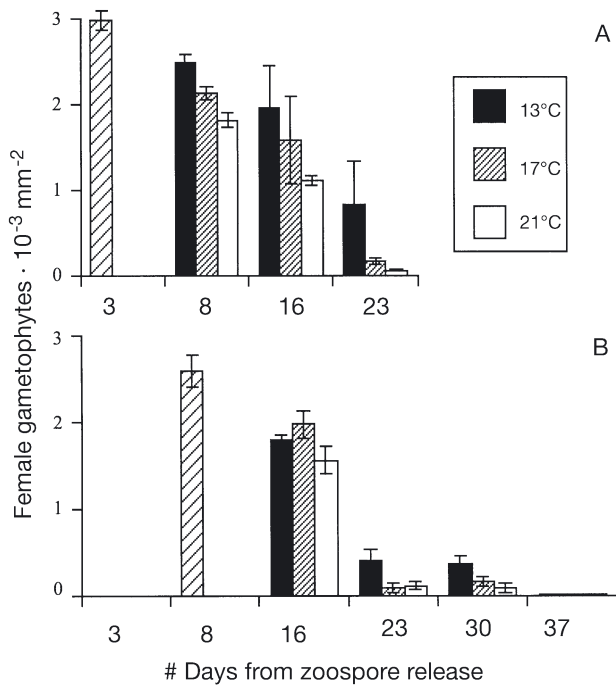


Fig. 4. *Undaria pinnatifida*. Density of female gametophytes derived from Monterey, California individuals and grown in laboratory culture at 13, 17, or 21°C. Zoospores were released and settled on glass slides at 13°C, and slides were moved into different temperature treatments on either Day 3 or 8. Data are mean densities of gametophytes \pm 1 SE ($n = 5$ replicate slides). The hatched bar at Day 3 represents the density of gametophytes on slides prior to the temperature treatments. Slides moved at (A) 3 d and (B) 8 d

Individuals were at least 4 wk old and 17 cm long before they began to produce sporophyll tissue. The mean age of maturation was 6 wk for the fall cohort; the one individual from the winter cohort that reached maturity became reproductive at 4 wk. In addition, we happened to observe spore release (which is a brief event) in the field from one 9 wk-old individual in the fall cohort. All of these factors indicate that the time from appearance of macroscopic individuals to reproduction can be short (within 2 mo).

The maximum percentage of individuals with grazer damage was twice as large for the winter cohort (100%) than for the fall cohort (50%; Fig. 5C). Although there was some apparent grazer damage to individuals in the fall cohort, this began after the recruitment pulse had ended and most *Undaria pinnatifida* individuals had reached larger sizes (mean total length \pm SD = 20 ± 1 cm; Fig. 5A). By contrast, grazer damage was first observed near the beginning of the winter recruitment event, when most individuals were much smaller (mean total length \pm SD = 7 ± 0.2 cm; Fig. 5A), and new recruits continued to exhibit grazer damage throughout the duration of the recruitment pulse.

A possible explanation for the high grazer damage in the winter cohort, and the very large difference in size and survivorship to maturity between cohorts, is the presence of juvenile kelp crabs *Pugettia producta* on the floating docks beginning in mid-February 2002. Crabs were present during every subsequent monitoring of the *Undaria pinnatifida* population. No other herbivores except occasional amphipods were observed grazing on *U. pinnatifida* during the study.

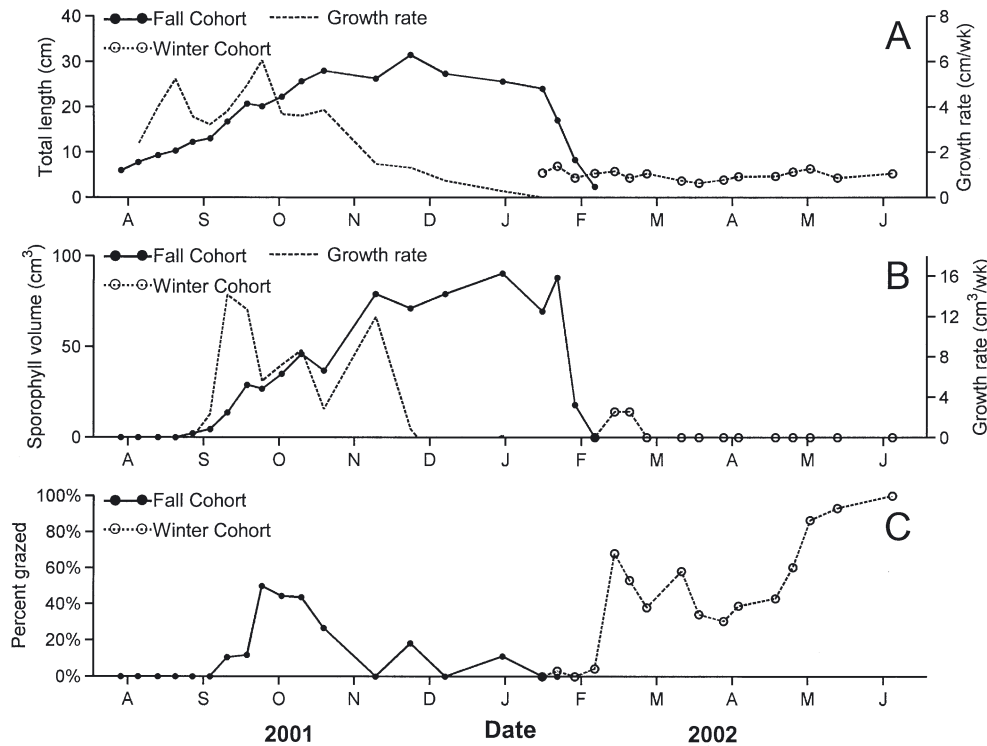


Fig. 5. *Undaria pinnatifida*. Population structure of the fall and winter recruitment cohorts at each sampling date. (A) Mean total length (cm) of all individuals and average weekly blade growth (cm). Growth is plotted only for the fall cohort due to the small number of tagged plants in the winter cohort. (B) Mean sporophyll volume (cm³) of all individuals, and average weekly sporophyll growth (cm³). Growth is plotted only for the fall cohort due to the small number of tagged plants in the winter cohort. (C) Percent of individuals with thallus grazer damage

Field studies: growth rates, lifespan

Growth rates and maximum lifespan also differed between the cohorts, which may be related to increased rates of grazer damage in the winter (see above). All individuals were tagged and followed in the fall cohort, and the mean growth rate varied weekly between 1 and 14 cm wk⁻¹ for individuals up to 15 wk old (Fig. 5A). The maximum recorded growth rate for one individual was 25 cm wk⁻¹. Growth was negligible for individuals older than 15 wk. All individuals in the fall cohort had died due to senescence by the beginning of February 2002 (Fig. 5A).

We were only able to track 18 out of over 300 individuals in the winter cohort—due to grazer damage the remainder never became large enough (4 cm minimum blade length) to be individually tagged and followed. Out of these 18 individuals, mean growth rates varied from 2 to 7 cm wk⁻¹, but after 4 wk, net growth ceased (Fig. 5A). However, there were no significant differences in growth rate for tagged individuals between the 2 pulses (Repeated measures ANOVA, $F_{1,9} = 0.064$, $p = 0.47$), which indicates that physical conditions during both times were amenable to

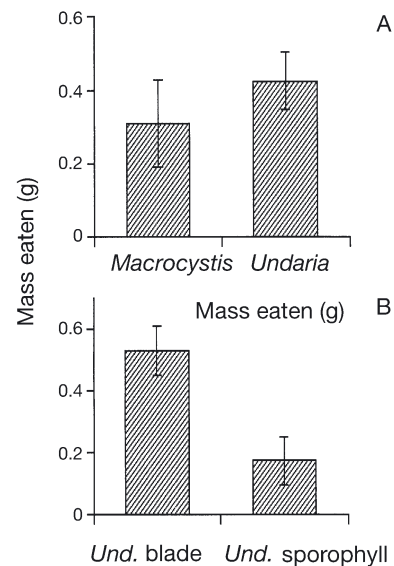


Fig. 6. *Undaria pinnatifida* and *Macrocystis pyrifera*. Feeding preference assays with the common kelp crab *Pugettia producta*. Data represent the mean mass eaten \pm 1 SE. (A) *Macrocystis* blades vs *U. pinnatifida* blades ($n = 13$ replicate containers). (B) *U. pinnatifida* blades vs *U. pinnatifida* sporophylls ($n = 16$ replicate containers)

growth. All tagged individuals in the winter cohort died after 6 wk; most untagged (grazed) individuals appear to have died within a similar time frame. The cohort disappeared completely by mid-June 2002 (Fig. 5A).

Laboratory grazing experiments

Pugettia producta readily consumed *Undaria pinnatifida* in the lab and did not distinguish between *Macrocystis pyrifera* and *U. pinnatifida* blades (paired *t*-test, $t_{12} = 0.873$ $p = 0.200$, Fig. 6A). However, *Pugettia* ate over 3 times more *U. pinnatifida* blade tissue than sporophyll tissue (paired *t*-test, $t_{15} = -4.716$, $p = 0.0003$, Fig. 6B).

DISCUSSION

Environmental controls on life history and demography

As has been shown in this and other studies, local environmental modifications can affect the population dynamics, and potentially alter the success, of species invading new habitats (Andrew & Viejo 1998, Ruiz et al. 2000, Valentine & Johnson 2003). The invasion patterns of *Undaria pinnatifida* in California provide a good example of how local physical factors may influence the phenology, demography, and ultimately the success, of an invasive species.

Our results suggest that persistent cold water temperatures (i.e. below approx. 15°C) may increase the potential for *Undaria pinnatifida* to form populations with continuous recruitment and overlapping generations, as has been previously observed in New Zealand (Hay & Villouta 1993). Preliminary observations suggest that this may be the case for the Monterey, California, population of *U. pinnatifida* (S. Lonhart pers. comm.), where water temperatures are much colder than Santa Barbara (Hickey 1979). The resulting occurrence of a persistent year-round *U. pinnatifida* canopy could greatly magnify the effect of this species on native algal communities. Alternatively, if *U. pinnatifida* populations occur in temporally discrete pulses regulated by ocean temperature cues as in the Santa Barbara and Catalina Island populations (this study and K. A. Miller pers. comm.), such populations will have greater temporal variability in macroscopic sporophyte densities, and thus the potential for impact on native communities may be decreased (Valentine & Johnson 2003). This is particularly true since the temperature regime of the Southern California Bight promotes senescence of *U. pinnatifida* during the summer

months when most temperate NE Pacific algal species flourish (Abbott & Hollenberg 1976). Indeed, a Catalina Island, California, *U. pinnatifida* population growing in a diverse assemblage of native kelp species, including *Pelagophycus porra* and *Macrocystis pyrifera*, has not (yet) negatively affected the native flora (K. A. Miller pers. comm.). However, *U. pinnatifida* may be more successful at invading natural substrates in southern California, because it becomes macroscopic at a time of year when there are few likely competitors. In spite of this asynchrony in seasonality, *U. pinnatifida* may have significant impacts on kelps that are macroscopic during the summertime, due to wintertime shading of their microscopic gametophytes by macroscopic (*U. pinnatifida*) sporophytes.

In addition, it is well known that temperature thresholds can be critical for the success and/or failure of invasive species establishment in new areas (Tyler et al. 2000, Mihulka & Pysek 2001). For example, the distribution of the invasive ctenophore *Mnemiopsis* sp. in US estuaries is restricted by low winter water temperatures (Purcell et al. 2001), and the range of the non-indigenous plant *Impatiens glandulifera* in the UK is climate-limited (Willis & Hulme 2002). Conversely, changing temperatures may have facilitated the invasion of some species that otherwise would not have become established (Stachowicz et al. 2002b).

In this study, we have demonstrated that recruitment of *Undaria pinnatifida* is linked to specific temperature cues. The strongest significant correlation ($r = -0.591$, $p < 0.05$) was between a drop in ocean temperature from approximately 17 to 13°C and the start of recruitment pulses 40 to 60 d following this temperature shift (Fig. 2). The magnitude of recruitment during a pulse is likely linked to temperature—during periods of recruitment, the strongest recruitment tends to occur in 2 wk periods when the average temperature approximately 60 d prior was below 15°C. By itself, it is difficult to conclude much from these observations, as we have a limited number of 'replicate' warm and cold periods. However, similar results have been found for native *U. pinnatifida* populations, where a drop in temperature is necessary for the appearance of recruits (Saito 1975), suggesting that this is a general phenomenon. Thus, ocean temperature may play a role in the observed differences between fall and winter recruitment pulses, and thereby could presumably affect the long-term local population expansion rate of this species.

Our laboratory culture data support our field observations on temperature effects of microscopic stages. We found the highest rates of survival in cultures raised at 13°C (i.e. below 15°C; Figs. 3 & 4). Cultures raised at higher temperatures had lower (but non-zero) densities of gametophytes and multicellular sporo-

phytes. Thus, although populations can persist (as microscopic stages) during periods of higher temperatures, larger macroscopic recruitment pulses would be expected in areas where ocean temperatures remain cooler. Had we continued our culturing experiment, we would have expected to see the appearance of macroscopic sporophytes (recruits) approximately 60 d post zoospore release (Saito 1975).

In addition, we did obtain viable zoospore release at 13°C (Monterey) and 17°C (Santa Barbara), indicating that these populations do not require the occurrence of higher water temperatures (Saito 1975) for zoospore release. This lower temperature is consistent with findings from New Zealand and Australian populations (Hay 1990, Campbell & Burridge 1998).

Native herbivore impacts on algal invaders

Native herbivores can be capable of effectively controlling the spread of newly invasive species (Broughton 2000, Dhileepan et al. 2000, Grevstad et al. 2003). In this study, we frequently observed the native kelp crab *Pugettia producta* grazing upon *Undaria pinnatifida*, preventing most individuals in the winter recruitment pulse from growing larger than a few centimeters in length, and virtually all individuals from reaching reproductive maturity. Our laboratory experiments confirmed that *Pugettia* consumes *U. pinnatifida* as readily as it consumes the native kelp *Macrocystis pyrifera*, its preferred food (Hines 1982), and that it significantly prefers vegetative blade tissue of *U. pinnatifida* to its reproductive sporophyll tissue. Differences in palatability between vegetative and sporophyll tissue have also been found for the kelp *Alaria marginata*, where the vegetative tissue was significantly more palatable (and less chemically defended) than its sporophyll counterpart (Steinberg 1984).

Often, trophic control is strongest at one stage of the life cycle (Rogers et al. 2002, Chase 2003). Thus, the effect of native herbivores may vary greatly depending upon the timing of introduction and the phenology of both invasive species and herbivore. New *Pugettia producta* recruits settle from the plankton throughout the year (Morris et al. 1980), and in Santa Barbara recruits are found year-round (C. Svedlund unpubl. data). However, their occurrence at any one point in space can be sporadic, as illustrated by the differences between our fall and winter observations. It is also plausible (but unlikely) that the higher density of *Undaria pinnatifida* recruits in the winter led to an herbivore aggregation in this study system, but in both pulses biweekly *U. pinnatifida* recruit density did not exceed 3 m⁻². Our results indicate that *P. producta* are probably much more effective in controlling *U. pinnat-*

ifida if they are present at the beginning of a pulse, when individuals are small and before they have formed less-palatable reproductive tissue. The present study is the first record of native herbivore control of invasive *U. pinnatifida* populations, although it is plausible in other regions where *U. pinnatifida* has invaded (e.g. New Zealand), where herbivorous fish have strong impacts on native algal assemblages (Jones & Andrew 1990). It remains to be seen whether native herbivores exert similarly strong effects on California populations of *U. pinnatifida* at larger spatial and temporal scales.

Potential for spread/impact on native communities

The rapid growth rate and onset of sporophylls (within 4 wk in some cases) indicate the potential for *Undaria pinnatifida* to rapidly increase its range along the western margin of North America, especially in areas where recruitment is not inhibited by warmer water temperatures (e.g. north of southern California). Individuals in Santa Barbara reached adulthood at smaller sizes (sporophyll onset began when individuals were less than 20 cm long) than have been reported from other locations (Casas & Piriz 1996, Campbell & Burridge 1998). Because initial *U. pinnatifida* invasions in California have been clustered around visiting slip docks in marinas (C. S. Thornber & S. Lonhart pers. obs.), it is likely that *U. pinnatifida* may continue to expand its range from one harbor to the next via accidental boat transportation, much like the green crab *Carcinus maenas* (Grosholz & Ruiz 1996).

It is well known that invasive species can profoundly change the structure of communities which they invade (Meinesz 1999, Grosholz 2002, Lohrer & Whitlatch 2002). For *Undaria pinnatifida*, the ultimate assessment of impacts on native communities depends upon the ability of populations to move out of harbors and colonize natural low intertidal and subtidal substrates, where native macroalgal assemblages occur. This has already happened in New Zealand (G. Thompson pers. comm.) and at Catalina Island, California (K. A. Miller pers. comm.).

However, as we show, the impact of California *Undaria pinnatifida* populations may be strongly influenced by environmental and biological factors determining phenology and demography. The west coast of North America has the highest diversity of native kelp species in the world (Druehl 1970). The dominant species in these assemblages are generally perennial, with occurrence of annual species facilitated by disturbance (Dayton et al. 1984). Persistent populations of *U. pinnatifida* may therefore be more likely to impact native kelp communities than discrete seasonal popu-

lations. If so, our results suggest the potential for stronger impacts of *U. pinnatifida* in central and northern California, where cooler water temperatures could promote year-round populations with overlapping generations. Future monitoring and control efforts should take account of local and regional factors promoting variation in *U. pinnatifida* population ecology.

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