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RESEARCH ARTICLE

# Effects of ocean temperature on the southern range limits of two understory kelps, *Pterygophora californica* and *Eisenia arborea*, at multiple life-stages

**Paul G. Matson · Matthew S. Edwards**

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**Abstract** Environmental factors have long been shown to influence species distributions, with range limits often resulting from environmental stressors exceeding organism tolerances. However, these abiotic factors may differentially affect species with multiple life-history stages. Between September 2004 and January 2006, the roles of temperature and nutrient availability in explaining the southern distributions of two understory kelps, *Pterygophora californica* and *Eisenia arborea* (Phaeophyceae, Laminariales), were investigated along the coast of California, USA and the Baja California Peninsula, Mexico, by limiting either: (a) tissue nitrogen uptake and storage by adult sporophytes during periods of elevated temperature, and/or (b) production of embryonic sporophytes by microscopic gametophytes. Results suggest that while adult sporophytes of both species are tolerant of high temperatures and low nutrients, reproduction by their microscopic stages is not. Specifically, while *E. arborea* produced embryonic sporophytes at both 12 and 18°C, temperatures commonly observed throughout the southern portion of its range, *P. californica* produced sporophytes at 12 but not at 18°C. As a result, it appears that the southern distribution of *P. californica*, which ends in northern Baja California, Mexico, may be limited by temperature acting on its microscopic stages. In contrast, the ability of *E. arborea*'s microscopic and adult stages to tolerate elevated temperatures allows it to persist in the warmer southern waters of Baja California, as well as to the north along the California coast where both species co-occur.

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P. G. Matson (✉) · M. S. Edwards
Department of Biology, San Diego State University,
San Diego, CA 92182, USA
e-mail: pmatson@gmail.com

## Introduction

Environmental gradients have long been known to significantly affect the distribution of species in both terrestrial and marine ecosystems, allowing species with wider ranges of tolerances to certain environmental conditions to have broader geographic distributions (Connell 1961; Root 1988; Stevens 1989). This may be especially true in subtidal habitats where local-scale variation in temperature, nutrients, turbidity, and wave exposure can negatively affect organism growth, fitness, and survival (Denny and Wethey 2001; Hochachka and Somero 2002). Regional-scale variation in oceanic climate may further result in reduced abundances of some species (Brown et al. 1996; Schiel et al. 2004; Edwards and Estes 2006), as well as shifts in their distributional limits (Holbrook et al. 1997; Edwards and Hernández-Carmona 2005). While our understanding of these biogeographical patterns comes primarily from studies on adult life-stages, growing evidence suggests that juvenile and dispersive (i.e. propagule) life-stages may also be influenced by changes in ocean climate (e.g. Hernández-Carmona et al. 2001; Zacherl et al. 2003). Therefore, a comprehensive assessment of the impact of environmental variability on the distribution of marine organisms necessitates consideration of these effects on multiple life stages.

The kelps (Phaeophyceae and Laminariales) are model organisms to investigate the effects of environmental stress on species' range limits. These large

brown algae are dependent on a suite of physical factors related to habitat (reviewed in Dayton 1985). Kelps demonstrate complex heteromorphic life histories that alternate between haploid (spores and gametophytes) and diploid (embryonic sporophytes) microscopic life-stages, and a diploid (adult sporophytes) macroscopic stage. While a growing list of studies have examined the ecology and physiology of these microscopic stages, our understanding of the geographic distribution of most kelp species comes primarily from studies on the adult macroscopic life stages. Therefore, to fully understand how their range limits are regulated, evaluation of how both the micro- and macroscopic life stages respond to latitudinal variation in ocean climate is necessary.

There is a large amount of work that has investigated the effects of abiotic factors on kelp survival, growth, and reproduction (e.g. Dayton 1985). However, given that kelp microscopic and macroscopic life stages may exhibit different physiological requirements (based on size, growth rates, and surface/volume ratios), it is important to investigate the effects of variability in temperature and nutrient conditions separately for each life-stage. Previous work has shown microscopic stages of some kelp species to be more tolerant of unfavorable abiotic conditions than macroscopic stages (reviewed by Carney and Edwards 2006). The effects of high temperature on the production of embryonic sporophytes are important in explaining biogeographical patterns (Dieck 1993) and responses to environmental variation (Ladah et al. 1999; Hernández-Carmona et al. 2001; Kinlan et al. 2003). If embryonic sporophyte production is limited, then adult recruitment will be reduced or perhaps absent altogether resulting in unstable population demography.

In addition to the effects on microscopic stages, high temperature and low nitrate availability have been shown to negatively affect survival and growth of adult kelps (Gerard 1982; Dean and Jacobsen 1984; Dayton et al. 1999; Hernández-Carmona et al. 2001), although the degree to which this occurs may vary among geographically separated populations due to local adaptation (Kopczak et al. 1991). However, some kelp species are capable of maintaining internal nitrogen reserves that sustain growth during periods of low nitrate availability (Chapman and Craige 1977; Sjøtun and Gunnarsson 1995) ranging from 2 weeks in *Macrocystis pyrifera* (Gerard 1982) to almost 7 months in arctic species such as *Laminaria solidungula* (Henley and Dunton 1997). It has been suggested that the storage ability of some temperate species make them more resistant to oceanographic disturbances such as El Niño Southern Oscillation (ENSO) events (Dayton et al. 1999) and may also facilitate extending the geographic distribution of some kelp into warmer, more nutrient-depleted waters (e.g. southern Baja California Sur, Mexico). However, this storage ability is only known for adult stages and, given that kelp propagule dispersal is generally limited to a few meters to kilometers (Reed 1988; Reed et al. 2004), it may be necessary for adults to be locally present in order to ensure successive generations (but see Carney and Edwards 2006 for a review regarding kelp 'seed banks').

Along the west coast of North America, the stipitate kelps *Pterygophora californica* and *Eisenia arborea* share similar geographic distributions, extending from Vancouver Island, British Columbia, Canada, to Baja California, Mexico (Abbott and Hollenberg 1976). However, while *P. californica* is the dominant understory kelp throughout most of this range (i.e. from Vancouver Island to Bahía Rosario, Baja California, Mexico), *E. arborea* extends farther to the south to Bahía Magdalena, Baja California Sur, Mexico (Fig. 1) where it dominates the understory and forms thick canopies capable of excluding *M. pyrifera* south of Bahía Rosario (Edwards and Hernández-Carmona 2005). In the southern California Bight, where *P. californica* and *E. arborea* occur in both monospecific and mixed stands, the adults often experience periods of high temperatures and low nutrients that can negatively affect their growth and survival (Dayton et al. 1992, 1999).

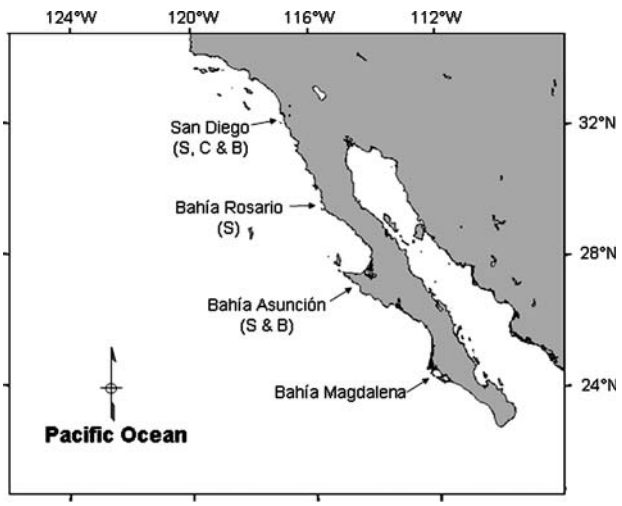


**Fig. 1** Map of west coast of southern California, USA and Baja California, Mexico, showing three locations where temperature data was collected: San Diego, CA, USA, Bahía Rosario; Baja California, Mexico; and Bahía Asunción, Baja California Sur, Mexico. Southern limit of *P. californica* is found at Bahía Rosario (Abbott and Hollenberg 1976), while southern limit of *E. arborea* is at Bahía Magdalena, Baja California Sur, Mexico. Temperature data is indicated below location name (*S* surface temperature collected by satellite; *C* surface temperature collected in situ; *B* bottom temperature collected in situ)

Both species are seasonal reproducers; spore development and release generally occurs from September through February with *E. arborea* releasing spores 1–2 months prior to *P. californica* (Abbott and Hollenberg 1976; Reed 1990; P. Matson unpublished data). As a result, this is also the period when recently settled microscopic stages inhabit the substrate. By comparing two closely related species with overlapping distributions, it may be possible to identify particular traits that may be responsible for regulating their distributional limits (Hoffmann and Blows 1994). Therefore, the purpose of this study is to identify whether environmental factors, namely temperature and nutrient availability, are responsible for maintaining the southern limit of *P. californica*, but not *E. arborea*, in northern Baja California, Mexico, by either: (a) reducing tissue nitrogen uptake and storage ability of the adult stages during periods of elevated temperature, and/or (b) inhibiting the survival and development of the microscopic stages, and thus production of embryonic sporophytes.

## Materials and methods

### Field observations

Sea surface temperatures were monitored at San Diego, CA, USA, Bahía Rosario, Baja California, Mexico, and Bahía Asunción, Baja California Sur, Mexico, while bottom temperatures were monitored at San Diego and Bahía Asunción during 2004 and 2005 (Fig. 1). These locations represent areas to both the north and south of *P. californica*'s (Ruprecht) southern limit at Bahía Rosario. To the south, *E. arborea* (Areschoug) occurs alone while to the north both species co-occur. Satellite-derived sea surface temperatures for Baja California and Baja California Sur, Mexico were provided by Mexico's Centro de Investigaciones Biologicas del Noroeste (CIBNOR) in La Paz, Baja California Sur, Mexico, analyzed as monthly means, and for southern California, USA from the Southern California Coastal Oceans Observing System's (http://www.sccoos.org/data/) sensor at Scripps Institution of Oceanography (SIO) Pier. Ocean bottom temperatures were determined using Stowaway Optical thermographs (Onset Computer Co.), provided for Bahía Asunción, Baja California Sur, Mexico by our own thermographs and for San Diego, CA, USA courtesy of P. Dayton at SIO. The combination of surface and bottom temperatures allowed for the examination of temporal variation of temperature within the water column and provided a surrogate for ambient nitrate levels (Jackson 1977; Zimmerman and Kremer 1984; Edwards and Estes 2006). Periods of low nitrate availability were determined by identifying periods when bottom temperatures exceeded 15°C for several days. While previous studies (Dayton et al. 1992, 1999) identified 16°C as the point at which ambient nitrate fell below 1 $\mu g\ ml^{-1}$, which is considered to be the minimum level to maintain growth (Jackson 1977), there was a paucity of days during this study in which bottom temperatures exceeded this temperature; therefore, a more conservative value of 15°C was used.

### Temporal variation in temperature and tissue nitrogen

To examine temporal variation in tissue nitrogen within *P. californica* and *E. arborea*, adult sporophytes (i.e. *P. californica* possessing four or more sporophylls and *E. arborea* possessing a bifurcated stipe) were collected semi-weekly from the Point Loma kelp forest, San Diego, CA, USA. Thirty-seven collections were made between 30 September 2004 and 27 September 2005 with a minimum period between each collection of 7 days and a maximum of 21 days. Longer periods between sampling resulted from inaccessibility to dive sites due to severe weather events. On each date, five whole individuals of each species were collected using SCUBA at 8–10 m depths in areas where they co-occur. All samples were immediately transported to the laboratory in a dark cooler where tissue samples were taken from both stipes and blades using a razor blade. All blade samples were taken from near the base of non-reproductive blades to avoid any bias during reproductive seasons. In the case of *P. californica*, this meant limiting sampling to the apical vegetative blade. Tissue samples were desiccated on silica gel (Activa Products Inc.) for a period of no less than 2 weeks. Samples were then removed from the silica gel, brushed to remove any remaining silica, and ground in a Wiley Mill plant grinder. Ground samples were analyzed for nitrogen and carbon content using a NCS 2500 elemental analyzer (Carlo Erba Instruments). Results from nitrogen and carbon analysis were reported as a percentage per dry weight of each sample.

Statistical analyses were performed using SYSTAT 10 (SPSS Inc.). Coefficients of variation were calculated for each species and tissue type in order to compare relative variability in tissue nitrogen content through time. Correlation analysis was used to identify possible relationships between tissue nitrogen concentrations in stipes versus blades within each species separately. Ocean temperature data was analyzed graphically to identify patterns between surface and bottom temperatures and linear regressions were used

to examine whether ocean temperature and duration of elevated temperature (above 15°C) correlated with temporal variation in tissue nitrogen levels for each species. To identify potential relationships with temperature, tissue nitrogen data were regressed against bottom temperature and reanalyzed multiple times using time lagged bottom temperatures for daily increments up to 29 days prior to collection. The resulting coefficients of determination ($r^2$) were then plotted as a function of time and analyzed graphically to determine which periods of time provided the best model fit. These analyses were run separately for each species and tissue type. Homoscedasity was examined with Cochran's test and normality by graphical interpretation of residuals (Underwood 1997).

### Embryonic sporophyte production

To examine the effects of elevated temperature and reduced nitrate availability on embryonic sporophyte production, fertile reproductive blades from adult *E. arborea* and *P. californica* were collected from 8 to 12 m depths using SCUBA within the Point Loma kelp forest. Blades of *E. arborea* and *P. californica* containing sori were collected on 13 October 2005 and 15 November 2005, respectively. These blades were placed in a dark cooler and transported back to the laboratory where they were cleaned with damp paper towels to remove epiphytic organisms and then desiccated in the dark at 15°C for 1 h. Following this, the blades were hydrostatically shocked to induce spore release by placing them in filtered seawater (Reed 1990). Spore densities were estimated using a hemocytometer and adjusted to approximately $1 \times 10^5$ spores $ml^{-1}$ by adding the appropriate amount of filtered seawater to the solution. For each species, one ml of this solution was then added to each of 30 plastic culture dishes (Falcon 100 mm × 15 mm, Fisher Scientific Co.) containing 20 ml of filtered seawater enriched with one of three levels of nutrients. The three levels of nutrient enrichment (high, medium, low) were made by diluting a stock solution of 25 ml of prepared culture media (Alga-gro®, Carolina Biological Co.) in one liter of filtered seawater. Dilutions from this stock solution of 1/3.2, 1/32, and 1/320 resulted in estimated concentrations of 20, 2, and 0.2 μmol $NO_3^-$ $l^{-1}$ (high, medium, low, respectively). Dishes were randomly assigned to one of two culture chambers (Percival Environmental Chambers Model E-36L) maintained at 12 and 18°C, which represent temperatures commonly seen along the coast of California and Baja California. For each species, five replicate dishes were randomly assigned to orthogonal combinations of temperature (two levels) and nutrient concentration (three levels). Light intensity within the incubators was initially set at approximately 40–60 μmol photons $m^{-2}$ $s^{-1}$ during a 12 h light:12 h dark cycle for the initial 6 weeks, and then increased to 80–100 μmol photons $m^{-2}$ $s^{-1}$ for the remaining 4 weeks. Nutrient solutions in the culture dishes were changed weekly during the 10-week experiment.

This study was composed of two separate 10-week trials: *E. arborea* was cultured from 13 October 2005 to 22 December 2005 and *P. californica* was cultured from 15 November 2005 to 24 January 2006. The sampling of *E. arborea* took place weekly for the entire 10-week period, while *P. californica* was sampled weekly for the first 6 weeks and again during week 10. During each sampling period, each dish was sampled nondestructively using an inverted microscope at 40× magnification with a light intensity of less than 50 μmol photons $m^{-2}$ $s^{-1}$ to avoid subjecting the gametophytes to light stress (levels greater than that in culture chambers), which could potentially damage the gametophytes and bias later sampling efforts. Embryonic sporophyte production was determined by counting the number of sporophytes per field of view (FOV = 10.18 $mm^2$) at five randomly selected locations in each dish and calculating the mean density per dish. In order to detect differences in sporophyte production due to temperature, separate two-sample *t*-test were used to compare sporophyte densities after weeks 6 and 10 for each species. Data for *E. arborea* were heteroscedastic and square-root transformed in order to meet the assumptions of the analysis (Underwood 1997). Nutrient level was removed from the analyses because no sporophytes were seen at any time in either medium or low-level treatments (see "Results" section).

## Results

### Field observations

Sea surface temperature along the California and Baja California coastline showed strong seasonal variation and consistently higher sea surface temperatures at lower latitudes (Fig. 2a). Interestingly, the maximum temperatures observed at Bahía Rosario and San Diego, locations where *P. californica* and *E. arborea* both occur, were similar but approximately 4–6°C colder than those observed at Bahía Asunción where only *E. arborea* occurs. Further, bottom temperatures at San Diego during the winter (late November–February) when spores are released and settlement occurs) were

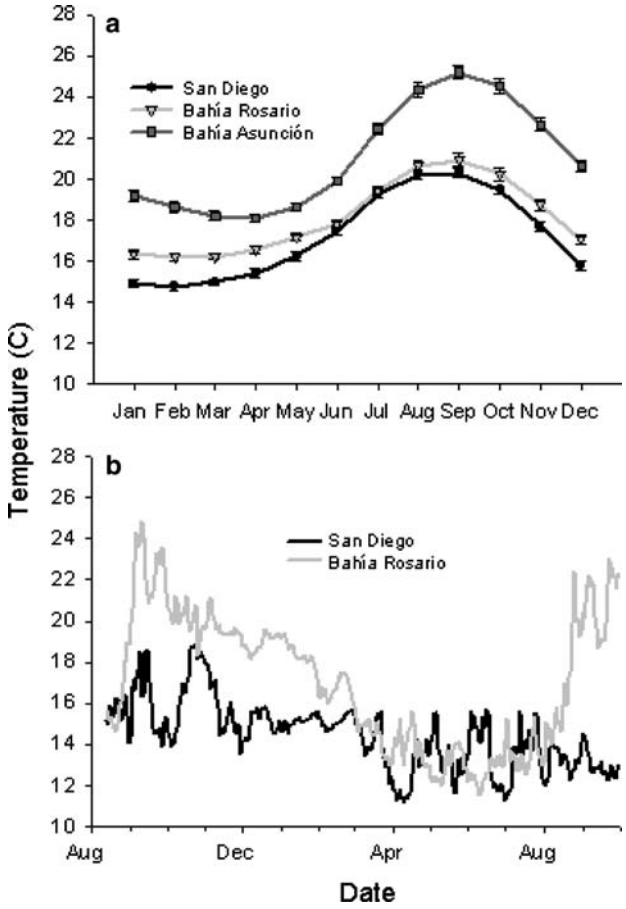


**Fig. 2** **a** Average monthly satellite-derived sea surface temperatures (means ± SE) from 1982 to 2001. **b** In situ bottom temperatures at San Diego, CA, USA and Bahía Asunción, Baja California Sur, Mexico from 13 August 2004 to 1 October 2005. Note change of time scale in two panels

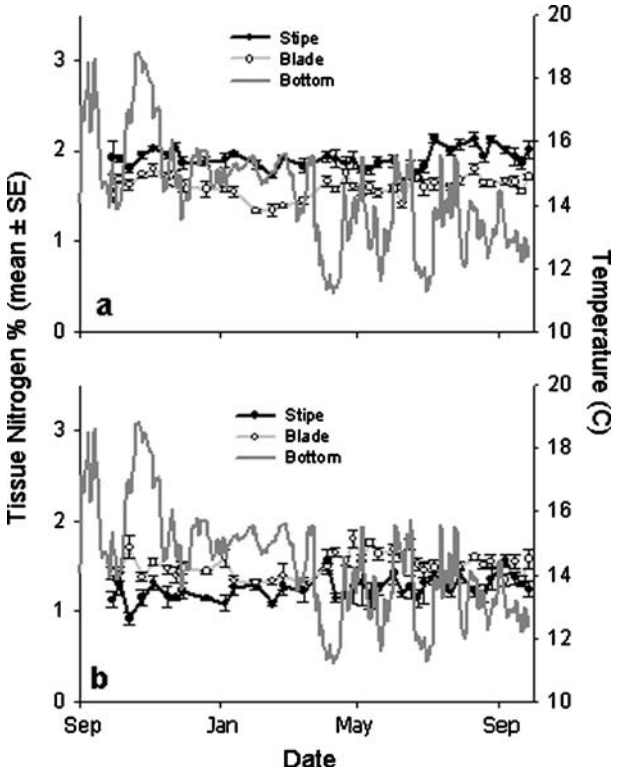


**Fig. 3** Tissue nitrogen percent (mean ± SE) of: **a** *P. californica* and **b** *E. arborea* from 30 September 2004 through 27 September 2005. In situ bottom temperatures (°C) from San Diego, CA, presented for same time period

below 18°C, while bottom temperatures during this period exceeded 18°C at Bahía Asunción (Fig. 2b). These results indicate that *E. arborea* and *P. californica* experience variability in temperature across their latitudinal ranges and differences in bottom temperature are greatest during the period when microscopic stages of *P. californica* would occupy the substrate.

## Temporal variation in temperature and tissue nitrogen

Changes in tissue nitrogen concentrations revealed no distinct temporal patterns regarding nitrogen accumulation and/or storage for either *P. californica* or *E. arborea*; tissue nitrogen was variable but with no discernable patterns (Fig. 3a, b). While both blade and stipe nitrogen fluctuated during the study in both species, *E. arborea* maintained higher nitrogen levels within blade tissue while *P. californica* maintained higher levels within stipe tissue (Fig. 3a, b). Analysis of the coefficient of variation for blades and stipes of each species revealed that relative variability in tissue nitrogen was greater in *E. arborea* (0.198 and 0.124) than *P. californica* (0.091 and 0.097). In addition, there was a significant positive correlation between blade and stipe tissue nitrogen in *P. californica* (Pearson correlation $r = 0.312$, $p \leq 0.001$), but no trend was found in *E. arborea* (Pearson correlation $r = -0.051$, $p \leq 0.491$) (Fig. 4). This suggests that tissue nitrogen within the stipes and blades in *P. californica* fluctuate synchronously, while the stipes and blades in *E. arborea* vary independently of each other.

Time-lagged regression analyses were used to identify whether bottom temperature correlated with fluctuations in tissue nitrogen in *P. californica* and *E. arborea*. While no strong relationships were seen for either species, some weak negative relationships were observed (Fig. 5). No relationship between tissue nitrogen and ocean temperature was observed in *P. californica* for either tissue type. Relationships were highly variable in *E. arborea* stipes and blades but no clear pattern was discernable. Regression analyses were again used to identify relationships between tissue nitrogen levels and duration of elevated temperatures as a proxy for limited nutrient availability in *P. californica* and *E. arborea*. Significant negative

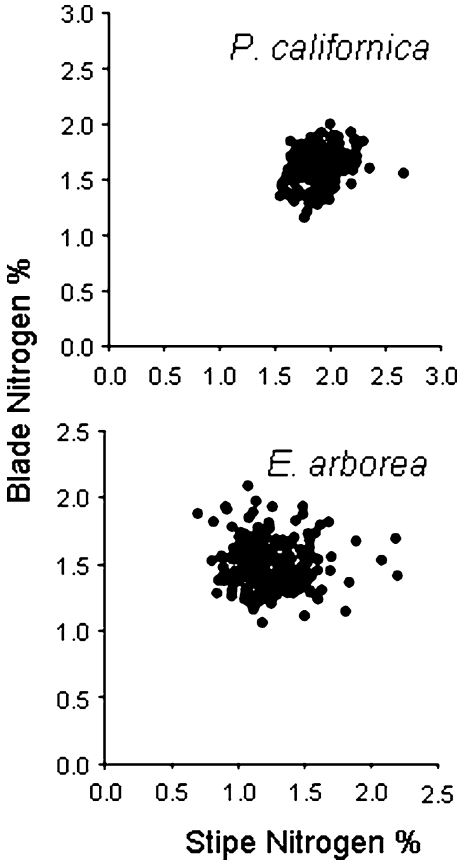


**Fig. 4** Correlations between mean stipe and blade tissue nitrogen percent for *P. californica* and *E. arborea* during each collection

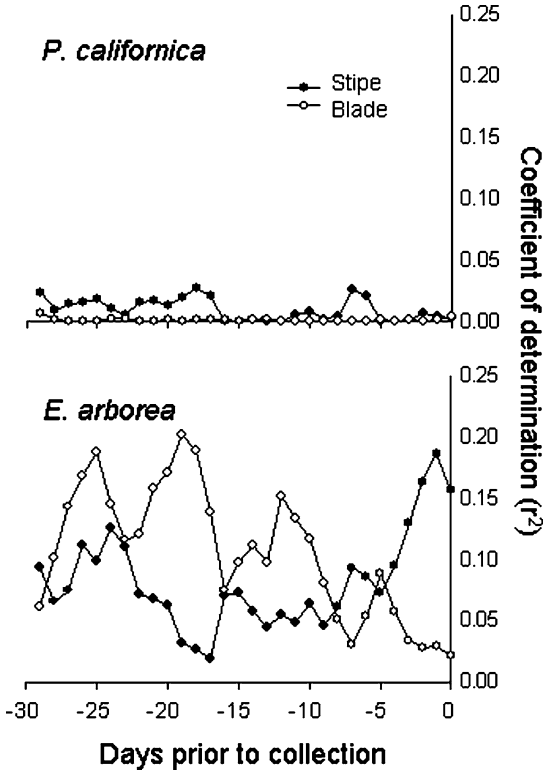


**Fig. 5** Relationships between tissue nitrogen percent and temperature expressed by coefficient of determination ($r^2$) for each day prior to collection

relationships between tissue nitrogen levels and ocean temperature were found in *E. arborea* (stipes, $p \leq 0.024$, $r^2 = 0.137$; blades, $p \leq 0.004$, $r^2 = 0.211$), but not in *P. californica* (stipes, $p \leq 0.970$; blades, $p \leq 0.332$).

## Embryonic sporophyte production

*E. arborea* embryonic sporophyte production was first observed in the high nutrient treatment during week four at both 12 and 18°C, while *P. californica* embryonic sporophyte production was first observed in the high nutrient treatment in week 2 but only in the 12°C treatments (Fig. 6). No *P. californica* sporophytes were observed at 18°C at any time during this experiment. Also, no sporophytes of either species were observed in the low or medium nutrient treatments during the experiment (data not shown). After 6 weeks, *E. arborea* exhibited a mean density of 0.024 ± 0.024 (±SE) sporophytes mm$^{-2}$ at 12°C and 0.102 ± 0.046 sporophytes mm$^{-2}$ at 18°C (Fig. 6); densities were not significantly different between the temperature treatments (*t*-test; $p \leq 0.166$). At this time, *P. californica*

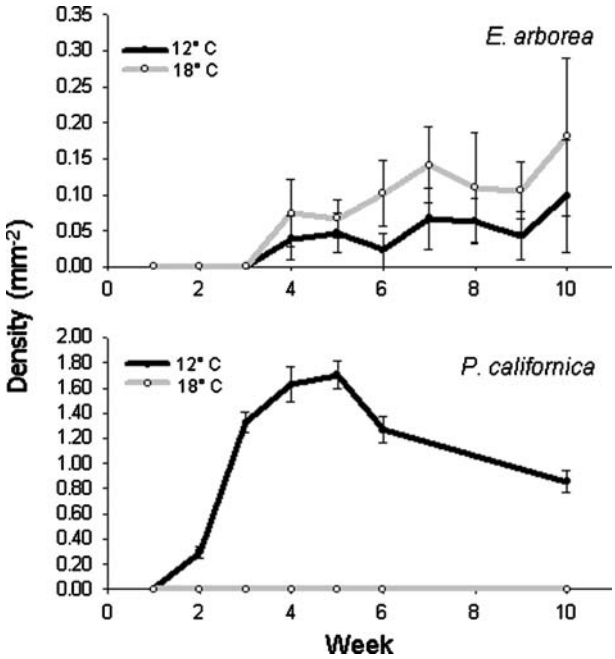


**Fig. 6** Embryonic sporophyte densities (mean ± SE) for *E. arborea* (*upper*) and *P. californica* (*lower*) during the 10-week period. *P. californica* not sampled in weeks 7, 8, and 9. Data from high nutrient treatments only. Note change of scale in two panels

exhibited a mean density of $1.265 \pm 0.11$ sporophytes $mm^{-2}$ at 12°, while no sporophytes were produced at 18°C (Fig. 6). Following this, irradiance was increased in all treatments for four additional weeks. At the end of 10 weeks, *E. arborea* sporophytes had increased to $0.098 \pm 0.079$ sporophytes $mm^{-2}$ and $0.181 \pm 0.11$ sporophytes $mm^{-2}$ at 12 and 18°C, respectively (Fig. 6), but differences between the temperature treatments remained non-significant (*t*-test; $p \leq 0.557$). Similar to week six, *P. californica* embryonic sporophyte density remained high at 12° ($0.857 \pm 0.085$) sporophytes $mm^{-2}$, but still had not appeared in the 18°C treatment (Fig. 6).

## Discussion

The influence of climate on species geographic distributions is well known for both marine and terrestrial ecosystems (e.g. Brown et al. 1996; Parmesan 1996), and there is increasing support for the importance of oceanographic currents in limiting distributions of marine species by acting as dispersal barriers (Gaylord and Gaines 2000; Zacherl et al. 2003). Due to the many environmental factors that can potentially affect organisms, it can be difficult to distinguish those which are most influential for the observed patterns of distribution. In this study, we compared two kelps with overlapping distributions, *P. californica* and *E. arborea*, in order to determine if temperature and nutrient availability contribute to maintaining the southern limit of *P. californica*, and if so, whether they act differentially on microscopic and macroscopic life-stages.

Along the coast of California, USA and the Pacific coast of the Baja California Peninsula, ocean temperatures generally tend to increase with decreasing latitude. Across this range, *P. californica* tends to be the dominant understory kelp in regions with cooler temperatures but absent in warmer southern waters. On the other hand, *E. arborea* tend to dominate in the warmer southern regions, but become much less common in the cooler northern waters (Abbott and Hollenberg 1976; P. Matson unpublished data; but see Spalding et al. 2003 for observations of deepwater (>30 m depths) populations of *E. arborea* in central California). In addition, regional temperature differences between surface and bottom waters fluctuate seasonally depending on the magnitude of upwelling and mixing of the water column, resulting in these species experiencing thermal and nutrient environments that are highly variable through time and with depth. This variability was found to have a strong effect on sexual reproduction in *P. californica*'s microscopic stages but not on *E. arborea*. The failure of *P. californica* to produce embryonic sporophytes at 18°C may preclude it from establishing stable populations in southern Baja California. During *P. californica*'s reproductive season (late November–February; Reed 1990), bottom temperatures of 12°C in southern California and northern Baja California are common, while temperatures of 18°C are rare. However, bottom temperatures of 18°C are common during this same period in southern Baja California. As a result, if *P. californica* were present in southern Baja California, its microscopic stages would most likely experience bottom temperatures that would prevent the production of embryonic sporophytes. This finding is strengthened by the fact that these results occurred at non-limiting nutrient levels, thereby isolating the temperature effect. The greater temperature tolerance of *E. arborea* may allow greater patch persistence during and/or recovery following periods of extreme temperature events, such as observed during El Niño events (Hernández-Carmona et al. 2001; Edwards and Hernández-Carmona 2005).

The adult sporophytes of *P. californica* appear tolerant of variability in temperature and nutrient availability. Bottom temperatures in Point Loma exceeded 18°C several times during this study with the longest duration being approximately two weeks, although no widespread declines in *P. californica* abundance were seen (personal observation), and tissue nitrogen concentrations remained consistently high. As a consequence, *P. californica* tissue nitrogen did not show any significant relationship with the duration of elevated temperatures. Based on these results, it seems likely that the southern distribution of *P. californica* may be limited by elevated temperatures inhibiting the production of its embryonic sporophytes and not the survival of its adult sporophytes. In contrast, *E. arborea* appeared quite capable of producing embryonic sporophytes when exposed to elevated temperature, possibly explaining why its populations extend further south into warmer waters. It is also interesting to note, however, that unlike *P. californica*, on several occasions *E. arborea* adults demonstrated coincident increases in blade tissue nitrogen with decreases in stipe tissue nitrogen. It is possible that these responses may be due to *E. arborea* blades developing sori while *P. californica* possess specialized reproductive blades, which were not sampled during this study. Reed et al. (1996) found C/N ratios in reproductive tissue of *P. californica* to remain relatively constant through time as compared to vegetative tissue. By maintaining more nutrients within reproductive tissue, adult fitness is increased by producing higher quality spores. It is

possible that this may explain why we found higher nitrogen levels within blades of *E. arborea*. However, further study is needed to better understand these patterns and relationships.

The ability of these two species to store nitrogen may also be very important in their resistance to large-scale disturbances such as ENSO events. Several studies have noted the resistance of both *P. californica* and *E. arborea* to ENSO events (Dayton et al. 1992, 1999; Edwards and Hernández-Carmona 2005), which have been shown to have strong negative effects on kelp exposed to extended periods of low nutrient availability followed by increased large wave events (Edwards and Estes 2006). It is possible that this resistance is due to the ability to maintain high levels of nitrogen combined with wave-tolerant morphologies (Gaylord and Denny 1997). Additionally, their close proximity to the substrate (<2 m above) may result in these two species occurring below the thermocline, while species such as *M. pyrifera* that extend throughout the water column may experience more stressful conditions. A related study found *M. pyrifera* to demonstrate stronger negative relationships with both temperature and the duration of elevated temperatures with minimal storage ability as compared to *P. californica* and *E. arborea* (Matson 2006), which supports previous work observing its weak resistance to ENSO events (Gerard 1984; Dayton et al. 1992; Hernández-Carmona et al. 2001; Edwards and Estes 2006). Although not addressed in this study, it is also possible that following the removal of *M. pyrifera* canopies by large disturbance events, the ability to maintain greater tissue nitrogen reserves may allow adult stages of understory kelps to rapidly respond with increased growth once benthic light levels are no longer limited (Watanabe et al. 1992), as observed for *P. californica* by both Reed and Foster (1984) and Dayton et al. (1992), and for *E. arborea* by Edwards and Hernández-Carmona (2005).

While local ecotypic adaptation has been shown in several genera of kelp (for *M. pyrifera*, Kopzack et al. 1991; *Laminaria saccharina*, Gerard 1990; *E. arborea*, Roberson and Coyer 2004), its role in microscopic stages is unclear (Bolton and Luning 1982; Gerard 1990). While our results showed that nutrient storage in adult *P. californica* in San Diego, CA is not strongly affected by ocean temperature, it is possible that nutrient-stress may be greater near its southern limit, thereby reducing its ability to tolerate further reductions in nitrate availability that occur during ocean warming. This is similar to observations of *M. pyrifera* populations at its southern limit near Bahía Asuncion, Baja California Sur, Mexico, following the 1997/1998 El Niño event (Edwards and Hernández-Carmona 2005). Conversely, while *E. arborea* can tolerate conditions across its northern distribution as shown in this study, it may be subject to increased stress levels in San Diego, CA as opposed to populations in Baja California Sur, Mexico, where it tends to be found at much greater densities (P. Matson unpublished data). It is possible that tissue nitrogen storage by *P. californica* at its southern limit may respond differently than those in San Diego, CA. However, due to logistical constraints, this has yet to be explored. The use of new genomic-based techniques such as expression of heat shock proteins (Hsps) may provide insight into relationships between abiotic stress and distributional boundaries (Hofmann et al. 2005), but more work is needed in this area.

This study further shows the importance of a multiple life-stage perspective in understanding the mechanisms regulating species distributions. By examining the effects of abiotic factors on multiple life-stages, we can begin to clarify the complex interactions of environmental variability on the distribution of species. This is increasingly important in light of changing global climate and the potential effects it may have on natural communities. Information from this type of research can be used to predict how these distributions may change in the future and be applied towards predicting potential range expansions of both threatened and fishery-targeted species as well as invasive species. Additionally, this type of work is important to understand how climate may affect whole ecosystems by focusing on foundation species, such as kelp, which can create essential habitats for many dependent species (Foster and Schiel 1985).

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