

Biogeographic variation in temperature drives performance of kelp gametophytes during warming

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ABSTRACT: The capacity for thermal adjustment or adaptation is critical to population persistence in a warming ocean. Understanding such performance across a species' range can give insights into the extent of possible adjustment as well as spatial variation in vulnerability. This study tested the effects of temperature on the density and size of gametophytes of the habitat-forming kelp *Ecklonia radiata*, across its Australian distribution (between ~9° and ~33°S). Gametophytes from warm, intermediate and cool biogeographic regions were cultured over a temperature gradient from 12 to 26°C, revealing optimum temperatures of ~18 to 23°C—well above current maximum temperatures in parts of the range—and a positive relationship between *in situ* temperature and thermal optima for performance. Optimum temperatures in warmer regions were more than 1°C higher than in cooler regions. Biogeographically, the thermal optima for gametophytes were more strongly linked to long-term temperature characteristics of a region (annual extremes, 3 yr range) than short-term variation (mean for the month prior) in sea temperature. These results document that present-day populations of *E. radiata* have adjusted their gametophyte thermal sensitivity according to their local environment, and further indicate that these differences are adaptive rather than phenotypic. Collectively, these findings suggest that the scope for thermal adaptation and gametophyte performance of *E. radiata* across most of its Australian distribution is within projected levels of future warming.

KEY WORDS: Adaptation · Ecotype · Growth · Ocean warming · Survival · Thermal optima

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INTRODUCTION

Species with broad geographical distributions, extending across multiple latitudes, commonly span large temperature gradients. In order to survive and optimise performance across their range, these species must adjust their physiology to local conditions and temperature regimes (Sunday et al. 2012). Therefore, thermal optima and latitudinal range of organisms are often directly linked (Somero 2005,

Oppliger et al. 2012, Sunday et al. 2012, Smale & Wernberg 2013). Thus, biogeographic-scale comparisons of temperature responses enable tests of adaptation beyond experimental observations (Brown et al. 1996, Ladah & Zertuche-González 2007, Sorte et al. 2011) and can inform on the capability of species to adjust their physiology to changing environmental conditions (Brown et al. 1996, Somero 2005). Any increase in temperature resulting from global climate change is likely to threaten marginal populations,

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that exist at the distributional limits of a species (Somero 2005, Harley et al. 2006, Wernberg et al. 2013). In most cases, the geographic distributions of species are expected to shift poleward, following rising temperatures (Walther et al. 2002). Organisms that cannot shift to a more suitable climate are physiologically susceptible to the effects of increased temperature, such as increased metabolic rates, cellular damage, limited nutrient uptake, photosynthetic inhibition, respiratory distress, reduced growth and productivity, delayed development, and eventually mortality (Davison & Pearson 1996, Harley et al. 2012).

Susceptibility to temperature stress is dependent on the life-history of the individual (Schiel & Foster 2006, Matson & Edwards 2007) and juvenile phases are often more sensitive than adults (Kordas et al. 2011). In intertidal and subtidal marine systems, the life cycle of many species has a planktonic phase, which is particularly susceptible to thermal stress; thus recruitment can be limited by temperature (Lotze & Worm 2002, Gilman 2006, Harley et al. 2006, Andrews et al. 2014). For example, comparisons of warm and cool climate marine invertebrate populations in both intertidal and shallow subtidal systems revealed differences in densities and a reduction in recruitment over an increasing thermal gradient (Somero 2005, Gilman 2006, Wernberg et al. 2010, Sorte et al. 2011).

Kelps (Order Laminariales) are important foundation species in marine ecosystems and many have broad geographic distributions (Steneck et al. 2002, Bolton 2010). Algae within the order Laminariales have a biphasic, heteromorphic life cycle where the adult, macroscopic sporophyte is diploid and the microscopic gametophytes are haploid (Lüning 1990). There are published observations of variation in thermal tolerances and survival limits of juvenile Laminariales depending on population location; for example, warm water species from Japan are able to tolerate considerably higher temperatures than other species from Arctic regions (tom Dieck 1993). Comparisons of populations *Lessonia nigrescens* and *Ecklonia cava* from different points along their distribution revealed that warmer-water inhabitants exhibited greater growth and survival and higher photosynthesis rates at higher temperatures, compared to their cool-water counterparts (Serisawa et al. 2001, Oppliger et al. 2012). Kelp populations under thermal pressure, such as those at the extremes of distribution, exhibit reduced physiological performance, and limited reproduction and recruit survival and growth, resulting in poor popula-

tion maintenance and reduced persistence (tom Dieck 1993, Matson & Edwards 2007, Wernberg et al. 2010, Eggert 2012).

The main habitat-forming macroalga in Australia is the kelp *Ecklonia radiata* (Wernberg et al. 2003b, Connell & Irving 2008), which is common in temperate waters around the entire continent. *E. radiata* beds support fish, invertebrate, and benthic communities (Goodsell et al. 2004, Irving et al. 2004, Wernberg et al. 2006, Vanderklift et al. 2009) many of which are commercially and recreationally important. Despite its ecological significance in Australasia, surprisingly little is known about the effects of temperature on this species, and how this might vary across its wide distribution. Knowledge of the impacts of increasing temperature on the microscopic stages of the life cycle of *E. radiata* is particularly deficient (Mabin et al. 2013). Therefore, we tested the effect of temperature on the performance of the early life cycle stages of *E. radiata* across the majority of its latitudinal distribution in Australia. By examining the effects of temperature on gametophytes from populations in warm, intermediate and cool climates, this study aimed to assess the variability in thermal optima across the distribution of *E. radiata* and the capacity for thermal adjustment or adaptation of this critical life-cycle stage in this ecologically important species. We hypothesised that populations from different climatic zones would have different thermal optima and that there would be a positive relationship between recent climatic conditions and optimum temperature for gametophyte performance.

METHODS

Sample collection

Kelp (*Ecklonia radiata*) were collected from 3 regions (>1500 km apart) spanning 2 biogeographic provinces (Heap et al. 2005, Waters et al. 2010) across the latitudinal and longitudinal extent of temperate Australia: Western Australia (WA; 34° 16'–38° 15' S, 115° 00'–118° 13' E), South Australia (SA; 35° 17'–35° 35' S, 137° 02'–138° 39' E) and Tasmania (TAS; 41° 51'–43° 29' S, 146° 58'–148° 19' E). These regions represent populations in the centre (SA), and at the northern (WA) and southern (TAS) limits of the species' latitudinal range (Fig. 1). In each region, 5 macroscopic kelp thalli were collected from each of 3 sites (1 to 5 km apart) within each of 3 locations (70 to 250 km apart). All sites were within a depth range of

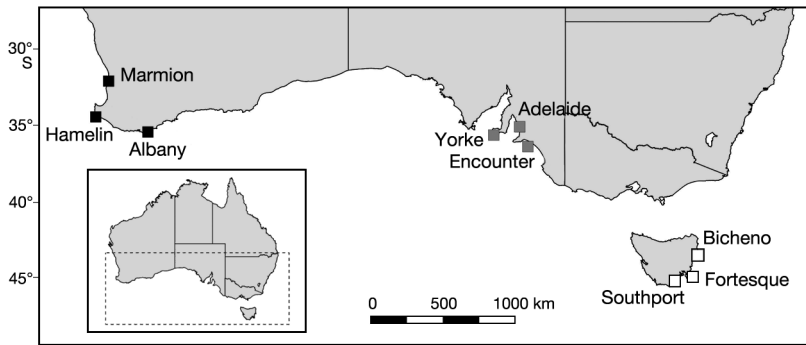


Fig. 1. *Ecklonia radiata*. Location of the 9 sampling sites in 3 study regions: Western Australia (black symbols), South Australia (grey symbols) and Tasmania (white symbols)

8 to 10 m. Kelps were collected on SCUBA by cutting the stipe just above the holdfast. Thalli were stored in a damp, labelled calico bag that was wrapped in plastic and kept on ice until processing (~24 h). The 15 thalli from each location were combined into one zoospore source resulting in 3 sets of data from each region. Collections and experiments were carried out in the Austral autumn in May 2011 (WA and TAS) and April 2012 (SA).

After 24 h, a total 150 to 200 g fresh weight of tissue containing visible sori was trimmed from the 15 combined thalli. For each of the 9 locations, a large plastic container was lined with 56 labelled glass microscope slides (76 × 25 mm, thickness 1.2 mm), and filled with 5 l of fresh seawater. After desiccating the sporogenic tissue at ambient temperature for 1 h, the tissue was submerged in the container and gently agitated over the following hour in order to promote zoospore release. Slides were left undisturbed for 18 h to allow settlement before being randomly allocated to their respective temperature treatments. Gametophytes were cultured for a total of 6 d, after which measurements were made, as this culture period is sufficient to determine significant differences in density among temperatures (Mohring et al. 2013a)

Laboratory experiment

Eighteen small aquaria (volume ~15 l) were set up in controlled environment rooms, and filled with seawater, and a 250 W Jager heater was used to heat each tank individually. Aquarium temperatures ranged from 12 to 26°C, with at least one treatment every 2°C. Temperature was measured every day using a digital thermometer, and the final treatment temperature was an average of the 6 d of culture

(temperature deviation was <0.5°C over 6 d). Light levels in the controlled environment rooms varied between 5 and 15 $\mu\text{E m}^{-2} \text{s}^{-1}$, corresponding to levels commonly encountered at the reef surface in Australasian kelp beds (Novaczek 1984a, Wernberg et al. 2005, Russell 2007). Replicates from all locations were randomly allocated so that all collection locations received similar light treatment overall.

Two small plastic containers (volume 650 ml each), filled with Provasoli Enriched Seawater (PES), were floated on the surface of each aquarium and aerated. PES was used so that thermal performance could be measured under non-limiting conditions, removing any potential influence of differences in nutrient concentrations of locally collected seawater. The enriched seawater was replaced after 3 d of growth, that is, halfway through the experiment. One microscope slide from each location was randomly allocated to each plastic container (i.e. 2 slides per treatment). The remaining slides ($n = 20$) were used as the initial (Day 1) sample prior to treatment. After 6 d, slides were examined under a compound microscope and 6 random photographs (0.17 × 0.13 mm) were taken from each slide, using an eyepiece camera. The number of gametophytes was counted in each photo and was averaged to give one density value (gametophytes mm^{-2}) for each replicate/slide. The size (area) of 6 randomly selected gametophytes from each temperature treatment were measured using the ImageJ photo analysis program (Rasband 2009). In the discussion, effects on survival and growth were inferred from density and size results at 6 d, assuming the starting point for all treatments was the same. The optimum temperature for density and size was determined as the mean temperature of treatments yielding the upper tenth percentile of gametophyte densities and sizes. This method is similar to quantile regression but does not require categorical data, and is particularly sensitive to detecting departures from mean conditions (Griffiths & Willcox 1978, Chen 2012).

In situ temperatures were determined from sea surface temperatures (SST) measured for each location for the month prior to experimentation, as well as the maximum and minimum temperatures during the year prior to sampling (Fig. 2a). The mean difference between the summer maximum and winter minimum temperatures for the 3 years preceding the sample period was also calculated. These time periods for

integrating temperature measurements were selected to represent a range of time periods over which kelp populations might be affected by local temperatures. SST has been shown to be a good broad proxy for local thermal conditions at 8 to 10 m depth (Smale & Wernberg 2009), although peak and absolute temperatures might be under and overestimated, respectively. Temperature data were retrieved from daily SST maps delivered by NOAA and accessed through the Commonwealth Scientific & Industrial Research Organisation (CSIRO; www.marine.csiro.au/remotesensing/oceancurrents/sst_s/). A single pixel (representing $\sim 20 \times 20$ km) was selected for each location every day for which temperature data were required and RGB values were converted to SSTs (Smale & Wernberg 2009). To assess whether thermal optima were related to local patterns of nutrient concentrations and phytoplankton biomass, the temperature responses were also compared to *in situ* chlorophyll concentrations sourced from NASA Earth observations (<http://neo.sci.gsfc.nasa.gov/Search.html>). Chlorophyll data were collected from 8 d composite satellite images, processed using the NASA Earth Observations online software, and values were obtained that represented an average concentration for the month prior to sampling, and the maximum and minimum concentrations (Fig. 2b).

Statistical analyses

Initial (Day 1) densities and sizes of newly settled gametophytes were compared using a 2-factor nested ANOVA to test for differences among regions (fixed factor) and locations (random factor nested within region). Potential effects of differences among regions in initial zoospore settlement densities on the experimental outcome were also tested. This was achieved by averaging the density and size of gametophytes at each location after 6 d into 3 temperature increments; <18 , 18 to 22, and $>22^\circ\text{C}$. Regressions were then used to compare the initial densities at each location to the

size and density of gametophytes in each of the 3 temperature categories. No density-dependent effects were detected (effect on density: $r^2 < 0.052$, $p > 0.05$; effect on size: $r^2 < 0.032$, $p > 0.05$).

Gametophyte density and size after 6 d of culture was compared between regions and locations, using a General Linear Model Analysis of Covariance, with temperature as a covariate. The optimum temperature for density and size was regressed against the mean SST for the month prior to sampling, mean 3 yr range in SST, and the maximum summer and minimum winter SSTs. Prior to analysis, homogeneity of variances were tested using Cochran's test, which suggested no transformations were required. All analyses were carried out using the statistical software GMAV5 for Windows (Underwood & Chapman 1998), Sigmaplot (Systat Software 2001) and Minitab (Minitab 2000).

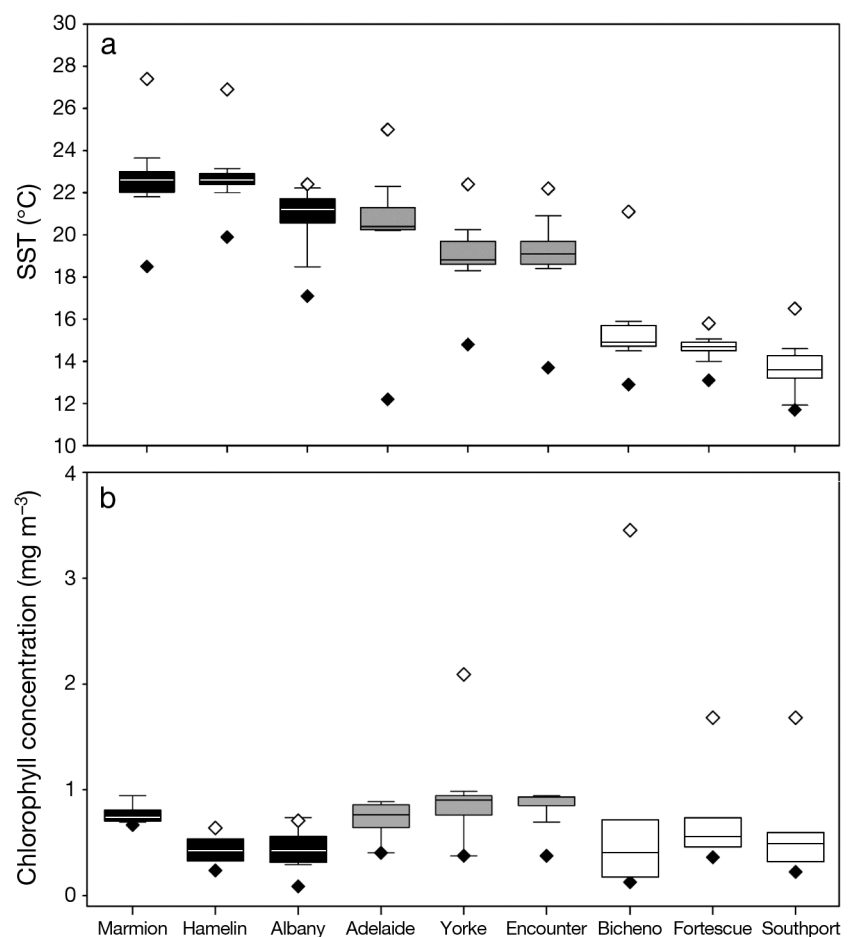


Fig. 2. *Ecklonia radiata*. (a) *In situ* sea surface temperature (SST) and (b) chlorophyll concentrations at each location for the 30 d prior to sampling. Box: median, 25th, and 75th percentiles; whiskers: 10th and 90th percentiles; (◇) maximum summer value; (◆) minimum winter value

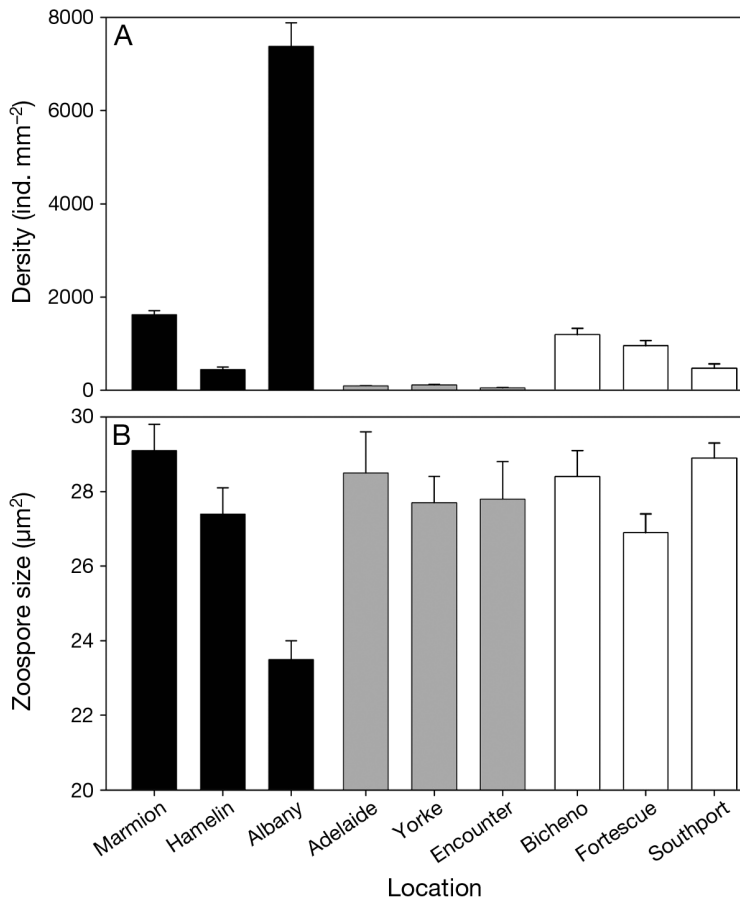


Fig. 3. *Ecklonia radiata*. (A) Density and (B) size (mean + SE, $n = 20$) of zoospores on experimental slides 18 h after zoospore release and immediately prior to initiating the temperature treatments for the 3 locations in each region. Black bars: Western Australia; grey: South Australia; white: Tasmania

RESULTS

Initial settlement densities

The initial densities of gametophytes settling onto the experimental slides differed significantly among regions ($F_{2,177} = 40.07$, $p < 0.001$), with densities from WA 3 to 30 times greater than in TAS and SA (Fig. 3). There were also significant differences among locations within regions ($F_{6,171} = 159.99$, $p < 0.001$). Kelp from Albany released by far the most zoospores, with the average density up to 140 times higher than at other locations, and this is likely to have driven the significant difference in density between WA and the other regions. The initial sizes of the gametophytes also differed among regions, although differences were not significant ($F_{2,177} = 3.01$, $p = 0.052$), and again there were significant differences in initial size among locations within regions ($F_{8,171} = 5.42$, $p <$

0.001 ; Fig. 3). Albany differed significantly from all other locations, with smaller initial sizes than recorded elsewhere.

Gametophyte survival and growth

Gametophyte densities after 6 d of culture were highly variable over the temperature gradient in all 3 regions (Fig. 4). While there was no significant difference in the density of gametophytes among the regions ($F_{(2,321)} = 3.71$, $p < 0.089$), there was a significant difference among locations within regions ($F_{(6,317)} = 10.20$, $p < 0.001$). The Tasmanian locations showed a distinct peak in gametophyte densities between 18 and 21°C, with markedly reduced gametophyte numbers in the lowest and highest temperature treatments. Gametophyte density peaked at Adelaide in SA, but no clear peaks were present at the other 2 locations. In general, increasing temperature had a negative effect on gametophyte numbers ($F_{1,314} = 8.92$, $p = 0.003$; ANCOVA coefficient -1.39). The lowest optimum temperature for gametophyte density was found in Adelaide, where gametophytes performed best at 18.6°C. Gametophytes from WA had higher temperature optima than the other regions, with gametophytes from Hamelin returning the highest densities at 22.3°C. At the lower temperatures gametophyte density from WA was constant but began to decline above 15 °C.

Gametophyte size showed distinct peaks between 19 and 21°C, and most showed a marked decline in the extreme temperature treatments (Fig. 5). Gametophytes from high latitude populations grew larger than those from lower latitude populations, and this was evidenced by a significant difference in gametophyte size among regions ($F_{2,962} = 46.10$, $p < 0.001$) and locations ($F_{6,958} = 17.85$, $p < 0.001$). The gametophytes collected from TAS were considerably larger than those from the other regions, and Western Australian gametophytes were the smallest. Overall, increasing temperature had a significant positive effect on the size of gametophytes ($F_{1,955} = 15.89$, $p < 0.001$; ANCOVA coefficient 0.02). The highest temperature optimum for size was recorded in WA, at Hamelin, with an optimum of 22.7°C. The location with the lowest optimal temperature for size was in TAS, at Fortescue, at 20.2°C.

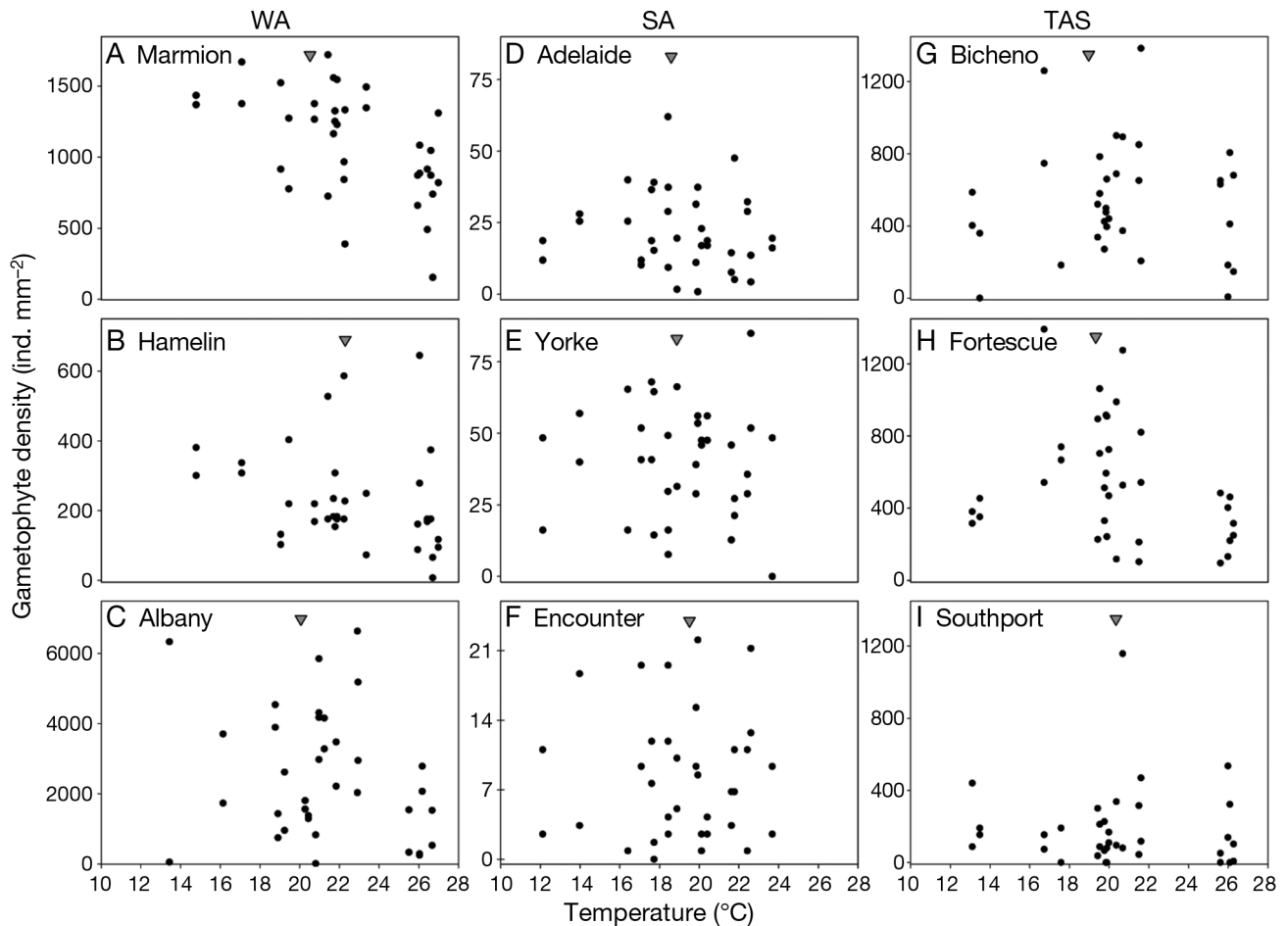


Fig. 4. *Ecklonia radiata*. Gametophyte density after 6 d of exposure to various temperatures at locations in Western Australia (WA; A-C); South Australia (SA; D-F) and Tasmania (TAS; G-I). Each point represents the average density on each replicate slide ($n = 2$). Note the different scales on the y-axes among the locations. (∇) Temperature where density is optimal, i.e. the mean temperature of treatments yielding the upper 10th percentile of gametophyte densities

In situ temperature and nutrient characteristics

Optimum conditions for gametophyte performance were significantly related to all *in situ* temperature characteristics, except the mean 3 yr temperature range (Table 1, Fig. 6A–C). There was a positive relationship between optimal culture temperature for density and the winter minimum SST ($r^2 = 0.56$, $p < 0.05$) but no relationship between summer maximum SST and the mean temperature of the preceding month. The significant regression statistics were stronger for comparisons of size ($0.58 < r^2 < 0.91$) compared to density ($0.12 < r^2 < 0.56$). Similar to density, the culture temperatures promoting maximum size were strongly related to *in situ* winter minimum ($r^2 = 0.91$, $p < 0.001$). There was also a significant positive relationship between the optimum culture temperature for size and *in*

situ summer maximum ($r^2 = 0.58$, $p < 0.05$) and the mean SST for the month prior to sampling ($r^2 = 0.62$, $p < 0.05$).

Chlorophyll concentrations (Fig. 2b) prior to sampling were significantly different among the regions ($F_{2,177} = 8.44$, $p = 0.001$) and locations ($F_{8,171} = 3.97$, $p = 0.002$). This difference was attributed to the higher chlorophyll values in SA, particularly in Encounter Bay, which returned significantly higher concentrations than Albany, Bicheno and Marmion. Despite the significantly different levels of chlorophyll in the coastal waters at these locations, optimum temperatures for gametophyte density and size could not be significantly ($r^2 < 0.21$, $p > 0.05$) related to chlorophyll concentrations (Fig. 6D–F). Consequently, thermal optima of gametophytes were not affected by productivity of the ocean waters where kelps were collected.

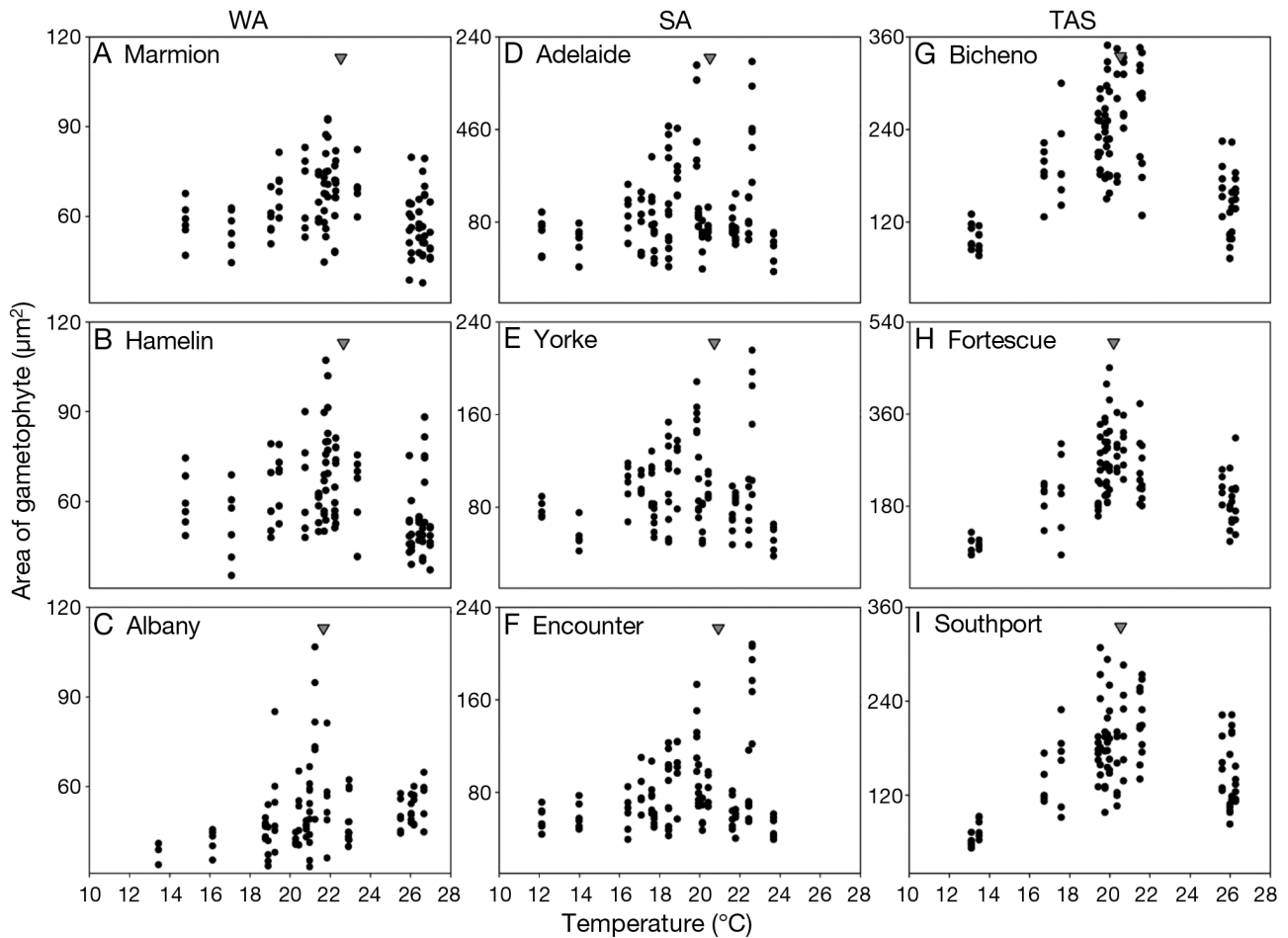


Fig. 5. *Ecklonia radiata*. Size of gametophytes after 6 d of exposure to various temperatures at locations in Western Australia (WA; A-C), South Australia (SA; D-F); and Tasmania (TAS; G-I). Each point represents a randomly selected gametophyte (n = 6); in some cases <6 gametophytes were available for measurement. Note the different scales on the y-axes among the locations. (▽) Temperature where size is optimal, i.e. the mean temperature of treatments yielding the upper 10th percentile of gametophyte sizes

DISCUSSION

This study revealed distinct biogeographic patterns in the effects of temperature on the early life-stage performance of kelp populations around temperate Australia. *Ecklonia radiata* gametophytes had

optimal survival (density) and growth (size) between 18 and 23°C, and generally, outside of these temperatures there was a decline in growth and survival. However, gametophyte performance reflected local climatic conditions, as there was a positive relationship between local SST (particularly winter minima)

and thermal optima for gametophyte survival and growth. These results not only demonstrate that *E. radiata* in Australian waters have varied thermal optima for growth and survival, but also that this variability is influenced by biogeography and, furthermore, that Australian kelp populations might exhibit adaptation to local temperature regimes.

The density and morphology of *E. radiata* populations are highly vari-

Table 1 *Ecklonia radiata*. Results of regression (slope, p-value and regression statistic) of optimum temperature for density and size against *in situ* temperature characteristics of the locations. **Bold:** significant

Sea surface temp.	Density			Size		
	Slope	p	r ²	Slope	p	r ²
Month prior to sampling	0.127	0.304	0.150	0.208	0.012	0.618
Summer max.	0.097	0.362	0.120	0.172	0.017	0.581
Winter min.	0.291	0.020	0.564	0.297	<0.001	0.908
Three year annual range	-0.336	0.069	0.397	-0.195	0.222	0.204

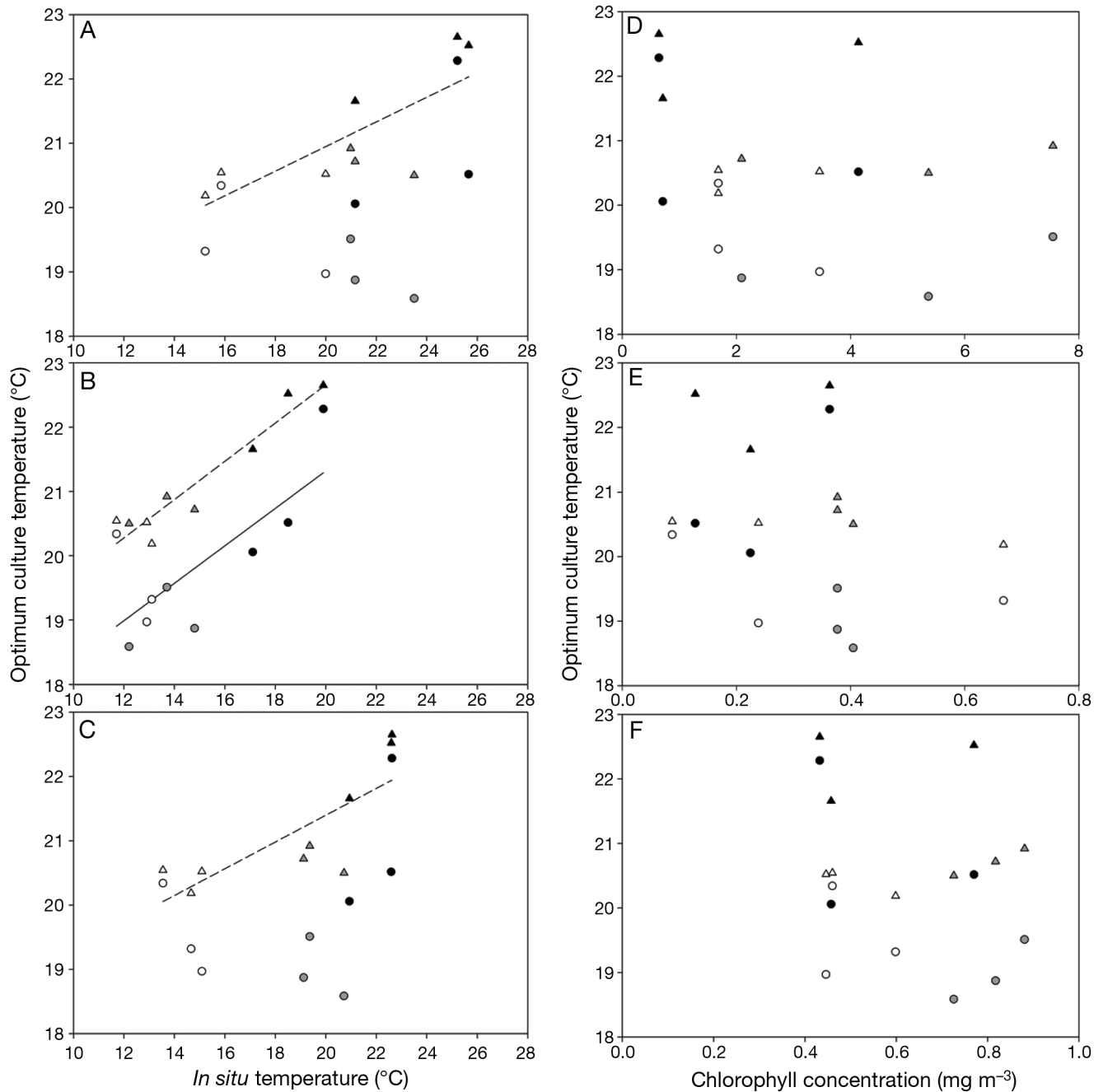


Fig. 6. *Ecklonia radiata*. Regression plots of temperature supporting optimum gametophyte density (●) and size (▲) against (A–C) temperature, and (D–F) chlorophyll concentration. (A) *In situ* summer maximum and (B) winter minimum temperatures, and (C) average temperature for the month prior to sampling. (D) *In situ* maximum, (E) minimum and (F) average chlorophyll concentration for the month prior to sampling. Symbol shades indicate locations in WA (black), SA (grey) and TAS (white). Solid and dashed lines: significant regressions for density and size, respectively

able across the species' distribution (Wernberg et al. 2003a, Goodsell et al. 2004, Irving et al. 2004, Fowler-Walker et al. 2005). This variability has commonly been attributed to local environmental and biological pressures (Wernberg et al. 2003a, Fowler-Walker et al. 2005, 2006, Mabin et al. 2013). There is also a high

level of genetic variability among *E. radiata* populations, even over distances of as small as tens of kilometres, with populations showing genetic divergence due to patterns in boundary currents around the continent (Coleman et al. 2009, 2011). In this study there were distinct differences in the growth of

gametophytes among regions and even locations. There were also differences in the survival of gametophytes among locations; however, these did not show evidence of a continental-scale pattern. This suggests that Australian populations of *E. radiata* may differ intrinsically, with differences in gametophyte characteristics reflecting the genetic variation around Australia. For example, densities at the Albany location were anomalous, and were considerably higher than all other locations. This highlights the spatial variability in reproduction occurring among population of this species, but may also be a result of temporal variation. While samples were collected as closely as possible (in time), previous work investigating the reproductive phenology of *E. radiata* reported significant fluctuations in spore production over time scales of weeks (Mohring et al. 2013b).

Adaptation to local temperature regimes is ecologically important, and is reflected in a range of marine and terrestrial environments (Somero 2005, Sorte et al. 2011). Few studies of Laminariales performance have reported a temperature signature in the ecology of kelp; thus local thermal conditions do not appear to define temperature optima or tolerance ranges of gametophytes. Several studies document no difference in temperature responses between spatially isolated populations, even if they are from differing *in situ* climate regimes (Bolton & Lüning 1982, Ladah & Zertuche-González 2007, Andersen et al. 2013). The effects of temperature on populations of 4 species of *Laminaria* spp. across the Northern Hemisphere were very similar, with near identical temperature optima for growth despite very different temperature regimes at the collection locations (Bolton & Lüning 1982). A comparison of 2 populations of *Macrocystis pyrifera* in California, one from the centre of its distribution and the other near its low latitude extreme, also demonstrated no effect of geographic location on survival of gametophytes from an experimentally simulated ENSO event and the resultant increased temperatures (Ladah & Zertuche-González 2007). In contrast, there is evidence of differing temperature responses among populations of *E. radiata*. In New Zealand, gametophytes from warmer-climate populations responded better to increased temperatures than cool-water populations (Novaczek 1984b). Here, there were differences in the thermal optima for survival and growth of gametophytes over various spatial scales, with variation between locations as little as 50 km apart, extending to differences over the entire distribution of the species. These differences could be linked with *in situ* temperatures at the locations, suggesting that *E. radiata* gametophytes have

adjusted their thermal characteristics in response to location-specific conditions, rather than having general characteristics across the entire biogeographical range of the species.

In this study, there was a significant relationship between winter minimum at each location and thermal optima with respect to gametophyte survival. However, growth was related to both short-term (average of the month prior to sampling) and long-term (summer maximum and winter minimum) *in situ* temperature patterns. The relationship between thermal optima and *in situ* conditions was much stronger for growth than survival, highlighting the fact that growth is a more temperature-sensitive process. Adaptation to long-term patterns and trends typically reflects the ability of a population to withstand gradual changes in the system through acclimatization (Somero 2005, Sorte et al. 2011). However, while links to short-term patterns demonstrate a population's ability to respond to temporary changes in the thermal environment, they do not provide evidence of ability to survive thermal extremes and long-term increases in temperature (Sorte et al. 2011). These ideas, and the fact that growth appeared linked to both short and long-term thermal characteristics of locations, suggest that *E. radiata* gametophytes have the capacity to withstand short-term thermal fluctuations, and that gradual long-term changes in temperature regimes may result in locally acclimated populations with differing temperature responses.

Where gametophytes are more sensitive to temperature, recruitment can be limited in extreme conditions, and the persistence of kelp populations can be threatened. For some species the gametophyte phase of the life cycle is more sensitive to temperature than the macroscopic sporophytes (Matson & Edwards 2007). In contrast, Novaczek (1984b) found that *E. radiata* gametophytes in New Zealand could grow at temperatures higher than those at which adults occur. These are not isolated findings. Mabin et al. (2013) found that *E. radiata* gametophytes could grow in temperatures up to 25°C but no sporophytes developed. Gametophytes of several Arctic Laminariales are able to tolerate up to 20°C, while the sporophytes live in -1.5 to 5°C; and, while tolerance of adult plants was not tested, it was assumed that they could not tolerate temperatures higher than this. Antarctic species, existing in <5°C water temperature, were able to produce gametophytes that could grow in 13 to 16°C (tom Dieck 1993). Similarly, 4 species of *Laminaria* had sporophyte populations with a temperature optima for growth and survival of 10 to

15°C, while their gametophyte phase grew best between 21 and 23°C (Bolton & Lüning 1982). These authors concluded that the limit of population distribution is determined by upper lethal limits of sporophyte populations rather than the gametophyte phase. In this work, the temperature range that macroscopic sporophytes were subjected to in 2011 (15.8 to 27.4°C) was marginally higher than our experimental temperature range. We found that gametophytes were able to survive and grow in all temperature treatments tested (12 to 26°C). Without testing a wider range of temperatures, outside those which *E. radiata* is subjected to *in situ*, conclusions cannot be drawn regarding which phase of the life cycle controls population persistence.

While the relationship between gametophyte performance and temperature was as expected, some results were unexpected. (1) There was a negative relationship between survival and culture temperature; however, growth was positively related to culture temperature. Since *E. radiata* exists in water temperatures above the thermal limits for most other species of the Laminariales (tom Dieck 1993), and reproduces when annual water temperatures are the warmest, the conditions for reproduction of this species promote gametophyte growth rather than being favourable for survival (Mohring et al. 2013b). However, gametophytes must still survive, and the gametes must still be viable for populations to persist, so the tolerance level for survival still has the potential to define this species' distribution. (2) The thermal optima for the most southerly populations were higher than temperatures the populations are ever subjected to naturally. So, the thermal optima for gametophyte performance are high relative to the thermal regime of *E. radiata* distribution, such that reproduction occurs when water temperatures are at annual maxima, and in some cases the water temperature never reaches levels high enough to promote optimum performance. This finding suggests that this species may be limited by cool temperatures at the southern end of its distribution. In combination, these findings suggest that cool-water populations can withstand greater increases in sea temperature than those closer to their limits. This also means that the effects of changing climates may differ among regions, since gametophytes from cool-water populations are growing in temperatures below optimum, they may perform better in future climates; while, an increase in sea temperatures will likely cause a decline in performance in warm-water populations.

In conclusion, *E. radiata* gametophyte performance reflected local climatic conditions as evidenced by a

positive relationship between local sea temperature and thermal optima for gametophyte survival and growth. Since variability in thermal optima was controlled by biogeographic position, Australian kelp populations appear to have the capacity to adapt to local temperature regimes and, potentially, to acclimatise to a changing climate. Importantly, cool-water populations of kelp responded better to increased temperature, and may have a greater capacity to tolerate larger increases in sea temperature than those closer to their warm-water limits.

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