Variation in the morphology, reproduction and development of the habitat-forming kelp *Ecklonia radiata* with changing temperature and nutrients

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ABSTRACT: Increasing ocean temperatures are a threat to kelp forests in several regions of the world. In this study, we examined how changes in ocean temperature and associated nitrate concentrations driven by the strengthening of the East Australian Current (EAC) will influence the morphology, reproduction and development of the widespread kelp *Ecklonia radiata* in south-eastern Australia. *E. radiata* morphology and reproduction were examined at sites in New South Wales (NSW) and Tasmania, where sea surface temperature differs by ~5°C, and a laboratory experiment was conducted to test the interactive effects of temperature and nutrients on *E. radiata* development. *E. radiata* size and amount of reproductive tissue were generally greater in the cooler waters of Tasmania compared to NSW. Importantly, one morphological trait (lamina length) was a strong predictor of the amount of reproductive tissue, suggesting that morphological changes in response to increased temperature may influence reproductive capacity in *E. radiata*. Growth of gametophytes was optimum between 15 and 22°C and decreased by >50% above 22°C. Microscopic sporophytes were also largest between 15 and 22°C, but no sporophytes developed above 22°C, highlighting a potentially critical upper temperature threshold for *E. radiata* in Tasmania. Lower nitrate concentration had no effect on *E. radiata* gametophytes and sporophytes. Given forecast increases in ocean temperature of between 2 and 3°C in southeastern Australia by 2100, these findings suggest that *E. radiata* is likely to be affected by a strengthening EAC and highlight the susceptibility of the development and growth of early life-cycle stages to these changes.

KEY WORDS: *Ecklonia radiata* · East Australian Current · Climate change · Morphology · Reproduction

INTRODUCTION

Projections of global climate change forecast rapid atmospheric and oceanic temperature increases over the next 100 yr (IPCC 2007), which will cause changes in the strength and pattern of winds and ocean currents (Cai et al. 2005, Poloczanska et al. 2007). Consequently, population declines and range shifts of species are predicted to occur, with ramifications for marine ecosystems (Sagarin et al. 1999, Parmesan 2006, Wernberg et al. 2011). Empirical studies support such predictions of climate impacts: changes in species phenology and distribution can alter community dynamics through flow-on effects to abiotic processes and food webs (Parmesan 2006, Holbrook et al. 2009, Beaugrand et al. 2002). Under-

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standing which life-cycle stages are most vulnerable to oceanographic changes and the mechanisms underpinning vulnerability (e.g. juveniles or adults) are critical to predicting the response of species to climate change (Russell et al. 2011).

In southeastern Australian coastal waters, the East Australian Current (EAC) is the dominant mode of oceanic input, particularly during summer (Ridgway 2007). EAC-associated waters are warmer and nitrate poor compared to the Antarctic-influenced waters that otherwise dominate the region, and recent strengthening of the EAC means warm and nitrate-poor waters are pushing farther south for longer periods of time (Rochford 1984, Cai et al. 2005, Cai 2006, Ridgway 2007). For example, long-term sea surface temperature (SST) datasets taken at the southern edge of the EAC (Maria Island, Tasmania) show an increase in annual average SST of >1°C since 1944 (Johnson et al. 2011). Additionally, at both Maria Island and a site that is approximately 8.5° latitude further north in New South Wales (NSW) (Port Hacking), SST is weakly negatively correlated with nitrate concentrations (Rochford 1984). Significantly, modeling predicts future extension of the February mean 20°C SST isotherm into currently cool-temperate Tasmanian waters, exposing that region to warm-temperate conditions by the end of the century (Bartsch et al. 2012). Overall, Tasmania's east coast marine communities are predicted to be exposed to increasing SSTs ~3.8 times the global average (2.0 to 3.0°C) and associated longer exposure times to low nitrate levels (i.e. nitrates <1 µmol l^{-1}) (Rochford 1984, Ridgway 2007).

Some major ecological effects of the strengthening of the EAC are already evident. These include the range expansion of the barrens-forming sea urchin *Centrostephanus rodgersii*, which is impacting subtidal kelp forests in Tasmania (Johnson et al. 2005, Ling et al. 2009a,b), and range shifts in a number of macroalgae (Wernberg et al. 2011) including the contraction and reduction in canopy cover of giant kelp *Macrocystis pyrifera* in Tasmania (Johnson et al. 2011). The effect of a strengthening EAC on habitat-forming temperate kelp and associated species is of major importance. Globally, kelp facilitate high levels of temperate marine biodiversity (Anderson et al. 1996, Smith et al. 1996, Wernberg et al. 2009), and in southern Australia, kelp habitat (particularly *Ecklonia radiata*) contributes to the world's highest rates of regional endemism in both marine algae and invertebrates (Bolton 1996, Phillips 2001, Kerswell 2006). In Tasmania, the economic importance of kelp is recognised through support to fisheries-based ecosystems,

particularly the southern rock lobster and abalone industries, worth more than AU\$ 160 million annually (Johnson et al. 2005, Ling et al. 2009a, ABARES 2011).

Temperature, nutrients and light generally limit kelp to mid-latitudes of between 40° and 60° in the Northern and Southern hemispheres (Steneck et al. 2002), although northern range limits of *Ecklonia radiata* in Australia extend to ~28°S (Guiler 1960, Kirkman & Kendrick 1997). Changes to temperature and nitrates can impair kelp photosynthetic, respiratory and cellular function in their expected ranges (Staehr & Wernberg 2009, Wernberg et al. 2010), leading to reduced growth and survivorship (Dayton et al. 1999, Graham et al. 2007) and ultimately range contractions or local extirpations (van Tussenbroek 1989, Edyvane 2003, Connell et al. 2008). Moreover, increases in ocean temperature associated with climate change have been linked to reduced resilience in kelp to anthropogenic and natural perturbations (Wernberg et al. 2010). Understanding the combined effects of temperature and nitrates on *E. radiata* will provide valuable information towards understanding climate change impacts and the future viability of *E. radiata* populations in southeastern Australia. In particular, an understanding of the impacts of climate change on the microscopic stages (gametophyte and juvenile sporophytes) of the life cycle is likely to be crucial (Hurd et al. 2009, Roleda et al. 2012), but to our knowledge, combined impacts of changes in temperature and nutrients on microscopic stages have not been examined in *E. radiata*.

Given the observed changes to the EAC and their influence on local-scale temperature and nitrates, there are likely to be important implications for the reproduction, development and growth of kelp. Our overall aim was to examine how the predicted scenario of a stronger EAC may influence the reproduction and development of the dominant habitat-forming kelp in temperate Australia, *Ecklonia radiata*. We addressed this aim by combining large-scale field surveys of *E. radiata* morphology and reproduction in 2 latitudinal regions in southeastern Australia (Tasmania and NSW) with laboratory culturing experiments to determine the effects of temperature and nitrates on different microscopic life-cycle stages. Specifically, we determined (1) the daily SST and wave power at sites in Tasmania and NSW, (2) differences in the morphology and the amount of reproductive tissue of *E. radiata* sporophytes among sites in Tasmania and NSW, (3) whether variation in the amount of reproductive tissue was explained by variation in thallus morphology, and (4) how increasing

temperatures and lower nitrates affected the growth and development of gametophytes and juvenile sporophytes of *E. radiata.*

MATERIALS AND METHODS

Study species

Ecklonia radiata (C. Agardh) J. Agardh is a perennial, subtidal, habitat-forming kelp (order Laminariales; Womersley 1967) with a wide latitudinal and depth range (Womersley 1981), making it the most important habitat-forming species in southeastern Australia. It has a typical laminarian life cycle consisting of microscopic male and female gametophytes and a macroscopic sporophyte stage. Sporophytes grow up to 2 m in length and consist of a stipe arising from a single conical holdfast. The central lamina (primary blade) arises from the stipe and basal meristem, with laterals (secondary blades) developing in distichous pairs along the central lamina (Womersley 1987). The lamina can be eroded by forces from wave action and grazing (Mann 1973, Kirkman 1981). Adult sporophytes develop sori along the central lamina and laterals typically at approximately 8 to 12 mo post fertilisation (Novaczek 1980, Kirkman 1981). Sori emerge from the distal (top) end of the thallus and grow down the central lamina and into the laterals towards their distal ends. Zoospores are released from sori, and after settlement, zoospores germinate into 1-celled male and female gametophytes that become fertile through gametogenesis. Gametophytes are dioecious and filamentous, exhibiting sexual dimorphism, and females (up to 400 μm in length) are larger than males (up to 100 μm in length) and less branched. Gametophytes are oogamous, and male gametophytes produce motile antherozoids that fertilise nonmotile eggs which have been liberated from elongated terminal cells, the oogonia (Womersley 1981), that then metamorphose into juvenile sporophytes (Womersley 1981). *E. radiata* is known to survive up to 10 yr in New Zealand (Novaczek 1981).

Study sites and sampling

We determined SST and wave power and sampled adult sporophytes, which we defined as reproductive
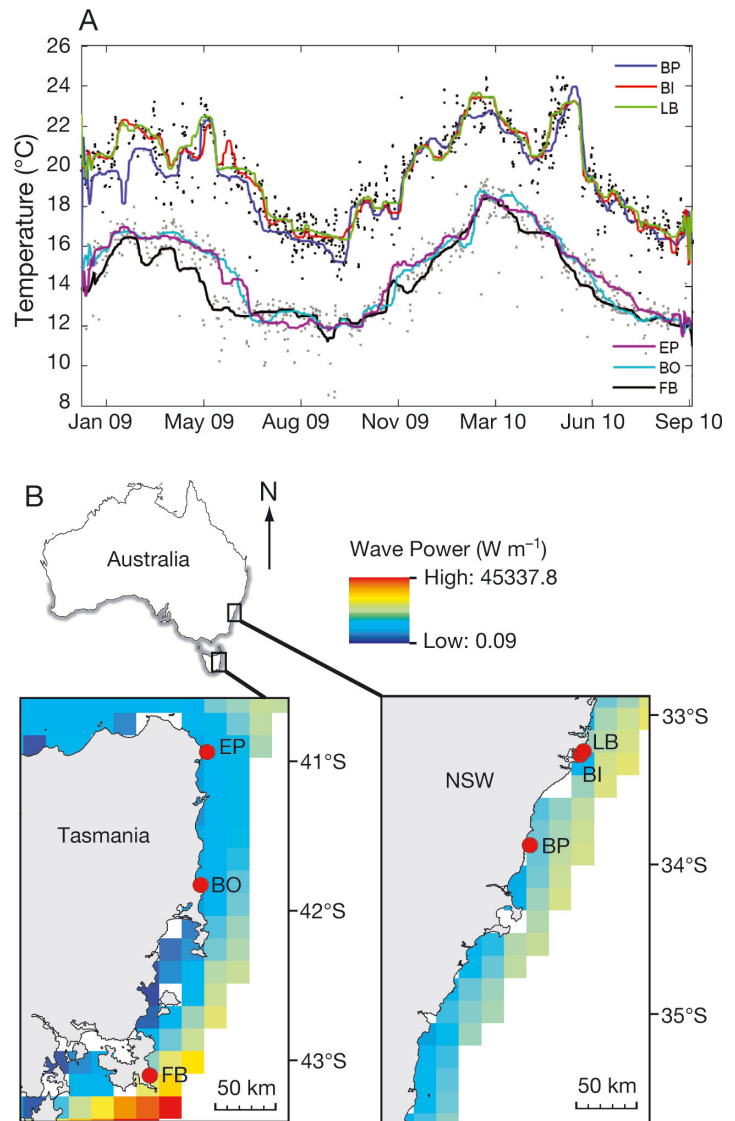

Fig. 1. (A) Temperature profiles of the 6 study sites from December 2008 to September 2010; Tasmania (grey dots): Fortescue Bay (FB), Bicheno (BO), Eddystone Point (EP); New South Wales (black dots): Bass Point (BP), Bare Island (BI), Long Bay (LB). (B) Map showing the 6 sites in southeastern Australia where *Ecklonia radiata* were sampled for sea surface temperature, morphology and reproduction, with insets showing average wave power (1997 to 2008); pixels indicate average W m^{-1} of wave crest

thalli or thalli of equivalent size and morphology to reproductive thalli, from 3 sites within each of 2 regions spanning ~10° of latitude (NSW and Tasmania, Fig. 1). Adult sporophytes were collected haphazardly from largely monospecific *Ecklonia radiata* forests between 7 and 10 m depth from sites exposed to year-round prevailing south to southeasterly swells (Guiler 1960, Wright 1976). As much as possible, we endeavoured to standardise large-scale environmental factors that are known to influence kelp

morphology (see Fowler-Walker et al. 2005, 2006), as local-scale drivers of morphology such as hydrology and sedimentation are highly complex to determine and measure.

Variation in SST and wave power

SST data were collected for the 6 sites using daytime data sourced from Bands 31 and 32 of the moderate resolution imaging spectroradiometer aboard the Aqua satellite, which is an effective proxy for *in situ* SSTs for depths of up to 10 m (Smale & Wernberg 2009). Image data are administered by Ocean Color Web, Ocean Biology Processing Group (OBPG) at NASA's Goddard Space and Flight Centre, Greenbelt, Maryland, USA (Feldman & McClain 2010) and were downloaded from the OBPG Web site (http://oceancolor.gsfc.nasa.gov/). Temporal and spatial resolutions are daily at 4×4 km. Using Matlab R2009b, data were extracted from the images (Feldman & McClain 2010) using a 5×5 pixel (20×20 km) window around each of the sampling sites, and data were interpolated by averaging temperature values within this region. Daily SST data were extracted for the previous 12 mo mean at each site for each sampling period. This 12 mo time period was chosen based on time to adulthood in *Ecklonia radiata* (Novaczek 1980, Kirkman 1981).

Wave power (W m^{-1} crest), estimated by the regional implementation of the WAM model (Greenslade 2001), provides an estimate of the time-averaged wave power that occurs on the Australian shelf. The WAM model integrates the basic transport equation describing the evolution of a 2-dimensional ocean wave spectrum, including dissipation due to whitecapping (Hasselmann 1988). Linear wave theory and water depth were used to calculate wave power from the WAM-derived significant wave height and period (Hughes & Heap 2010). The estimated time-average wave power was obtained by averaging the power record over the available time series. Data were extracted from the model output to describe the time-average wave power at each of the sample sites.

Variation in morphology and reproduction

Morphology and reproduction of adult *Ecklonia radiata* sporophytes were quantified at each site on 3 occasions (May, July and September 2010). Each time, 23 to 24 Stage 3 *E. radiata* sporophytes (see Kirkman 1981, 1984) were collected (no collection

was done in July from Bass Point due to bad weather). Thalli were returned to the lab, where 7 morphological traits (May and July only) and 1 reproductive trait were measured (Fig. 2). The 7 morphological traits (thallus length, lamina length, lamina width, lateral length, lateral width, stipe length and stipe thickness) reflect the overall size and shape of *E. radiata* thalli and are a subset of traits measured previously by others (see Wernberg et al. 2003, Fowler-Walker et al. 2005, 2006, Wernberg & Thomsen 2005). The total amount of reproductive tissue down the central lamina of a thallus was measured as the distance from the distal end where sori emerge to where sori terminate (Fig. 2). We focused on this measure of reproductive tissue, as the majority of reproductive tissue occurs down the central lamina (~90%) compared to the laterals; sori coverage on laterals was patchy, and sori-bearing laterals always occurred within the margins of central lamina sori. While this measure does not reflect all aspects of reproduction (Patten & Yarish 1993), it is a meaningful relative measure that allows quantitative among-site comparisons. Moreover, there is a link between sorus area and spore release density (Mohring et al. 2013). In Tasmania, *E. radiata* reproduction output peaks between May and July (Sanderson 1990); however, this is not known for NSW. Thus, our sampling coincided with the time when reproduction was
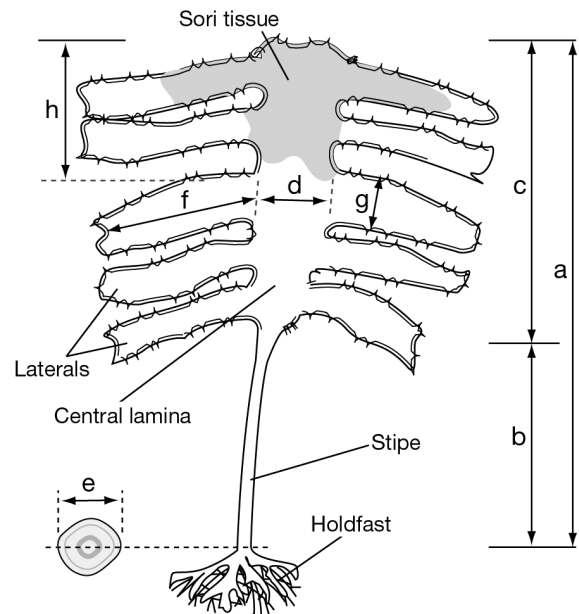

Fig. 2. *Ecklonia radiata*. Seven morphological measurements taken on adult sporophyte: (a) total thallus length; (b) stipe length; (c) central lamina length; (d) central lamina width; (e) stipe diameter; (f) lateral length; (g) lateral width. Sori extent down the central lamina is also shown (h)

high and is a meaningful test of the link between variation in morphology and reproduction. In September, we only measured lamina length and stipe length, focusing on those morphometrics that were good predictors of reproduction.

Testing for effects of temperature and nitrates on growth and development

Microscopic stages of *Ecklonia radiata* were grown from zoospores liberated from reproductive tissue (sorus) from 10 reproductive sporophytes collected at Bicheno in July 2010. To liberate zoospores, sori were placed into a cool, dry and dark place for approximately 1 h and then briefly sterilised in an antiseptic solution (1 ml Betadine l^{-1} distilled water) for ~1 min so as not to harm the spores whilst reducing contamination by associated epiflora (Wright et al. 2004). Excessive mucilage was wiped away with a lint-free cloth. Sori were then submerged into 500 ml of 0.2 µm filtered, autoclaved seawater and placed under controlled light conditions. Zoospores were released within 7 h. Then, 100 µl of zoospore solution (~2.8 × 10^5 zoospores ml^{-1}, pooled from all 10 plants) was pipetted into cylindrical, autoclaved plastic culture jars (43 mm diameter, 45 mm depth) containing seawater media (see below) and 2 coverslips as the settlement substratum, to be used for destructive sampling of microscopic parameters at 2 times, post-settlement (gametophytes) and post-fertilisation (sporophytes). Jars (n = 3 replicates of each temperature × nitrate concentration combination) were placed into an aluminium temperature-gradient plate (730 × 370 mm) forged with 36 wells (6 × 6 grid, 44 mm diameter, 45 mm depth). Lighting consisted of 4 parallel 40 W Sylvania standard cool white globes (Model F40W/133-RS) set to a 16 h light:8 h dark cycle, the optimum lighting regime for *E. radiata* development (Novaczek 1984a). Light flux density ranged from ~17 to ~42 µmol photons m^{-2} s^{-1}. The growth and development of *E. radiata* gametophytes do not differ within this light range (Novaczek 1984a,b).

A temperature gradient across the aluminium plate was maintained by water baths at either end (12 and 26°C), resulting in 6 experimental temperatures: 13.5 ± 0.1°C, 15 ± 0.1°C, 16.5 ± 0.1°C, 19 ± 0.1°C, 22 ± 0.1°C, and 25.5 ± 0.1°C. High temperatures reflected the predicted average SST increase of 2 to 3°C off the Tasmanian coast by the year 2100, based on oceanographic CO_2 models (Ridgway 2007, Ridgway & Hill 2009). The second highest temperature (22.0°C) fulfilled this objective, while the maximum temperature

(25.5°C) tested for the effects of an extreme increase in temperature on the microscopic stages of Tasmanian *Ecklonia radiata*.

Two nitrate concentration treatments of 0.5 µmol l^{-1} and 3.0 µmol l^{-1} were created using f/2 media (reviewed by Andersen 2005), where sodium nitrate ($NaNO_3$) was adjusted accordingly to achieve the desired nitrate concentrations. Nitrate levels were set to reflect normal and depleted dissolved nitrate levels off Maria Island (Rochford 1984). Sodium dihydrogen phosphate dihydrate ($NaH_2PO_4 \cdot 2H_2O$) was also adjusted to retain the N:P ratio of the f/2 media. Silicates were omitted from the recipe to reduce the likelihood of diatom contamination, which eliminated the need to use germanium dioxide (GeO_2). GeO_2 is used as a diatom suppressant in *Laminaria* culturing due to its effect of arresting diatom cell division (Lewin 1966, Shea & Chopin 2007); however, GeO_2 may have inhibitory effects on kelp gametophytes (Shea & Chopin 2007). Media was changed weekly.

One coverslip was removed from each culture jar at 16 d (post-settlement, for male and female gametophytes) and the second at 32 d (post-fertilisation, for sporophytes) to determine growth and development. Once removed, coverslips were inverted onto a microscope slide, and up to 100 photographs were taken haphazardly from each coverslip at a magnification of between 200× and 400×. Images were randomly selected until 5 male and 5 female gametophytes were measured per coverslip (n = 15 per sex, per crossed nitrate × temperature treatment). Two measurements were made on each gametophyte; 2-dimensional surface area and the number of cells of the gametophyte. Surface area was measured in ImageJ 1.43 using the trace tool with the scale calibrated to 0.1 mm using a digital image of a calibrating slide (Wild Heerbrugg, Model 310345). Cells were counted manually from images. Only surface area was measured on juvenile sporophytes (3 per coverslip, n = 9 per crossed treatment) using the same methods as those used for gametophytes. Surface area measures growth (Shea & Chopin 2007), while cell count measures development via cell division rates (Novaczek 1980) under the different treatments.

Statistical analyses

Multivariate differences in *Ecklonia radiata* morphology were examined using nested permutational multivariate ANOVA (PERMANOVA; Anderson 2001) with the factors Region (random), Site (ran-

dom) nested within Region and Time (fixed). We used untransformed Gower dissimilarities (Gower 1967), as we had variables measured at different scales and ran 9999 permutations to calculate F-statistics. Permutational tests of multivariate dispersion (PERMDISP; Anderson et al. 2008) were done to assess the effect of the dispersion of observations about their centroid on the centroid′s position in multivariate space. Finally, pseudo-variance components were then calculated for each of the spatial levels each month (region, sites and within sites) (e.g. Benedetti-Cecchi 2001). To visualise multivariate differences in *E. radiata* morphology, non-metric multidimensional scaling (nMDS) was done using Gower′s dissimilarities. Ordinations were based on average centroids for sites each month to limit the number of observation points on plots. All multivariate analyses were run using PERMANOVA+ for PRIMER. Differences in individual morphological traits were determined using 3-factor nested ANOVA with the factors (all random) Region (Tasmania vs. NSW), Site (nested within Region) and Time (May and July 2010).

Differences in reproduction (extent of sori down the central lamina) between regions and among sites within regions at each time (May, July and September) were determined using nested analysis of covariance (ANCOVA). The effect of time was not included in this analysis. Total length of the central lamina was used as a covariate to take into account effects of lamina size on reproductive tissue. To meet ANCOVA assumptions, data were $\log_n(x + 1)$ transformed and homogeneity of slopes was examined. Despite the transformation, this assumption was violated in July and September (see 'Results').

To test for relationships between the extent of sori down the central lamina and particular morphological traits of thalli, multiple regressions were performed separately for May and June, with the extent of sori down the central lamina as the dependent variable and all morphological measures, excluding total thallus length, as predictor variables. Data were $\log_n(x + 1)$ transformed.

Differences in the surface area and cell count of gametophytes were analysed separately with 4-factor nested ANOVA with the factors Temperature (fixed), Nitrate concentration (fixed), Sex (fixed) and Jar (random and nested within the Temperature × Nitrate interaction). Both these dependent factors were $\log_n(x + 1)$ transformed. Differences in the sur-face area of sporophytes ($\log_n$ transformed) was analysed with 3-factor nested ANOVA with the factors Temperature (fixed), Nitrate (fixed) and Jar (random and nested within the Temperature × Nitrate interaction).

RESULTS

Variation in SST and wave power: Tasmania vs. NSW

Average SST in NSW and Tasmania differed by approximately 5°C. NSW sites showed a minimum of 13.7°C, a maximum of 24.4°C and a mean of 19.3°C (±0.07°C). Tasmanian sites ranged between 8.4 and 19.9°C with a mean of 14.5°C (±0.07°C). Strong seasonal patterns occurred for sites in both regions, with maximum temperatures in February to March and minimum temperatures in June to August (Fig. 1A). Average wave power from 1997 to 2008 varied among sites and was highest at Bass Point (NSW) (9285.03 W m^{-1} crest) and lowest at Fortescue Bay (3350.57 W m^{-1} crest). Generally, average wave power was greater at NSW sites (7549.543 ± 867.74 W m^{-1}, mean ± SE) compared to Tasmanian sites (5326.64 ± 1120.84 W m^{-1}, mean ± SE), although the magnitude of difference was small (Fig. 1B).

Differences in morphology between regions

PERMANOVA indicated significant variation in kelp morphology at the scales of Region, Site within Region and a significant Site within Region × Time interaction (Table 1). Pseudo-variance components highlighted large spatial variation at the scales of Region and Site within Region and, in particular, at

Table 1. *Ecklonia radiata.* Results of nested PERMANOVA testing the effects of Region (Tasmania vs. New South Wales), Sites within Region and Time (May and July 2010) on morphology. There were 3 sites per region except for New South Wales in July, when 1 site could not be accessed. Significant (p < 0.05) factors in **bold**

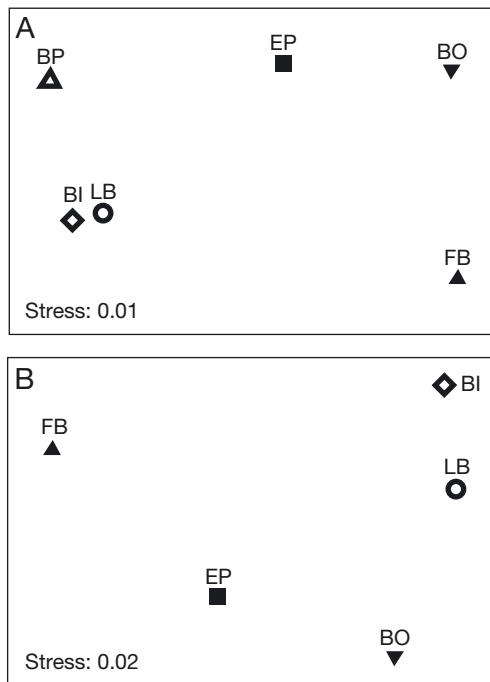| Source	df	MS	Pseudo-F	p (perm)	% of total variance
Region	**1**	**10313**	**4.829**	**0.032**	**23.7**
Site (Region)	**4**	**2322.1**	**15.758**	**<0.001**	**17.3**
Time	1	2361.1	3.967	0.328	5.1
Region × Time	1	595.14	1.468	0.297	1.1
Site (Region × Time)	**3**	**405.3**	**2.751**	**0.006**	**3.6**
Residual	253	147.36			49.2

Fig. 3. *Ecklonia radiata*. Non-parametric multidimensional scaling analyses showing morphological variation at sites in (A) May and (B) July. Site abbreviations as in Fig. 1. Filled symbols: Tasmania; open symbols: New South Wales

the smallest spatial scale (among individuals within Sites), which accounted for >50% of the variation (Table 1). Visual inspection of nMDS plots reflected the results from the PERMANOVA; although there was some evidence of grouping of sites within regions each month, there was still large separation among sites within regions (Fig. 3).

Most individual morphological traits showed significant variation among sites within regions (Table 2, Fig. 4). Two traits that reflect overall thallus size (total length and lateral length) were significantly larger in Tasmania compared to NSW, while 2 other traits (lamina width and lamina length) varied across regions and time (significant Region × Time interaction, Table 2). Lateral width was also highly variable [significant Site (Region) × Time interaction], but stipe diameter did not vary with any factors (Table 2).

Differences in reproduction between regions

In May, adult sporophytes from Tasmania had significantly more reproductive tissue on the central lamina than plants from NSW (region, $F_{1,4}$ = 6.032, p = 0.028; site, $F_{4,136}$ = 0.499, p = 0.736; lamina length, $F_{1,136}$ = 49.484, p < 0.001; Fig. 5). By contrast, in both

Table 2. *Ecklonia radiata*. ANOVA testing the effects of Region (Tasmania vs. New South Wales), Site within Region and Time (May and July 2010) on 7 morphological traits of morphology. Significant (p < 0.05) factors in **bold**

Source	df	MS	F	p
Total length				
Region	**1**	**31292.6**	**23.431**	**0.008**
Time	1	9481.60	8.761	0.207
Site (Region)	**4**	**1335.50**	**5.365**	**<0.001**
Region × Time	1	1082.30	4.437	0.126
Site (Region) × Time	3	243.90	0.980	0.403
Residual	251	248.90		
Stipe length (log₁₀)				
Region	1	4.028	5.379	0.081
Time	1	0.450	0.810	0.534
Site (Region)	**4**	**0.749**	**10.611**	**<0.001**
Region × Time	1	0.556	5.836	0.095
Site (Region) × Time	3	0.095	1.348	0.259
Residual	251	0.071		
Lamina length (log₁₀)				
Region	1	1.152	1.785	0.253
Time	1	0.545	1.690	0.417
Site (Region)	**4**	**0.645**	**40.476**	**<0.001**
Region × Time	**1**	**0.323**	**55.731**	**0.005**
Site (Region) × Time	3	0.006	0.363	0.780
Residual	251	0.016		
Lamina width (log₁₀)				
Region	1	0.175	0.422	0.558
Time	1	0.134	0.992	0.604
Site (Region)	**4**	**0.415**	**45.082**	**<0.001**
Region × Time	**1**	**0.135**	**345.846**	**<0.001**
Site (Region) × Time	3	0.000	0.042	0.988
Residual	251	0.009		
Stipe diameter				
Region	1	0.029	0.232	0.655
Time	1	0.315	3.629	0.307
Site (Region)	4	0.126	2.108	0.080
Region × Time	1	0.087	0.584	0.500
Site (Region) × Time	3	0.149	2.487	0.061
Residual	251	0.060		
Lateral length				
Region	**1**	**9411.50**	**66.512**	**0.001**
Time	1	260.200	2.694	0.348
Site (Region)	4	141.500	1.762	0.137
Region × Time	1	96.600	0.477	0.539
Site (Region) × Time	3	202.600	2.522	0.058
Residual	251	80.300		
Lateral width (log₁₀)				
Region	1	1.099	3.310	0.143
Time	1	0.266	10.161	0.194
Site (Region)	**4**	**0.332**	**22.045**	**<0.001**
Region × Time	1	0.026	0.386	0.579
Site (Region) × Time	**3**	**0.068**	**4.508**	**<0.001**
Residual	251	0.015		

July and September, there were no differences between regions but significant differences among sites within regions (July: region, $F_{1,3}$ = 0.626, p = 0.488; site, $F_{3,115}$ = 5.101, p = 0.002; lamina length, $F_{1,115}$ =
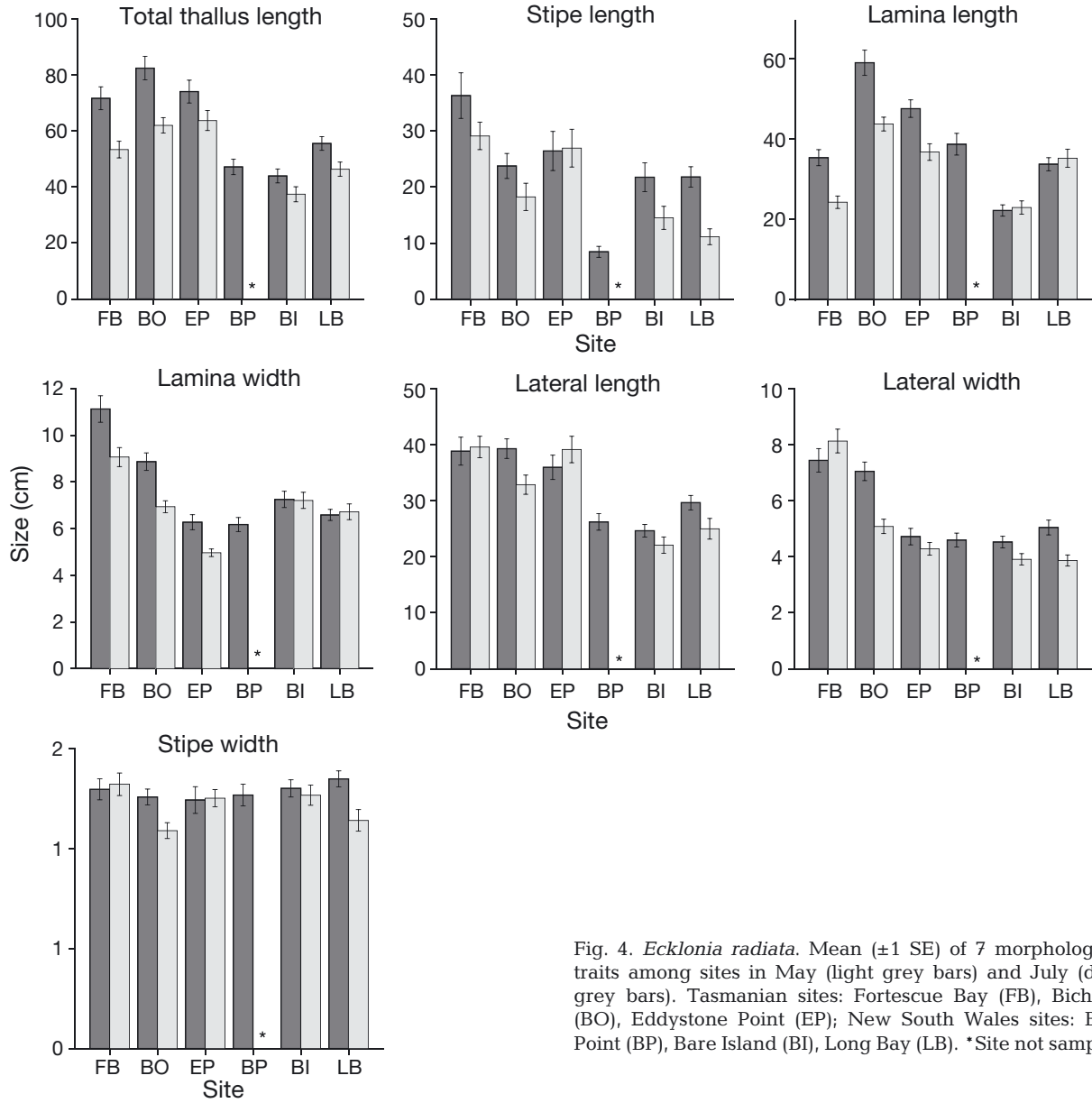
Fig. 4. *Ecklonia radiata.* Mean (±1 SE) of 7 morphological traits among sites in May (light grey bars) and July (dark grey bars). Tasmanian sites: Fortescue Bay (FB), Bicheno (BO), Eddystone Point (EP); New South Wales sites: Bass Point (BP), Bare Island (BI), Long Bay (LB). *Site not sampled
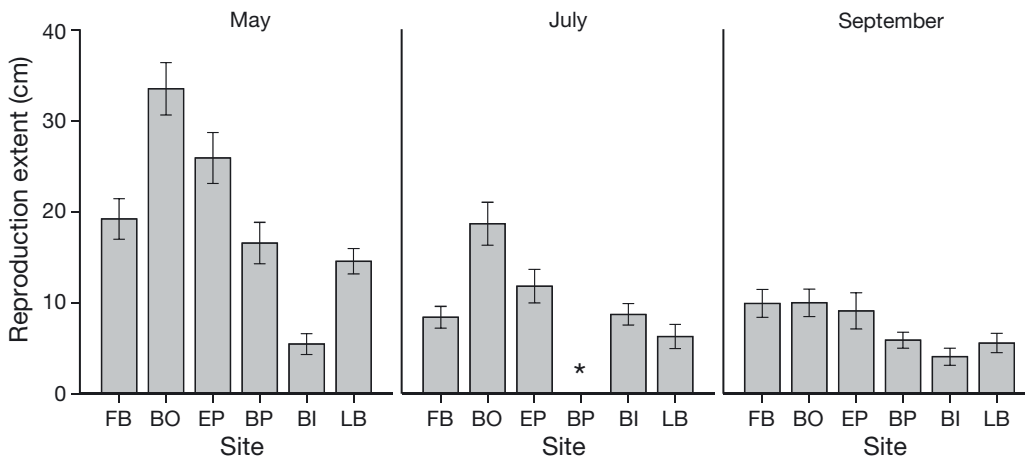

Fig. 5. *Ecklonia radiata.* Amount of reproductive tissue down the central lamina of thalli at sites in May, July and September. Site abbreviations as in Fig. 4. *Site not sampled. Bars show mean ±1 SE

21.924, p < 0.001; September: region, $F_{1,4}$ = 0.872, p = 0.403; site, $F_{4,136}$ = 4.084, p = 0.004; lamina length, $F_{1,136}$ = 31.036, p < 0.001). In June and September, there were also violations of the ANCOVA homogeneity of slope assumption, highlighting the large site-to-site variation in reproduction but limiting the interpretation for these months (see 'Discussion'). For all sites, reproduction declined over the duration of the study (May to September) with the exception of Bare Island (NSW) from May to July. Reproduction then declined at this site from July to September (Fig. 5).

Table 3. *Ecklonia radiata*. ANOVA testing the effects of temperature, nitrates and sex on gametophyte surface area with jar replicates included as a nested term. Surface area data were $\log_{10}$ transformed prior to analysis to meet ANOVA homogeneity of variance assumptions. Significant (p < 0.05) factors in **bold**

Source	SS	df	MS	*F*	p
Temperature	**7.344**	**5**	**1.469**	**32.219**	**<0.001**
Nitrate	0.117	1	0.117	2.574	0.122
Sex	**0.472**	**1**	**0.472**	**15.609**	**0.001**
Temperature × Nitrate	0.185	5	0.037	0.810	0.554
Temperature × Sex	0.108	5	0.022	0.713	0.620
Nitrate × Sex	0.047	1	0.047	1.561	0.224
Temperature × Nitrate × Sex	0.173	5	0.035	1.141	0.366
Jar (Temperature × Nitrate)	1.094	24	0.046	1.506	0.161
Sex × Jar (Temperature × Nitrate)	0.726	24	0.030	1.539	0.054
Residual	5.664	288	0.020		

Do morphological traits predict reproduction?

In May, approximately 73% of the variation in the extent of reproduction tissue down the central lamina was explained by kelp morphology (R^2 = 0.727, $F_{6,136}$ = 60.469, p < 0.001), while in July, only 37% of the variation in the extent of reproduction tissue down the central lamina was explained this way (R^2 = 0.374, $F_{6,113}$ = 11.234, p < 0.001). Of all predictor variables, lamina length and stipe diameter were the only two with significant and positive linear relationships with the amount of reproduction. Examination of the partial residual plots for these 2 factors against reproduction showed that only lamina length was a strong and significant predictor of the extent of reproduction tissue down the central lamina (May: R^2 = 0.667, p < 0.001; July: R^2 = 0.324, p < 0.001), while stipe diameter, although significant, was weakly correlated with reproduction (May: R^2 = 0.043, p = 0.015; July: R^2 = 0.054, p = 0.012).

Effects of temperature and nitrates on growth and development

The surface area of gametophytes 16 d after spore release differed significantly between sex and temperature (Table 3). Males had a larger surface area than females, while at temperatures less than 15°C and greater than 22°C, gametophytes were significantly smaller than at temperatures between 15 and 22°C (Fig. 6). Noticeably, gametophytes grown at 25.5°C were significantly smaller in surface area than those grown at all other temperatures. There was no effect of nitrates on growth and no significant Tem-
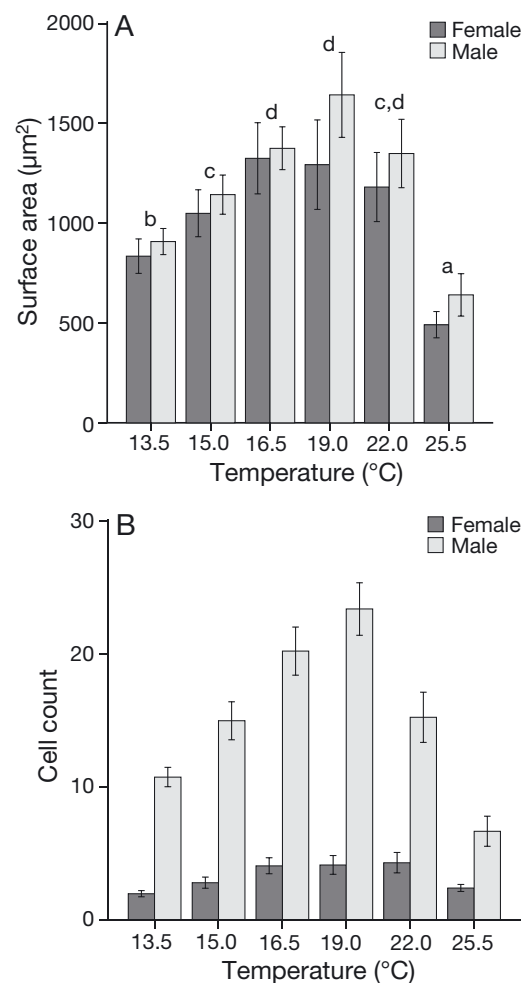

Fig. 6. *Ecklonia radiata*. (A) Variation in surface area of male and female gametophytes across 6 temperatures; (B) variation in cell count of male and female gametophytes across 6 temperatures. Bars show mean ±1 SE. For (A), means sharing letters are not significantly (p > 0.05) different from one another

Table 4. *Ecklonia radiata*. ANOVA testing the effects of temperature, nitrates and sex on gametophyte cell count with jar replicates included as a nested term. Cell count data were $\log_{10}$ transformed prior to analysis to meet ANOVA homogeneity of variance assumptions. Significant (p < 0.05) factors in **bold**

Source	SS	df	MS	*F*	p
Temperature	5.443	5	1.089	52.181	<0.001
Nitrate	0.121	1	0.121	5.788	0.024
Temperature × Nitrate	0.303	5	0.061	2.903	0.035
Sex	28.338	1	28.338	1341.175	<0.001
Nitrate × Sex	0.008	1	0.008	0.370	0.549
Temperature × Sex	1.257	5	0.251	11.903	<0.001
Temperature × Nitrate × Sex	**0.319**	**5**	**0.064**	**3.018**	**0.030**
Jar (Temperature × Nitrate)	0.501	24	0.021	0.987	0.512
Sex × Jar (Temperature × Nitrate)	**0.507**	**24**	**0.021**	**1.731**	**0.020**
Residual	3.516	288	0.012		

Table 5. *Ecklonia radiata*. ANOVA testing the effects of temperature and nitrates on sporophyte surface area with jar replicates included as a nested term. Sporophyte surface area data had heterogeneous variances (Cochran's *C*-test: p < 0.05) and were $\log_{10}$ transformed prior to analysis to meet ANOVA homogeneity of variance assumptions. Significant (p < 0.05) factors in **bold**

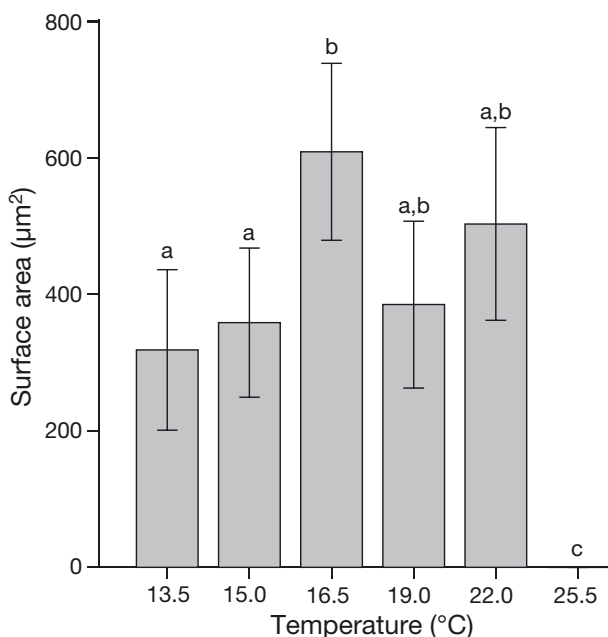| Source	SS	df	MS	*F*	p
Temperature	**187.269**	**5**	**37.454**	**83.501**	**<0.001**
Nitrate	1.003	1	1.003	2.236	0.148
Temperature × Nitrate	5.789	5	1.158	2.581	0.053
Jar (Temperature × Nitrate)	10.765	24	0.449	0.493	0.973
Residual	65.449	72	0.909		

Fig. 7. *Ecklonia radiata*. Variation in the surface area of microscopic sporophytes in 6 treatments of temperature. Bars show mean ±1 SE. Means sharing letters are not significantly (p > 0.05) different from one another

perature × Nitrate interaction. In contrast to surface area, the number of cells per individual was highly variable. There was a significant Temperature × Nitrate × Sex interaction (Table 4), indicating that within each Temperature × Nitrate × Sex combination cell count was variable and the main effects above this term for cell count cannot be further interpreted. There was also significant random variation among jars for each treatment combination [significant Sex × Jar (Temperature × Nitrate)] (Table 4).

For sporophyte surface area, there were significant differences among temperatures but no significant effect of nitrate and no significant Temperature × Nitrate interaction. Most notably, no sporophytes developed in the 25.5°C treatment. Sporophytes at 16.5°C had a significantly larger surface area than those of the 2 lower temperatures, while there were no significant differences in surface area for sporophytes grown in the 16.5°C, 19°C and 22°C treatments (Table 5; Fig. 7).

DISCUSSION

Globally, the world's oceans are becoming warmer and major ocean currents are shifting, resulting in demographic and distributional shifts in important marine species (Parmesan 2006, Poloczanska et al. 2007). Stronger EAC penetration into southeastern Australian coastal waters is already causing shifts in species distributions (Johnson et al. 2005, Ling et al. 2009a,b, Johnson et al. 2011, McLeod et al. 2012a,b), with SST in the region predicted to increase by up to 3.0°C by the year 2100 (Rochford 1984, Ridgway 2007). Because increased temperatures and reduced nitrates represent forcing factors for kelp, understanding how they impact the reproduction and development of *Ecklonia radiata*, the most abundant and widely distributed canopy-forming kelp in Australia, is important. Our findings show clear effects of increasing temperature (but not reduced nitrates) on the development and growth of microscopic life-cycle stages and indicate that because reproduction is linked to morphology, any temperature- or nitrate-driven changes to morphology may also have implications for reproduction.

Morphology

The morphology of *Ecklonia radiata* was highly variable within and among 6 eastern Australian sites, in line with previous broad-scale observations of *E. radiata* morphology among NSW, South Australia and Western Australia (WA) (Wernberg et al. 2003, Fowler-Walker et al. 2005) and along a 6° latitudinal gradient on the WA coast (Wernberg et al. 2010). Our study incorporated a strong latitudinal aspect (~8.5°), and some differences in traits occurred between NSW and Tasmanian sites. This suggests that although there is high local-scale variation in *E. radiata* morphology, there are also regional-scale differences, as suggested by previous studies (Chesson 1996, Fowler-Walker et al. 2005). Tasmanian populations of *E. radiata* typically had a larger morphology compared to NSW populations, especially for thallus length and lateral length. Nonetheless, the large variation in *E. radiata* morphology within and among sites was notable; a striking example of this occurred between the 2 closest sites in NSW, Bare Island and Long Bay, for thallus length and lamina length. This local variation makes interpreting the overall causes of local-scale morphological patterns difficult but highlights the importance of small-scale processes such as wave exposure, water depth (Fowler-Walker et al. 2005) and nitrates that may be associated with localised anthropogenic input. Currently, there appears to be slightly greater wave power in NSW than eastern Tasmania. Given that wave height and speed are forecast to increase globally (Young et al. 2011), it is likely that wave activity will continue to modify the morphology of wave-exposed *E. radiata*.

Temperature and nitrates, among other factors, are recognised as key drivers for large-scale growth and, hence, morphological differences in adult laminarians (Dayton 1985, Fowler-Walker et al. 2005, Graham et al. 2007), with age often being a weaker predictor of growth and morphology (Chapman 1986). For example, in WA, *Ecklonia radiata* growth rates are reduced when water temperatures exceed 20°C (Hatcher et al. 1987) and adult *E. cava* transplanted from warmer to cooler water increased in size relative to their non-transplanted cohorts, highlighting a plastic response in adults to temperature (Serisawa et al. 2002). The morphological differences between Tasmania and NSW (annual mean SSTs: Tasmania ~14.0°C; NSW ~19.5°C) suggest both morphological and growth responses to temperature variation. However, SST may not be the only large-scale contributing forcing factor to the patterns observed. On regional scales, nitrates may also influence growth

and morphology, and in the field, they are negatively correlated with temperature. *In situ* nitrate addition experiments with *Macrocystis pyrifera* demonstrated increased survivorship, growth rates and larger phenotypic plasticity in response to high nitrate levels compared to *M. pyrifera* in low nitrate (and higher temperature) conditions associated with El Niño events in California (Dayton 1985, Dean & Jacobsen 1986).

Furthermore, the extent to which the morphological differences reflect genetic vs. environmental influences is not clear, as the heritability of these traits is not known. There are genetic differences between *Ecklonia radiata* from Tasmania and NSW (Dolman & Coleman 2008), but phenotypic plasticity for *Ecklonia* morphology has been demonstrated in transplanted individuals (Serisawa et al. 2002, Fowler-Walker et al. 2006). Regardless of the degree to which morphology is plastic or heritable, because *E. radiata* generally have a smaller size in the warmer waters of NSW than in Tasmania, increased temperatures from EAC strengthening may contribute to a reduction in adult *E. radiata* size in southeastern Australia. Under such a scenario, there are implications for kelp forest architecture and potentially how *E. radiata* engineers the surrounding environment (Wernberg & Thomsen 2005) and impacts associated species.

Reproduction

Although quantifying the amount of reproductive tissue per thallus by measuring the extent of reproductive tissue down the central lamina, from the distal end of the thallus, is only one method for quantifying reproduction (Patten & Yarish 1993), it allowed for a rapid and relative comparison of reproduction (as a function of lamina length) over biogeographical scales. Laminarians generally exhibit seasonal variation in reproductive output which can vary with location and depth due to changes in temperature and light (Bolton & Levitt 1985, Joska & Bolton 1987). Reproductive seasonality in *Ecklonia radiata* has been previously recorded in Tasmania (Sanderson 1990) and WA (Mohring et al. 2013) and is likely to occur in NSW. The differences in *E. radiata* morphology are important, as central lamina length was a strong predictor of reproduction in May when reproduction was highest. Lamina length was still a strong predictor of reproduction in July and September when reproduction declined and when the ANCOVA assumption of homogeneity of slopes was violated.

For July and September, heterogeneous slopes are interpreted as the relationship between reproduction and the covariate (lamina length) differing between regions and/or among sites within regions, highlighting the high variability for reproduction in these months. This variability may be an effect of sampling outside the main reproductive window of *E. radiata* at these locations (Mohring et al. 2013). Positive size-fecundity relationships often occur in sessile organisms including plants (Aarssen & Clauss 1992) and laminarians (Reed et al. 2004, Underwood et al. 2000). The regional differences in reproduction may also reflect a response to higher mean annual temperatures (i.e. NSW) as observed for other kelp (e. g. *Laminaria longicruris*, Patten & Yarish 1993), a response to lower nitrates as observed in *Macrocystis pyrifera* (Reed et al. 2004) or a response to a combination of both factors (Dayton 1985, Dean & Jacobsen 1986). Because lamina length covaries with reproduction, smaller size in *E. radiata* under higher temperatures suggests reduced reproductive capacity.

Effects of temperature and nitrates on *Ecklonia radiata* development

Temperature also had strong effects on the development of microscopic stages of *Ecklonia radiata*. Both the gametophyte stage (measured at 16 d post-settlement) and sporophyte stage (measured at 32 d post-settlement) experienced optimum growth between temperatures of 16.5 and 22.0°C. In suboptimal temperatures (above 22.0°C), gametophytes grew the least, and no sporophytes had emerged by Day 32, highlighting a potential temperature threshold for *E. radiata* development. The 25.5°C temperature treatment reduced but did not stop gametophyte growth. The absence of sporophytes at this temperature does not necessarily deem them incapable of growth at this temperature but suggests that no successful fertilization occurred. The mechanism by which this may happen is not known but may result from arrested development of male or female gametes due to gametes being infertile or not functioning normally (e.g. antherozoids being unable to swim or respond to pheromones) or post-fertilisation mortality (Muñoz et al. 2004). This may also reflect a temperature-mediated seed bank strategy in *E. radiata*, with gametogenesis occurring within a narrower temperature range than gametophyte growth and survival (tom Dieck 1993). Furthermore, the optimum temperature range may influence the timing of fertilization, as gametogenesis may be a function of temperature. We were unable to determine the precise moment of temperature-dependent gametogenesis from our photographs, but this is an area for future research.

As nitrates did not have a significant impact on gametophytes and sporophyte growth, temperature-driven latitudinal effects appear more important and may determine upper survival temperature thresholds for microscopic *Ecklonia radiata* in Tasmania. An upper survival temperature of 28°C was found previously for Tasmanian *E. radiata* gametophytes (tom Dieck 1993). In New Zealand, *E. radiata* gametophytes sourced from cooler waters exhibited lower maximum temperature thresholds and followed the same pattern of reduced growth and no reproduction when exposed to such temperature extremes (Novaczek 1984a), suggesting localised adaptation to local temperature. Our cultured spores were sourced from Stage 3 adults in Bicheno, Tasmania, at a depth of 10 m (latitude ~42°S), where temperatures fluctuate annually around a mean of ~15°C with a summer maxima of ~19.0°C. Upper survival temperature thresholds may be different for gametophytes and juvenile sporophytes (Novaczek 1984a, tom Dieck 1993) in NSW, where the average annual temperature is ~20°C. Examining the tolerance of gametophytes and juvenile sporophytes sourced from multiple locations across latitudes, to the same experimental temperatures and nitrate concentrations, could determine whether similar tolerances occur or whether juveniles from warm-water locations are adapted to those conditions. In contrast to other experiments where optimum temperatures were found for kelp gametophyte cell count (e.g. *E. maxima*, Bolton & Levitt 1985), there was high variability in gametophyte cell count across treatments, suggesting variable levels of cell division and growth. The number of cells in male gametophytes peaked at 19°C and presumably allows an excess of antheridia production and a higher probability of fertilisation success. The absence of a difference in the surface area of gametophytes or sporophytes between high and low nitrates concurs with results for high (9 µmol l^{-1} NO$_3$) and low (~2 µmol l^{-1} NO$_3$) nutrient effects on the surface area *Macrocystis pyrifera* sporophytes in California under different light conditions (see Kinlan et al. 2003) but contrasts to findings for *M. pyrifera* in Chile, where females grew larger at high nitrate concentrations (although nitrate concentrations were not stated, Muñoz et al. 2004).

Generally, Laminariales gametophytes have a higher temperature tolerance than macroscopic adults (sporophytes) (tom Dieck 1993). If experimen-

tal results for microscopic stages of *Ecklonia radiata* are translated into a field scenario, the temperature tolerance of macroscopic adults may be a limiting factor for *E. radiata* distribution. However, the finding of an upper temperature threshold for sporophyte development suggests temperature effects on the microscopic stages may be critical.

CONCLUSION

Climate-induced changes to ocean temperatures and currents which affect important habitat-forming species, such as *Ecklonia radiata*, will have broad impacts on coastal food webs. Our study highlights some of the likely consequences for *E. radiata* morphology, reproduction and development given future climate scenarios. Such information is important for predicting impacts of EAC strenghtening on southeast Australian kelp forests, and can contribute to reducing uncertainty for stakeholders with a vested interest in kelp ecosystems, whilst contributing information towards human adaption to climate change.

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