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Reproductive seasonality and early life temperature sensitivity reflect vulnerability of a seaweed undergoing range reduction

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ABSTRACT: Temperature is a major determinant of the performance and geographical ranges of marine species. Changes in temperature can therefore result in localised mortality and shifts in species distributions, but the phenology and temperature sensitivity of many important habitat-forming seaweed species has not yet been investigated. Through field observations and culture growth experiments, the present study investigated the temperature sensitivity of reproductive timing, early post-settlement growth and survival, and recruitment success of the widespread foundation seaweed *Scytothalia dorycarpa* in Australia. In culture, the highest settlement densities and lowest mortality rates were achieved at 15°C, and optimal temperatures for germling fertilisation occurred at 18°C, whereas temperatures greater than 20°C delayed germling settlement and significantly increased mortality rates, with no germlings surviving at temperatures greater than 23°C. Experimental findings were consistent with field observations that found adult reproductive development and gamete release to occur in synchronous pulses throughout the winter months, when seawater temperatures were ~18°C. Surveys of the latitudinal distribution of *S. dorycarpa* recruits showed significantly lower recruit densities in warmer, low-latitude reefs where summer maximum temperatures often exceed 23°C compared to much higher recruit densities in cooler pole-ward reefs where average summer maximum temperatures are 21 to 22°C. The timing of reproduction, latitudinal distribution of recruits and culture temperature optima all indicate high temperature sensitivity among the early life stages of *S. dorycarpa.* These findings help to explain the rapid range contraction of this species following a 2011 marine heatwave off the southwest coast of Australia.

KEY WORDS: Thermal tolerance · *Scytothalia* · Macroalgae · Reproduction · Recruitment · Germling · Distribution · Range contraction · Extreme event · Heat wave · Western Australia

INTRODUCTION

Temperature directly affects the survivorship, growth, reproduction and recruitment of most marine organisms, including seaweeds (Bolton & Lüning 1982, Lüning et al. 1990, Kordas et al. 2011), and temperature is a strong driver of species distributions (Setchell 1915, Van Den Hoek 1982, Breeman 1988, Tuya et al. 2012). Knowledge of the physiological responses of individual species to temperature, knowledge of their thermal limits to performance and identification of the life stages most susceptible to temperature variability is therefore necessary to understand the causes of geographical range expansion or contraction resulting from global warming and extreme climatic events

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*Corresponding author: thomas.wernberg@uwa.edu.au (e.g. Walther et al. 2002, Root et al. 2003, Wernberg et al. 2011a). Understanding the physical thresholds leading to changes in species distributions holds particular significance for functionally important species whose addition or removal can result in cascading and often devastating effects on other species within the ecosystem (Ling 2008, Wernberg et al. 2013).

In the austral summer (January to April) of 2011, habitat-forming seaweeds along the south-western coast of Australia were severely affected by a marine heatwave, whereby soaring sea surface temperatures reached unprecedented levels >3°C above long-term monthly averages for several consecutive weeks (Feng et al. 2013, Pearce & Feng 2013, Wernberg et al. 2013). In the wake of this 'marine heatwave', many biological effects were reported, including extensions and contractions in species distributions, variations in recruitment and growth-rates, impacts on trophic relationships and altered catch rates of exploited species (Pearce et al. 2011, Depczynski et al. 2012, Smale & Wernberg 2012, Wernberg et al. 2013). Dominant seaweeds were particularly impacted, with large-scale decimations of important habitat formers. For example, the laminarian kelp *Ecklonia radiata* and the endemic fucoid *Scytothalia dorycarpa*, which jointly contribute ~70% of the local seaweed canopy cover, significantly decreased due to the stressful conditions induced by the localised high temperatures (Wernberg et al. 2013). Strikingly, *S. dorycarpa* was completely eradicated from its northern range edge, resulting in a poleward contraction of up to 100 km (Smale & Wernberg 2013).

Canopy-forming seaweeds play a key role in maintaining marine biodiversity by facilitating whole communities of organisms through habitat creation (Dayton 1972, Stachowicz 2001, Irving et al. 2004, Thomsen et al. 2010), and therefore, the loss of *Scytothalia dorycarpa* is likely to have widespread ecological consequences (Smale & Wernberg 2013). However, very little is currently known about this habitat-forming fucoid, which is highly abundant throughout southern Australia. For example, online searches for articles in the ISI Web of Knowledge database currently return only 8 results for *Scytothalia*, which is substantially less than for the co-occurring canopy species *Ecklonia* and *Sargassum* which return 131 and 90 records, respectively (search performed 10 September 2013; for each genus, the search term included 'AND Australia'). The monospecific genus *Scytothalia* is endemic to southern Australia (Huismann 2000), having likely evolved from the cool temperate Tethyan marine flora on the south coast (Phillips 2001). The microscopic propagule stage and the early post-settlement stage of seaweeds are generally more susceptible to physical and biological stresses than adults (Brawley & Johnson 1991, Lotze et al. 2001) and often represent a 'bottleneck' in the development and maintenance of seaweed populations (Steen & Scrosati 2003). Nevertheless, recruitment is ultimately important for the maintenance of most seaweed populations and plays a substantial role in stabilising densities of adults (e.g. Deysher & Norton 1981, Kendrick & Walker 1994). Whilst strong correlative evidence between declining *S. dorycarpa* abundance and increasing water temperatures along latitudinal gradients has led to suggestions of its value as an indicator species for climate impacts (Smale et al. 2010, Wernberg et al. 2011b, Smale & Wernberg 2013), very little is known about the seasonal timing of development and thermal tolerance throughout its life history. Developing our understanding of such processes is critical in order to understand the capacity of such species to cope with both gradually increasing ocean temperatures and extreme events, such as the 2011 marine heatwave.

The aim of the present study, therefore, was to determine the seasonal timing of gamete development and release of *Scytothalia dorycarpa* and to identify the optimal and lethal temperatures for its settlement, early post-settlement growth and survival. We then aimed to examine whether these temperatures were reflected in its geographical patterns of recruitment within cooler and warmer locations along its west coast distribution. Given the species' observed vulnerability to the 2011 marine heat wave, we predicted that optimal settlement and growth temperatures would reflect water temperatures found at the cooler end of the species range (<20°C), whereas lethal limits would occur in waters similar to summer maxima in northern populations (23°C). Furthermore, we predicted that recruitment rates of *S. dorycarpa* would be highest at the cooler locations and lowest toward the warm water limit of its geographical distribution.

MATERIALS AND METHODS

Study region

The temperate west coast of Australia is characterised by a relatively shallow (5 to 15 m) subtidal limestone platform, which extends 5 to 10 km out from the intertidal zone and runs virtually uninterrupted along the coast between Geraldton (~28° S) and Cape Leeuwin (~34° S), beyond which sandstone and granite intrusions dominate the reef geomorphology. *Scytothalia dorycarpa* is abundant along the coast poleward of ~31° S, the current range edge of the species (Smale & Wernberg 2013). The sea water temperature for this coast is highly influenced by the warm, poleward-flowing Leeuwin current and ranges between mean summer maxima of 22 to 24°C and winter minima of approximately 17 to 19°C for Hamelin Bay and Jurien Bay respectively (Fig. 1). Due to the directional flow of the current, upwelling is suppressed (Pearce 1991), resulting in consistently low nutrient concentrations (Lourey et al. 2006, Wernberg et al. 2010) and a gradual temperature gradient of 1 to 3°C (Smale & Wernberg 2009). Seaweed grazing pressure from herbivorous fishes and invertebrates is also relatively low and consistent among locations (Vanderklift et al. 2009), creating relatively consistent biotic and environmental conditions throughout the region with the exception of temperature (Smale & Wernberg 2009, Wernberg et al. 2010).

Field observations of receptacle development

From January to September 2012, 20 collections of *Scytothalia dorycarpa* specimens were made from 3 subtidal reefs (at least 1 km apart) within Marmion Marine Park, Perth, Western Australia (31° 47.5′ S, 115° 42.0′ E; Fig. 1). At each collection, 12 large individual seaweeds were sampled from each reef. Receptacles (reproductive structures) were examined under a dissecting microscope, and the reproductive maturity of *Scytothalia* was recorded by assessing the frequency of individuals with receptacles containing (1) mature gametes, (2) developing gametes or (3) empty gametangia (section of reproductive structure in which the gametes are produced). In the fucoid life cycle, a diploid adult produces haploid eggs and spermatozoids, which, following fertilisation, develop directly into diploid juveniles and grow into adult thalli. In the present paper, we refer to haploid stages as 'gametes' and post-settlement fertilised stages as 'germlings'. Receptacles were classified as holding 'mature gametes' based on the presence of either already extruded gametes in an external mucilage layer surrounding the receptacle and/or gametes being extruded

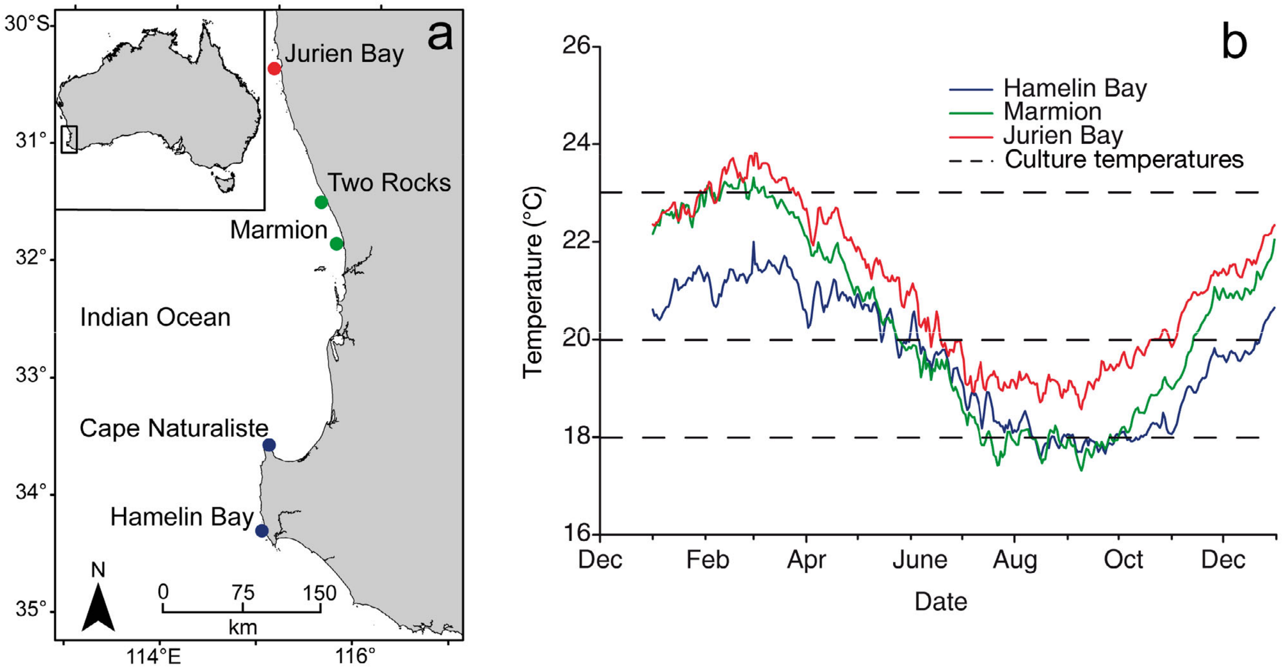


Fig. 1. (a) South-western Australia: blue spots illustrate the 'cool' study locations, green spots illustrate the 'warm' study locations, and the red spot marks the former range edge of *Scytothalia dorycarpa* up until 2011 (Smale & Wernberg 2013). (b) Daily mean seawater temperature averaged from 2006 to 2010. The black dashed lines illustrate 3 of the 4 temperatures from the germling culture experiment. Temperature data comes from values averaged across 3 long-term Tidbit temperature loggers recording at ~10 m depth within each of the respective locations. The Hamelin Bay and Marmion loggers were situated within 1 to 3 km of the study sites

through the conceptacle (pits within the reproductive structures where the gametes are formed). Receptacles were classified as holding 'developing gametes' if there were visible signs of gametogenesis, such as swollen receptacles with darkened conceptacle pits (e.g. Fig. 2 insert), and if, upon dissection, the gametangia were visibly holding immature gametes.

Culture of early post settlement stages

Germling growth was recorded over 4 temperature treatments: 15°C, 18°C, 20°C and 23°C with 3 replicate 10 l aquaria (280 × 200 × 150 mm) within each treatment. Temperatures were chosen to reflect the annual temperature range of reefs along *Scytothalia dorycarpa's* west coast distribution. Each tank contained unfiltered seawater and was lined with 12 sand-blasted acrylic settlement plates (30 × 100 mm). Accurate, stable temperatures (±0.2°C) were provided using 50 W adjustable Jager aquarium heaters, individually calibrated using HOBO temperature loggers. The coolest treatment temperature tanks (15°C) were immersed in a 'cool bath' held at 13°C by a TECO TR10 chillier unit. Each treatment received natural light with an average daily maximum between 10 and 20 µmol m^{-2} s^{-1} and natural photoperiod (~11.5 to 12 daylight hours). Individual aquaria were vigorously aerated throughout the duration of the experiment using 200 mm aquarium air stones. A total of 25% of the seawater in the experimental aquaria was changed every 3 d, the salinity was monitored daily with a hand-held refractometer, and levels were kept constant by adding small amounts of deionised water as required.

Collection and treatment methods of *Scytothalia dorycarpa* for the growth experiment were developed from previous studies on similar fucoids (e.g. Pollock 1970, McLachlan et al. 1971, Norton 1977, Niemeck 1978). Four adult *S. dorycarpa* with fertile receptacles were collected from 3 subtidal reefs (n = 12) within Marmion Marine Park, Western Australia (described above), on 9 September 2012 and transported to the laboratory in darkness using moist calico bags. The seaweeds were brushed to eliminate surface epiphytes, vigorously washed with deionised water for several minutes and laid out to dry on paper tissue at room temperature at an irradiance of ~30 µmol photons m^{-2} s^{-1}. After 1 h, 12 thallus sections (~10 cm in length) containing high densities of receptacles were excised from each seaweed, mixed together and evenly distributed among the replicate aquarium tanks. Seaweed sections were left in the aquaria for 24 h to induce the release of gametes, after which time they were discarded to avoid interferance with settlement.

After 12 h, 36 h, 3 d, 1 wk and 2 wk of treatment, 2 randomly selected settlement plates were destructively sampled from each replicate tank. The total number of settled germlings, fertilisation status and mortality were observed for each slide using a light microscope. Fertilisation was categorised as any early sign of cell division or asymmetry of the germling, and germlings that had structurally collapsed were considered dead.

Latitudinal distribution of recruits

Recruit densities were sampled along a ~400 km stretch of north-south running coastline in the southwest of Australia, covering the latitudes 34° S to 31° S (Fig. 1). Northern locations were Two Rocks (31° 29.0′ S, 115° 32.1′ E) and Marmion (31° 47.3′ S, 115° 01.1′ E). Southern locations were Cape Naturaliste (33° 32.0′ S, 115° 02.0′ E) and Hamelin Bay (34° 15.2′ S, 115° 01.1′ E). At each location, 3 reefs were sampled (at least 1 km apart). Sites were selected based on the presence of mixed seaweed canopies, consisting of *Scytothalia dorycarpa*, *Sargassum* spp. and *Ecklonia radiata*. '*Sargassum*' in the present paper is used to denote a complex of several species, primarily from the *Arthrophycus* subgenus, which cannot be differentiated as recruits. At each reef, the density of adults and recruits were recorded within 20 randomly placed 0.5 × 0.5 m quadrats (each at least 10 m apart). Recruits were classified into 3 size classes (0–5 cm, 5–10 cm and 10–20 cm) and did not have receptacles. All reefs were sampled in austral autumn (28 April 2012 to 2 May 2012) and resampled in winter (2 July 2012 to 8 July 2012).

Statistical analysis

One-way analysis of variance (ANOVA) using R statistical software (R Development Core Team 2012) was used to test the null hypothesis that no differences in settlement densities (living and non-living), survivorship (total surviving settled germling densities) and percentage of survivorship among temperature treatments (fixed factor) would be found throughout the culturing experiment after (1) 3 d, (2) 1 wk and (3) 2 wk. Data were checked for normality and homogeneity of variance through visual inspection of scatter plots and the distribution of residuals.

Percentage of survivorship was transformed for the analyses using a square root-arcsine transformation to account for the bound structure of the data. Tukey's HSD post-hoc analyses were performed on significant results, to determine the among-treatment differences in surviving germling density and fertilisation rates.

Permutational analysis of variance (PERMANOVA; Anderson 2001) using Primer 6 software was used to test (1) the null hypothesis that no differences in recruit densities would be detected among seasons (fixed, orthogonal factor) and locations (fixed factor) for each of the 3 seaweed species (*Scytothalia dorycarpa*, *Ecklonia radiata* and *Sargassum* spp.) and (2) the null hypothesis that no differences in recruit densities would exist among seasons and locations for 3 *S. dorycarpa* recruit size categories (0–5, 5–10 and 10–20 cm). These analyses were based on Euclidian distances and 999 permutations of the residuals under a reduced model. An *a priori* planned contrast (Two Rocks and Marmion vs. Dunsborough and Hamelin Bay) tested for differences between southern and northern latitudinal regions.

RESULTS

Field observations of receptacle development

Monthly observations of the development of *Scytothalia dorycarpa* receptacles indicated that gametes started to develop in late March (Fig. 2). Samples collected on 24 March showed the first sign of swollen receptacles with darkened surfaces (e.g. Fig. 2a inset). In any one individual, the development of receptacles was at a similar state of maturity. However, there was considerable variation among individuals. The percentage of *S. dorycarpa* sampled with developing gametes steadily increased from March to May. Developing gametes were not considered mature until they were found to excrete gametes, which first occurred 6 wk after the first signs of development on 5 May. Throughout May to August, >70% of *S. dorycarpa* were consistently found to release mature gametes, whilst still developing immature gametes. Throughout July and August, specimens had developing and mature gametes on almost all occasions. September was the first month in the reproductive season that the percentage of receptacles with mature gametes (75%) exceeded those still developing gametes. Receptacles on 42% of *S. dorycarpa* had empty gametangia, potentially indicating the final pulse of release for the season.

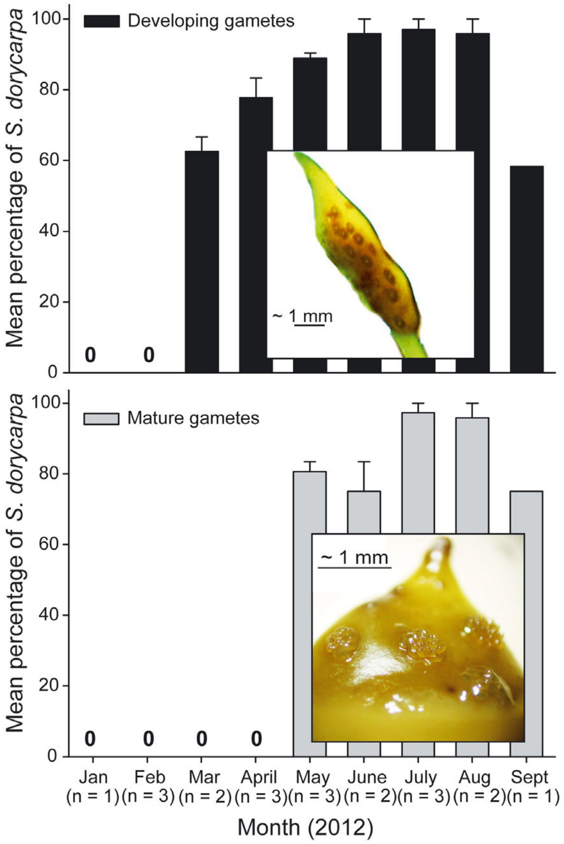


Fig. 2. Seasonality of receptacle development of *Scytothalia dorycarpa*. Mean percentage of *S. dorycarpa* sampled (a) with developing gametes (inset: swollen receptacles with darkened patches = conceptacles) and (b) with mature gametes (inset: mature gametes being extruded through receptacle osteole). Mean values ± 1 SE (n = number of collection days)

The expulsion of gametes in *Scytothalia dorycarpa* was a repeated synchronous occurrence, with all mature individuals in the same stand extruding their gametes simultaneously (spawning). Following an extended stormy period in May/June, *in situ* observations recorded that the receptacles of 94% of *S. dorycarpa* were bearing gametes externally in an outer mucilage layer (e.g. Fig. 3). In calm conditions following the storm, the receptacles had 'shed' their gametes within 5 d. There were no evident patterns of expulsion associated with lunar or tidal cycles, and the exact timing of expulsion varied among locations.

Culture of early post-settlement stages

Settlement densities increased over time in the 15, 18 and 20°C treatments; however, very few germlings were observed at 23°C, and of those few, zero survived (Fig. 4). Significant differences among tem-

Fig. 3. *Scytothalia dorycarpa* receptacles holding gametes externally in mucilage, June 2012

perature treatments were observed after 3 d, 1 wk and 2 wk (Table 1a), and the 15°C treatment had higher densities of alive germlings than both the 20 and 23°C treatments at every time interval (Fig. 4). The 18°C treatment had significantly higher living germling densities than 23°C at every time period but did not statistically differ from the 20°C treatments, despite averaging slightly higher densities. Despite a substantial rise in settlement densities after 2 wk across 3 of the culture temperatures, survivorship significantly decreased with increasing temperature, and at 20°C, 90 % of these germlings were dead after 2 wk, whilst no surviving germlings were found at 23°C (Table 1c).

Temperature also significantly affected fertilisation rates, with the percentage of fertilised germlings significantly higher in 15°C and 18°C treatments throughout the duration of the experiment (Fig. 5). The 15°C and 18°C treatments consistently displayed significantly higher fertilisation rates than the 20°C treatment and in particular the 23°C treatment, where no fertilised individuals were observed throughout the experiment. Germling growth rates varied markedly within treatments, and their size (excluding rhizoid) ranged from 300 to 700 µm after 2 wk. Germination of germlings (e.g. Fig. 6b) was faster at 18°C, with over 50 % having fertilised within 12 h (Fig. 5) compared to no fertilisation of germlings cultured at 15°C over the same time. After 3 d, 100 % of the surviving germlings cultured at 15°C and 18°C and 20°C had fertilised.

Latitudinal study of recruit densities

Recruit densities for *Scytothalia dorycarpa* were significantly higher in southern locations (16.2 ± 16.5 recruits m^{-2}) compared to northern locations (1.5 ± 2.6 recruits m^{-2}; Table 2, Fig. 7). For each size category, recruit densities in southern locations were significantly higher than recruit densities in northern locations and were consistently higher in southern locations over both autumn and winter. There were consistently more *S. dorycarpa* recruits at Cape Naturaliste than at all the other locations in autumn and winter. Small *S. dorycarpa* recruit densities were ~4-fold higher at Cape Naturaliste than all other locations, and there was a significant difference in the densities of this size category for locations interacting with the season (Fig. 7, Table 2c).

Ecklonia radiata recruit densities were significantly different amongst locations (Table 3), and although there was no significant difference between regions, densities were generally higher in southern locations (3.5 ± 4.6 recruits m^{-2}) than northern locations (2.4 ± 2.6 recruits m^{-2}). There were significant interactions between season × location and season × region for *Sargassum* recruit densities (Table 3). *Sargassum* recruits were the most abun-

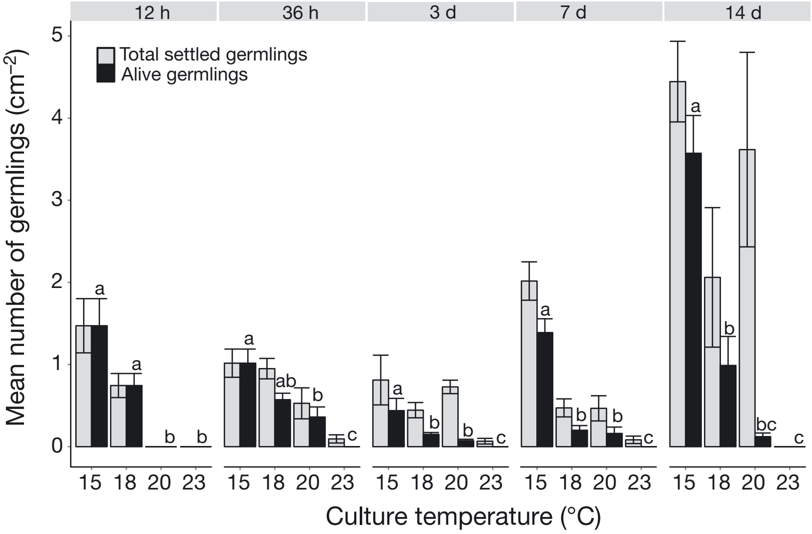


Fig. 4. *Scytothalia dorycarpa.* Mean (±1 SE) settlement densities (cm^{-2}) of germlings cultured at 15, 18, 20 and 23°C (n = 4). Bars indicate mean densities of (grey bars) total settled germlings (dead and alive) and (black bars) living settled germlings. Letters indicate significant differences in the number of 'Alive germlings' among the 4 temperature treatments, based on Tukey HSD post-hoc results. Separate ANOVAS were performed for each time period

Table 1. Single-factor analysis of variance (ANOVA) testing for differences in *Scytothalia dorycarpa* germling (a) settlement density (total number of settled germlings, dead and alive), (b) survivorship (total number of alive germlings) and (c) survivorship percentage (square-root arcsine transformed) between different temperature treatments ranging from 15 to 23°C at 3 d, 1 wk and 2 wk of culture. Values in **bold** are significant with $p < 0.05$

Source	df	3 d			1 wk			2 wk		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
(a) Settlement density										
Temperature	3	610.00	4.17	**0.02**	3970.70	31.90	**<0.01**	20640.10	6.47	**<0.01**
Error	20		146.10			124.49			3191.6	
(b) Survivorship										
Temperature	3	199.90	6.44	**<0.01**	2212.80	43.55	**<0.01**	6638.50	43.55	**<0.01**
Error	20		31.10			50.81			50.81	
(c) Survivorship percentage										
Temperature	3	1.51	15.65	**<0.01**	0.99	17.86	**<0.01**	1.48	32.40	**<0.01**
Error	20		0.07			0.06			0.05	

dant of all species, with densities averaging 22.1 ± 21.5 recruits m^{-2} in southern locations, which was similar to the densities in northern locations (19.3 ± 20.9 recruits m^{-2}).

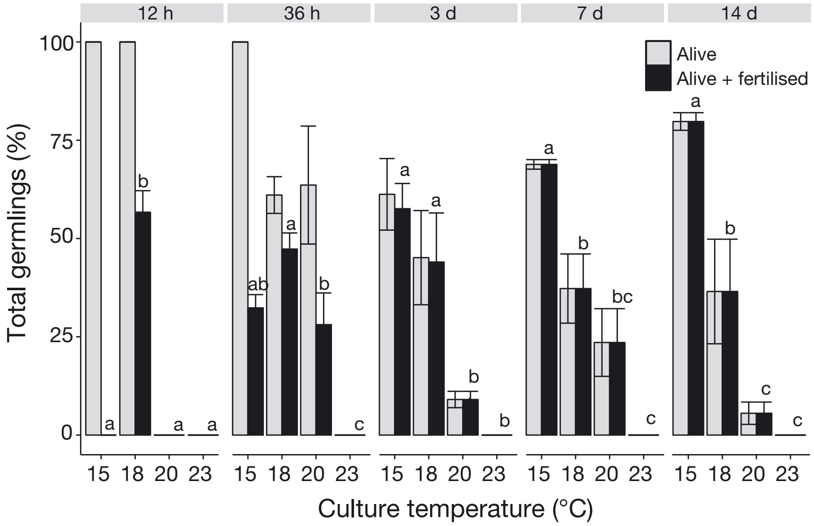
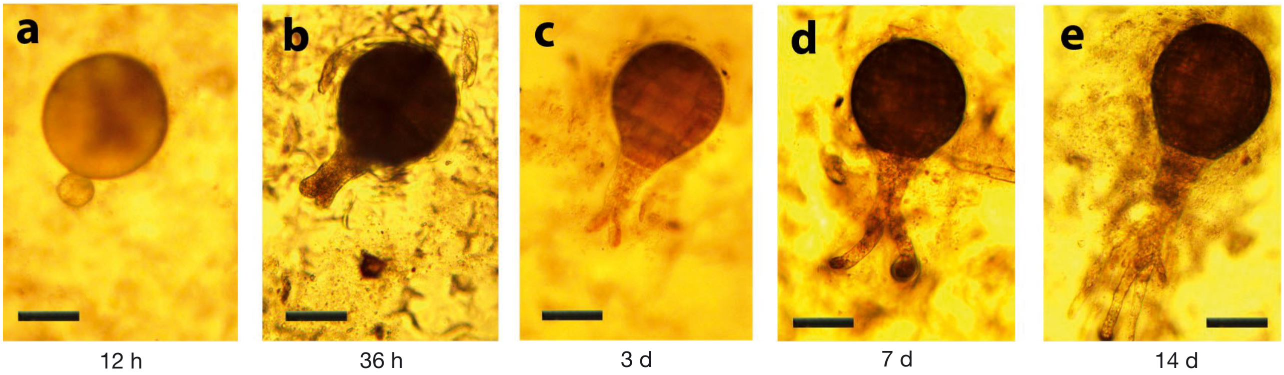


Fig. 5. *Scytothalia dorycarpa*. Mean (±1 SE) percentage of living settled germlings cultured at 15, 18, 20 and 23°C (n = 4). Grey bars indicate mean percentage of living germlings, and black bars indicate the mean density of fertilised germlings. Letters indicate significant differences in the percentage of fertilised germlings among the 4 temperature treatments, based on Tukey HSD post-hoc results. Separate ANOVAS were performed for each time period

DISCUSSION

The results from the present study highlight the thermal sensitivity of the pre- and early post-settlement stages of *Scytothalia dorycarpa*. In culture, temperatures > 20°C delayed germling settlement and significantly increased mortality. These findings were strongly supported by a sharp drop-off in the number of *S. dorycarpa* recruits on reefs from cool to warmer climates, and reproduction was constrained to winter months, coinciding with sub-20°C water temperatures.



12 h 36 h 3 d 7 d 14 d

Fig. 6. *Scytothalia dorycarpa.* Images of germling development at 15°C across the 5 observed time intervals (cf. Fig. 5). Scale bar = 200 µm

Table 2. Three-factor permutational analysis of variance (PERMANOVA) for *Scytothalia dorycarpa* recruit densities in size categories large (10 to 20 cm), intermediate (5 to 10 cm) and small (0 to 5 cm) with season (autumn vs. winter), location, region (*a priori* planned contrast; north representing northern locations Two Rocks and Marmion and south representing southern locations Cape Naturaliste and Hamelin Bay), Season × Location interaction and Season × Region interaction. Values in **bold** are significant with $p < 0.05$

Source	df	10–20 cm			5–10 cm			0–5 cm		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
Season	1	0.62	2.23	0.17	0.08	0.60	0.47	0.51	6.56	0.19
Location	3	7.35	8.85	**<0.01**	1.08	7.93	**<0.01**	2.07	26.64	**<0.01**
Region (North vs. South)	1	7.32	31.50	**<0.01**	2.67	17.54	**<0.01**	3.92	14.87	**<0.01**
Season × Location	3	0.39	1.40	0.26	0.10	0.76	0.54	0.66	8.44	**<0.01**
Season × Region	1	0.98	2.21	0.06	0.01	0.04	0.84	0.24	0.91	0.39
Error	23	0.28			0.14			0.07		

Table 3. Three-factor permutational analysis of variance (PERMANOVA) for *Scytothalia dorycarpa*, *Ecklonia radiata* and *Sargassum* spp. recruit densities with season (autumn vs. winter), region (*a priori* planned contrast; north representing northern locations Two Rocks and Marmion, south representing southern locations Cape Naturaliste and Hamelin Bay), Season × Location interaction and Season × Region interaction. Values in **bold** are significant with $p < 0.05$

Source	df	*S. dorycarpa*			*E. radiata*			*Sargassum*		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
Season	1	0.49	0.06	0.89	0.55	3.39	0.08	14.57	1.23	0.30
Location	3	25.53	3.26	**0.02**	0.65	3.96	**0.02**	9.51	0.81	0.49
Region (North vs. South)	1	60.33	8.46	**<0.01**	0.44	1.99	0.17	3.08	0.21	0.65
Season × Location	3	1.10	0.14	0.98	0.12	0.76	0.55	59.46	5.04	**0.01**
Season × Region	1	2.38	20.33	0.69	0.08	0.39	0.54	94.80	0.02	**0.03**
Error	23	7.84			0.16			11.81		

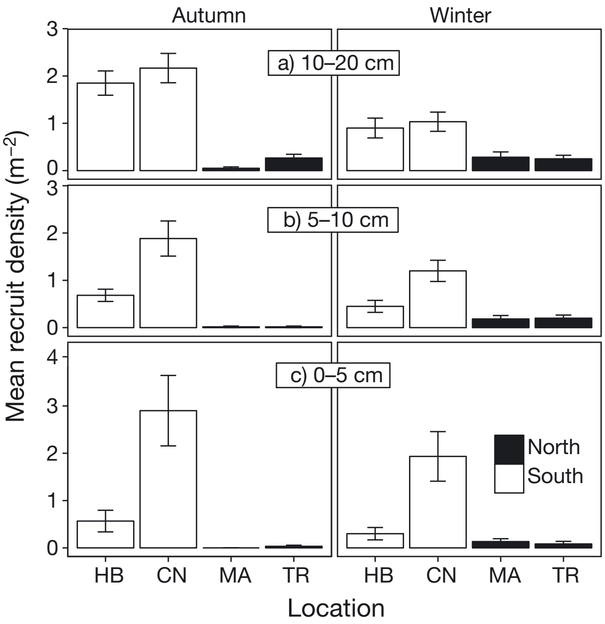


Fig. 7. *Scytothalia dorycarpa.* Mean (±1 SE) number of recruits m^{-2}, sampled in autumn and winter 2012 (n = 3 reefs), reported in each size bin (10–20 cm, 5–10 cm and 0–5 cm). White bars: locations in the southern region (HB: Hamelin Bay; CN: Cape Naturaliste); black bars: locations in the northern region (MA: Marmion; TR: Two Rocks)

Thermal sensitivity of early post-settlement stages

The early life history stages of *Scytothalia dorycarpa* were sensitive to high temperatures, particularly those above 20°C. In culture experiments, temperature significantly affected germling survivorship, which was highest at the coolest treatment temperature (15°C). Mortality rates at the 2 highest treatment temperatures (20°C and 23°C) were 90% and 100% respectively. Low rates of surviviorship and the observed structural collapse of germlings at high temperatures may be associated with thermally sensitive processes, such as the denaturation of proteins, and damage to heat-labile enzymes or membranes (Lüning et al. 1990).

In the most extensive review of the temperature tolerance of seaweeds, Lüning (1984) found upper temperature limits for germling survival in brown seaweeds to range from 18°C (*Chorda tomentosa*) to 28°C (*Fucus vesiculosus* and *F. spiralis*). More recently, Chu et al. (2012) reported that germlings of the intertidal fucoid *Sargassum thunbergii* exhibited rapid growth and low mortality when exposed to warming conditions and were able to tolerate culture temperatures of 35°C, several degrees higher than adult *S. thunbergii* lethal limits (Hiroko et al. 2005). Ultimately, however, if the lethal limits of a particular ontogenetic stage or population overlap with the ambient ocean temperatures for prolonged periods, it will impact the demographic structure of the population or cause a range contraction of the species to cooler conditions (e.g. Edwards & Hernández-Carmona 2005, Wernberg et al. 2011a). For *Scytothalia dorycarpa,* the persistence of adult populations in locations where summer temperatures exceed 23°C suggests that the species undergoes an ontogenetic shift to slightly higher thermal tolerance, enabling the new cohort and adult the population to survive throughout the austral summer.

Latitudinal distribution of recruits

The marked differences in *Scytothalia dorycarpa* recruit densities between southern and northern locations were consistent with the thermal sensitivities of early post-settlement germlings observed in the present study. Field studies of the latitudinal distribution and abundance of recruits found significantly lower *S. dorycarpa* recruit densities in northern reefs at which summer temperatures consistently exceed 23°C and sub-20°C conditions last for ~5 mo compared to much higher recruit densities in southern reefs where average summer maximum temperatures peak at ~22°C, and sub-20°C conditions persist for 6 to 7 mo. Post-settlement processes and recruitment are tightly coupled and often confine the abundance of fucoid species (Serrao et al. 1996, Johnson & Brawley 1998, Berndt et al. 2002, Schiel & Foster 2006). Low densities of *S. dorycarpa* recruits in northern locations might therefore be a direct reflection of the sensitivity of early post-settlement stages and the shorter window of time available for recruits to establish before warm, lethal summer temperatures commence.

Smale & Wernberg (2013) found that conditions during the 2011 marine heat wave in south-western Australia exceeded the lethal limit for *Scytothalia dorycarpa* and were likely to have had detrimental physiological effects on adult stands. It is therefore possible that temperatures in northern locations may have temporarily exceeded the absolute limits for *S. dorycarpa*'s persistence and led to recruit mortality and/or reproductive and recruitment failure in the subsequent 2011 winter. For seaweeds that hold reproductive structures throughout the entire year, such as *S. dorycarpa*, extreme temperatures during summer months may stress adult stands and potentially impact subsequent winter reproduction.

Reproductive seasonality

The timing of reproduction in *Scytothalia dorycarpa* to coincide with the coolest winter months was consistent with the optimal and lethal temperatures observed in the culturing experiment. Winter temperatures range from an average of 17 to 19°C across the geographical range observed in the present study, consistent with the 15 to 18°C temperatures found to optimise settlement and survivorship in culture. In *S. dorycarpa*, although reproductive structures (receptacles) are present throughout the entire year (Naylor 1949), the present study found gametogenesis (the development of gametes) to be seasonally constrained to winter months. This seasonal pattern contrasts with co-existing canopy formers that concentrate their reproductive outputs during the summer months, when the water temperature ranges from 20 to 23°C. For example, local *Ecklonia radiata* populations reproduce from mid-summer to the end of autumn (Mohring et al. 2013), and local *Sargassum* spp. recruitment peaks in February (Kendrick & Walker 1994). At the warm margin of a species range, reproduction during summer may expose sensitive early life history stages to stressful temperature and light conditions. In contrast, germlings such as *S. dorycarpa,* which settle in cooler months, may experience a more benign thermal environment. However, the challenge for *S. dorycarpa* is that on the west coast of Australia, sea temperatures are close to the early life stage lethal limit; therefore, slight increases in temperature may constrain reproduction by restricting the species' 'reproductive window'. Seasonally, *S. dorycarpa* has no room to move to escape warming conditions, so the only option for the species is to shift its geographical distribution poleward.

CONCLUSIONS

Our findings highlight the vulnerability of a key foundation species, *Scytothalia dorycarpa*, to changing ocean temperatures. Temperature-controlled culture experiments combined with seasonal and latitudinal observations indicated that the pre- and early post-settlement stages of the *S. dorycarpa* life cycle are sensitive to waters warmer than 20°C. Whilst the acute temperature sensitivity of *S. dorycarpa* implies that it holds significant value as a bio-indicator of changes due to localised seawater warming, its long-term survival and recovery prospects around its current northern (warm) range limit are at risk under continued warming. Given the poleward flow of the Leeuwin current and negatively buoyant non-motile eggs of *S. dorycarpa*, natural recovery of northern populations is unlikely or will be extremely slow at best. Further studies of the ecology and population biology of *S. dorycarpa* will help to improve our understanding of the survival of this foundation species and the potential for its targeted rehabilitation in affected marginal populations.

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