Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range

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Abstract

Global climate change is leading to redistribution of marine species and altering ecosystem dynamics. Given recent poleward range extension of the barrens-forming sea urchin *Centrostephanus rodgersii* (Diadematidae) from mainland Australia to Tasmania, there is a need to understand the population dynamics of this ecologically important species in the Tasmanian environment. This paper informs possible population dynamics of *C. rodgersii* in Tasmania by examining its reproductive ecology in this new environment. Reproductive periodicity (gonad index and propensity to spawn) was assessed bimonthly over 18 months at four sites in eastern Tasmania spanning ~2° in latitude. At all sites, *C. rodgersii* displayed a strong seasonal cycle in gonad production with major spawning occurring in winter (~August) at minimum annual water temperature. Gametes from Tasmanian *C. rodgersii* were viable as determined by fertilization and early development trials. However, development to the two-arm stage at ~3 weeks was strongly dependent on water temperature across the 8–20 °C temperature range, with poor development occurring below 12 °C. The range of temperatures tolerated by Tasmanian *C. rodgersii* larvae was similar to that of larvae from its native New South Wales range, indicating that this species has not undergone an adaptive shift to the cooler Tasmanian environment. There was also no evidence for an adaptive shift in reproductive phenology. Importantly, coastal water temperatures in eastern Tasmania during the peak spawning in August fluctuate about the 12 °C larval development threshold. Recent warming of the eastern Tasmanian coast and further warming predicted by global climate change will result in an environment increasingly favourable for the reproduction and development of *C. rodgersii*.

Keywords: Centrostephanus rodgersii, climate change, gonad index, larval development, macroalgae, poleward range shift, reproductive phenology, temperate rocky reef, temperature threshold, urchin barrens

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Introduction

Range extensions provide important opportunities to investigate the underlying mechanisms defining a species distribution (Holt & Keitt, 2005; Parmesan *et al.*, 2005). For changes in species ranges to be detectable, range modifications must occur over large spatial scales of tens to hundreds of kilometres, therefore, causal mechanisms must also operate over large spatial scales. In the marine environment, global climate change is a

mechanism that has already resulted in, and is predicted to further lead to, widespread redistribution of species ranges (e.g. Fields *et al.*, 1993; Barry *et al.*, 1995; Holbrook *et al.*, 1997; Hughes, 2000; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Beaugrand, 2004; Chevaldonné & Lejeusne, 2004; Harley *et al.*, 2006; Poloczanska *et al.*, 2007).

Consistent with long-term climate change and species range shifts around the globe during the last ~40 years (e.g. Holbrook *et al.*, 1997; McGowan *et al.*, 1998; Sagarin *et al.*, 1999; Zacherl *et al.*, 2003), the temperate coastal environment of eastern Tasmania has undergone warming primarily as a result of increased southward pene-

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tration of the East Australian Current (EAC) (Ridgway, 2007). While some warmer water species have become regular members of the Tasmanian coastline, some of these species appear sporadically and generally only occur as juveniles (Edgar, 1997). Of the new species now present in Tasmania, the Diadematid sea urchin *Centrostephanus rodgersii* (Agassiz) is one of the most conspicuous and ecologically important due to its ability to catastrophically overgraze macroalgal beds and maintain an alternative and stable 'barrens' habitat (Fletcher, 1987; Andrew & Underwood, 1989, 1993; Andrew, 1991, 1993; Hill *et al.*, 2003; Johnson *et al.*, 2005). Historically, *C. rodgersii* in Australia has been largely restricted to the coast of New South Wales (NSW, see Fig. 1) where the associated barrens habitat is estimated to constitute 50% of all near-shore reef habitat (Andrew & O'Neill, 2000).

Undergoing a poleward range extension, *C. rodgersii* was first recorded in the Kent Group of Islands in the late 1960s; northeast Tasmania in 1978; southeastern Tasmania in mid-1980s; and southwestern Tasmania in 2005 (Fig. 1). Since first detected, the sea urchin's abundance has increased and expansive barren areas

now occur in some locations (Johnson *et al.*, 2005). The threat of widespread barrens, as found in NSW, poses major concerns for biodiversity on Tasmanian reefs and for reef associated fisheries (worth AUS$300 M yr^{-1}) that are dependent on macroalgal habitat (Johnson *et al.*, 2005; S. Ling, unpublished manuscript). Dartnall (1980) interpreted the discovery of *C. rodgersii* in northeastern Tasmania as perhaps a temporary bulge in the species range limit, stating 'We await evidence that this population is reproductively self-maintaining . . .'. A scenario whereby *C. rodgersii* is capable of completing its life cycle within Tasmanian waters is likely to allow for a more rapid population expansion and greater ecological impacts than if Tasmanian populations are only maintained by occasional cohorts of larvae transported south via the EAC (see Fig. 1). Therefore, information on the reproductive status of this species in eastern Tasmania is vital to the assessment of spread of this organism and the associated ecological consequences for rocky reef ecosystems in Tasmania.

Reproduction of *C. rodgersii* involves dioecious adults that spawn gametes into the water column where fertilization occurs (King, 1992; Huggett *et al.*, 2005). Fertilized eggs rapidly develop into a two-armed planktotrophic larval stage that exists in the water column for 100 days before settling to reef substratum (Huggett *et al.*, 2005). This feature facilitates long-distance dispersal in oceanographic currents, thus it is likely that the southward incursion of *C. rodgersii* in eastern Tasmania has occurred due to increased larval dispersal driven by changes to patterns of the EAC (see Ridgway, 2007). Within its native distribution, *C. rodgersii* displays a seasonal cycle in gamete production with the major spawning activity occurring in winter (King *et al.*, 1994; Byrne *et al.*, 1998). Given the cooler water temperatures in eastern Tasmania (winter minimum 11 °C) relative to NSW (winter minimum 14 °C), the ability of *C. rodgersii* to develop functional gonads, viable gametes and undergo normal larval development may be compromised in the Tasmanian environment. This paper assesses the reproductive capability of *C. rodgersii* in eastern Tasmania by examining evidence for the existence of a reproductive cycle, its ability to produce functional gametes and to undergo successful larval development.
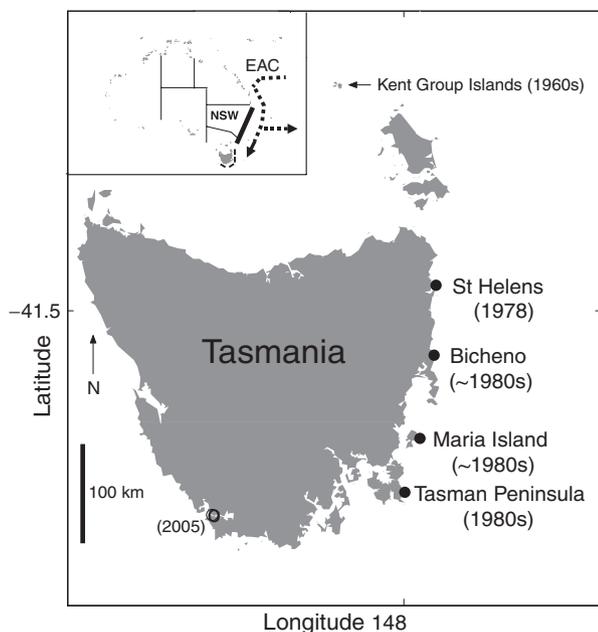

Fig. 1 Map of sites used to monitor the reproductive cycle of *Centrostephanus rodgersii* in eastern Tasmania, and the timeline of first sightings. Inset displays mainland Australia and the direction of the East Australian Current (EAC); the 'native' distribution of *C. rodgersii* on mainland (solid line, after Andrew & Byrne, 2001); and the recent range extension of the sea urchin (broken line, after Johnson *et al.*, 2005). The timing of discovery of *C. rodgersii* along the Tasmanian coastline is shown in parentheses (after Johnson *et al.*, 2005); the south western range limit is shown as an open circle (J. Valentine, personal observation).

Materials and methods

Study sites

Reproduction of *C. rodgersii* was investigated at Elephant Rock, St Helens (41°14′56″S; 148°20′18″E); The Gulch, Bicheno (41°52′29″S; 148°18′27″E); Mistaken Cape, Maria Island (42°38′34″S; 148°9′17″E); and The

Lanterns, Tasman Peninsula (43°8′19″S; 148°0′21″E) (Fig. 1). At all sites, *C. rodgersii* was collected from macroalgal habitat by divers at 8–15 m depth. Temporal variability in temperature was determined on the sea floor at each site using temperature loggers (Optic Stowaway©® by Onset Computer Corp., Bourne, MA, USA) fixed at a depth of 9 m.

Determination of reproductive seasonality

Evidence for reproductive periodicity was investigated by tracking mean gonad index (GI) obtained approximately bimonthly from a sample of 30 adult *C. rodgersii* from each of the four sites over an 18-month period from October 2003 to June 2005. Collections were aimed at sea urchins within the size range of 80–110 mm test diameter (TD) to reduce potential size-related biases in GI. Sea urchins were dissected fresh and drained of coelomic fluid plus any free-surface water. Gonads were removed and sexed where possible by the unaided eye (unmagnified swab). Sex ratios were generated for each site by summing males and females across sampling times where sex was determinable for all individuals. Sex ratios for each site, and across eastern Tasmania as a whole (summing sexes across all sites), were examined for departure from a 1 : 1 ratio using χ^2-tests. Drained gonads, test and spines, gut and contents, and the Aristotle's lantern were weighed separately. GI for each individual was expressed as (gonad weight/total body weight) × 100%. To assess the capacity to spawn, on each sampling occasion an additional 10 sea urchins from each site were injected with 4 mL of 0.5 M KCl through the peristomal membrane. The number of individuals artificially induced to spawn were recorded and expressed as a percentage.

Effect of temperature on fertilization and larval development

The effect of temperature on fertilization and larval development was assessed under constant laboratory conditions. Thirty sea urchins (TD 80–110 mm) were collected from the Tasman Peninsula (southern most site) near the 2005 peak in GI (23 August 2005) and held in aquaria overnight at ambient water temperature (12 °C) before commencement of experiments. Adults were selected randomly and injected with 4 mL of 0.5 M KCl. Profusely spawning urchins were individually inverted on top of 500 mL glass beakers to collect gametes 'dry' until gamete release slowed (10–15 min). Ambient 12 °C, 0.2 μm filtered seawater (FSW) was added carefully to each beaker and the gametes diluted into stock solutions. Eggs from individual females were serially diluted to make stock solutions of approximately 100 eggs mL^{-1} determined by count-

ing eggs in 1 mL aliquots using a dissecting microscope. The density of sperm in stock solution was standardized by a series of sperm dilutions and haemocytometer counts on sperm inactivated by Lugol iodine. A spectrophotometer was then used to calibrate the absorbance (at 340 nm) of the desired sperm solution to allow delivery of 500 sperm to one egg in each jar which is the optimal sperm to egg ratio in this species (King, 1992). Replicate cultures consisted of sperm and eggs from a different male–female pair.

The culture system consisted of 70 mL polystyrene jars arranged in 12 columns × 6 rows across an aluminium temperature-gradient block that maintained each column at 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19 and 20 °C (temperature loggers revealed a constant temperature regime for the entire trial period). The six rows in each temperature 'column' allowed three replicate gamete sets to be run concurrently. Additional jars containing FSW at each of the test temperatures were also kept on the temperature-gradient block to enable isothermal water changes in cultures twice weekly. When functional guts had developed (early pluteus stage, C. King, personal communication), larvae were fed a mixed diet of *Nannochlorpsis oculata*, *Chaetocerus muelleri* and *Isochrysis galbana* (Tahitian strain) at a density of 50 000 cells mL^{-1} following each water change. Because of the need for intensive sampling during embryonic and early larval development, replicate trials with different gamete sets were commenced 1 day apart.

At the start of each trial, jars were filled with 25 mL of egg solution and equilibrated to the treatment temperatures. An additional 25 mL of isothermal FSW was then added to each jar to obtain a culture density of approximately 50 eggs mL^{-1} before addition of 0.01 mL of sperm solution (containing 1.25 × 10^6 sperm) with a micropipette. To assess fertilization rates, 1 mL of eggs was sampled (by taking a random transect across the bottom of the jar) from each temperature treatment 20 min after the addition of the sperm solution and transferred to 5 mL vials containing 2 mL of 10% formosaline. Fertilization rate was calculated as the percentage of eggs displaying a fertilization membrane and the effect of temperature was examined with linear regression using appropriate tests of assumptions. To document development, embryos and larvae were sampled from jars at 2 h and at intervals of 30 min over the first 4 h, and at increasing intervals thereafter. The developmental stage that each culture had reached was assigned as the stage that accounted for >50% of the embryos per larvae in the sample. Extractive sampling of cultures was ceased after 1 day and development was then followed directly in jars using a dissecting microscope (× 20). The yield of advanced stage two-arm plutei for each temperature treatment was calculated as

the relative contribution, expressed as a percentage, of the total yield of advanced stage two-arm plutei from each trial. To assess the possibility of acclimation by *C. rodgersii* to the cooler Tasmanian environment, average development time to the two-arm plutei stage was taken for each temperature treatment and examined with respect to values for NSW-reared larvae (data from King, 1992).

Results

Determination of reproductive seasonality

Tasmanian *C. rodgersii* produced gonads similar in appearance to those of NSW *C. rodgersii* (C. King, personal observation). The distribution of sexes at each site and for eastern Tasmania as a whole did not deviate significantly from a 1 : 1 sex ratio (for individual sites minimum $P = 0.09$; for eastern Tasmania as a 'whole', $\chi^2 = 1.1$, $P = 0.30$). Across all sites, *C. rodgersii* displayed a strong seasonal cycle in gonad production, with major spawning activity occurring in winter (August) as evidenced by a rapid decline in GI (Fig. 2a and c). The capacity of *C. rodgersii* to undergo induced spawning at each site cycled in a clearly defined pattern with maximal induction of spawning occurring in July–August (Fig. 2b). This pattern displayed strong overlap with the timing of the marked decline in GI and was similar at all four sites (Fig. 2a and b). The relative decline in GI between gravid (July) and spent states (end of August to early September) was 51% at St Helens, 70% at Bicheno, 60% at Maria Island and 70% at Tasman Peninsula. The cycle in GI was the inverse of relative gut weight indicating a normal echinoid pattern of resource acquirement and subsequent transfer of energy to gonad production before spawning (Fig. 2c). The reproductive cycle of *C. rodgersii* in eastern Tasmania correlated strongly with water temperature. Increasing GI broadly tracked spring–summer periods of increasing water temperature with peak GIs reached during late autumn and maximum spawning activity occurring during August when water temperatures reached their annual minimum (Fig. 2d).

Effect of temperature on fertilization and larval development

Gametes produced by Tasmanian *C. rodgersii* were viable, with eggs readily fertilized, during the peak winter spawning period. Embryonic and larval development was normal and the two-arm pluteus stage was readily reached. While there was a small increase in fertilization rate with increasing temperature (95–99% fertilized), variation around this trend was large and so
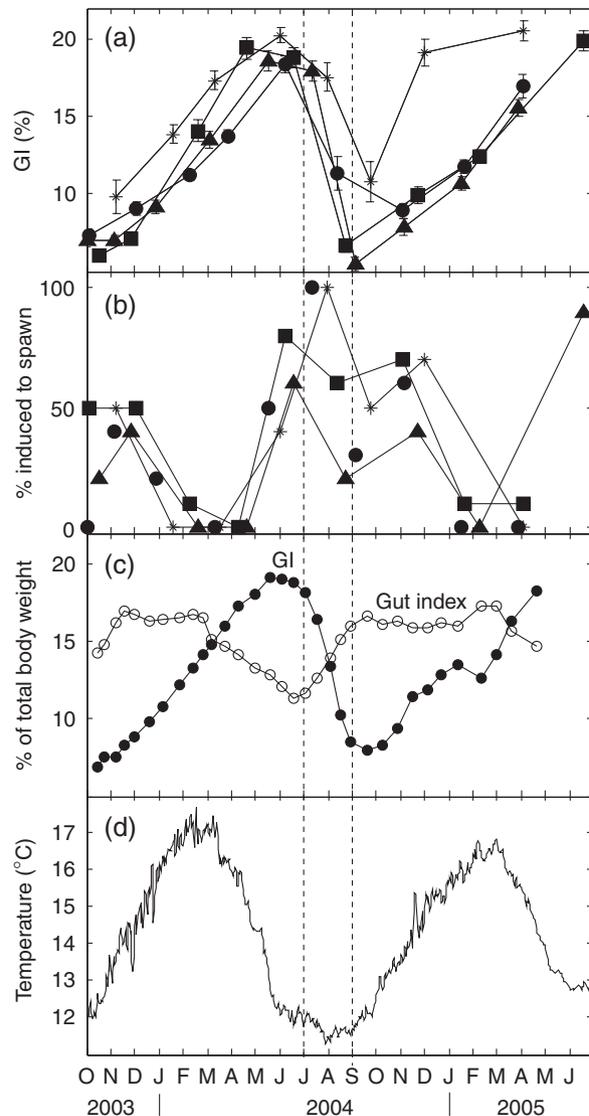

Fig. 2 Reproductive cycle of *Centrostephanus rodgersii* at four sites in eastern Tasmania, October 2003 to June 2005. (a) Gonad index, data are means ±SE, $n = 30$. St Helens, *; Tasman Peninsula, ▲; Bicheno, ●; Maria Island, ■. (b) Capacity of population to spawn, symbols as above. (c) Smoothed cycles of gonad (filled symbols) and gut (open symbols) indices; data represent the running mean calculated on four consecutive samples through time. (d) Mean daily temperature on the benthos. Temperature data have been pooled across the four monitoring sites (note: data before 23 November 2004 is daily mean for St Helens and Bicheno only). Area within the dotted vertical lines indicates the major period of spawning.

temperature was considered to have little biological effect on fertilization success over the 8–20 °C range examined (Fig. 3). There was, however, a strong effect of water temperature on development, with minimal successful development to two-arm plutei occurring in cultures below 12 °C. Rates of development increased
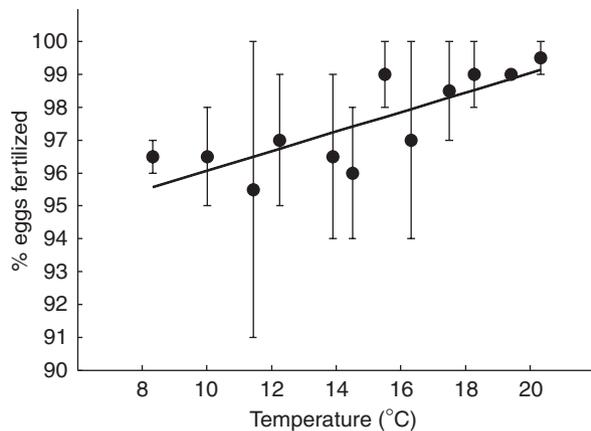
Fig. 3 Temperature-dependent fertilization rates of Tasmanian *Centrostephanus rodgersii*. Data are means for 100 randomly selected eggs from two replicate trials, ±SE. While linear regression revealed a significant positive trend (treatment: $F_{1,10} = 18.29$, $P = 0.0016$), the fit was relatively poor ($R^2 = 0.65$) and the size of the effect small ($y = 0.297x + 93.10$).

with increasing temperature up to 19 °C, however, development rate decreased and became highly variable across replicate trials in the 20 °C treatment (Fig. 4). The relative yield of two-arm plutei across temperature treatments peaked at the mid-range of temperatures tested, (i.e. between 14 and 15 °C; Fig. 5). Temperatures below 12 °C did not yield any advanced stage two-arm plutei (stage 22) and yield similarly declined with temperatures >16 °C, with very few stage 22 larvae observed in the 20 °C treatment. Indicating a lack of acclimation within the extended range, temperature-dependent patterns in development rate were similar for Tasmanian and NSW larvae (Fig. 6).

Discussion

Reproductive cycle

Seasonal reproductive activity of *C. rodgersii* in eastern Tasmania strongly indicates that this sea urchin is capable of completing its life cycle in its new range. Monitoring of gonad indices and spawning capacity over 18 months revealed a similar pattern at four sites spanning eastern Tasmania, with a strong seasonal cycle in gonad production and spawning in winter (̴ August). Maximum population GIs were recorded in June or July at each site (18.4–20.1%), while minimum population GIs occurred from September to November (5.5–9.8%). The clearly defined spawning period over 1–2 months contrasts the findings of Byrne *et al.* (1998) within the native range of *C. rodgersii* in NSW, which describe a pattern of increasing spawning period with increasing latitude. Northern NSW populations had a

short 1-month spawning period; mid-NSW populations spawned over several months; while southern populations spawned over 5–6 months (Byrne *et al.*, 1998). *C. rodgersii* may undergo prolonged low-intensity 'dribble' spawning over a longer period in eastern Tasmania (a more detailed histological examination of gonads is required), however, it is clear that the main period of gamete release, indicated by abrupt changes in the GI, occurs over a 1–2-month period.

The magnitude of reproductive investment in eastern Tasmania (maximum population GI = 20.1%; maximum individual GI = 29.3%) appears to be greater than that within the native NSW range where relatively low GIs (maximum population GI ≈ 14%) have been reported (King *et al.*, 1994; Byrne *et al.*, 1998). This pattern is diametrically opposite that of many other studies, chiefly of terrestrial plants, which describe trends of decreasing reproductive output toward the edges of species' ranges (e.g. Woodward, 1990; Despland & Houle, 1997; García *et al.*, 2000; Jump & Woodward, 2003). The high population GIs at the southern range limit of *C. rodgersii* likely reflects abundant food provided by dense Tasmanian macroalgal beds in combination with lower population densities compared with the dense populations and widespread barrens with limited food on the NSW coast (Byrne *et al.*, 1998; Blount & Worthington, 2002; Worthington & Blount, 2003). The notion that Tasmanian populations, within macroalgal habitat, are not food limited is further supported by the large individual size attained by *C. rodgersii* in eastern Tasmania. Individuals were commonly observed above the 120 mm maximum TD reported in NSW (Andrew & Byrne, 2001), with the largest individual recorded at 133 mm TD and weighing ̴ 600 g (drained of coelomic fluid). Furthermore, the GI cycle in eastern Tasmania tracked the temporal cycle in gut index indicating a normal pattern of echinoid food acquirement and subsequent transfer of energy reserves to gonad production (see Byrne *et al.*, 1998 for histological examination), emphasizing the importance of food availability in procuring large GIs.

Lack of adaptive shift in temperature dependency of larval development

The strong reproductive condition of Tasmanian *C. rodgersii* was reflected in viable gamete production and larval development in accordance with normal patterns described for *C. rodgersii* from NSW (King, 1992; King *et al.*, 1994; Huggett *et al.*, 2005; see Fig. 4). While there was little detectable effect of temperature on fertilization success at temperatures ranging from 8 to 20 °C, there was a strong effect of water temperature on larval development. Larval development was poor
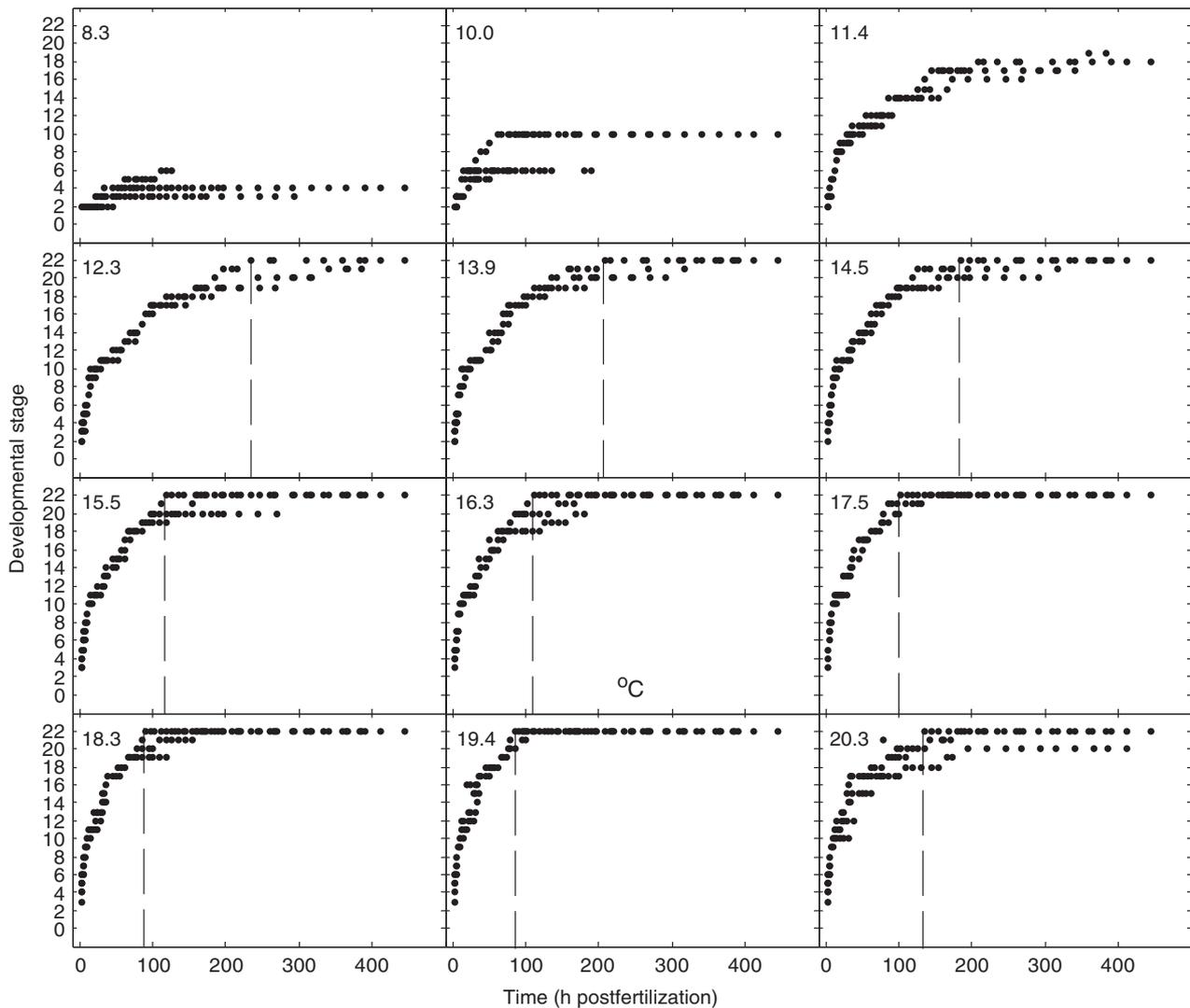
Fig. 4 Temperature-dependent development rates of Tasmanian *Centrostephanus rodgersii* reared at 8.3–20.3 °C. Stages of larval development are (after King, 1992): stage 1, unfertilized egg; stage 2, fertilized egg; stage 3, two-cell embryo; stage 4, four-cell embryo; stage 5, eight-cell embryo; stage 6, 16-cell embryo; stage 7, 32-cell embryo; stage 8, 64-cell embryo; stage 9, morula; stage 10, early blastula; stage 11, mid-blastula; stage 12, hatched blastula; stage 13, early gastrula; stage 14, mid-gastrula; stage 15, late gastrula; stage 16, early prism; stage 17, mid-prism; stage 18, late prism; stage 19, early pluteus; stage 20, early two-arm pluteus; stage 21, mid two-arm pluteus; stage 22, advanced two-arm pluteus. Broken vertical line indicates the minimum time required to reach the advanced two-arm pluteus. The advanced two-arm pluteus stage was not reached in treatments <12 °C [also not observed up to 35 days (840 h) post-fertilization]. Rates of larval development increased with increasing temperature up to 19.4 °C; however, development rate slowed and became highly variable across replicate trials in the 20.3 °C treatment.

below 12 °C, and optimum larval yields and developmental rates occurred at ~14–16 °C. Importantly, Tasmanian *C. rodgersii* larvae appear to develop at similar rates to their counterparts in warmer NSW waters (Fig. 6). The only evidence for deviation in rates of development was the poor performance of Tasmanian reared larvae at the warmest temperature examined (20.3 °C). This may indicate heat stress to gametes and/or embryos at temperatures ≥8 °C higher than the ambient temperatures experienced by parents. Moreover, there was no evidence of acclimation of larvae to cooler Tasmanian waters because a similar larval development threshold of ~12 °C is also evident in NSW (King, 1992). This finding supports the 'recent' nature of the *C. rodgersii* range extension given that adaptive shifts to thermal tolerance would likely require many generations to evolve within the cooler Tasmanian environment.
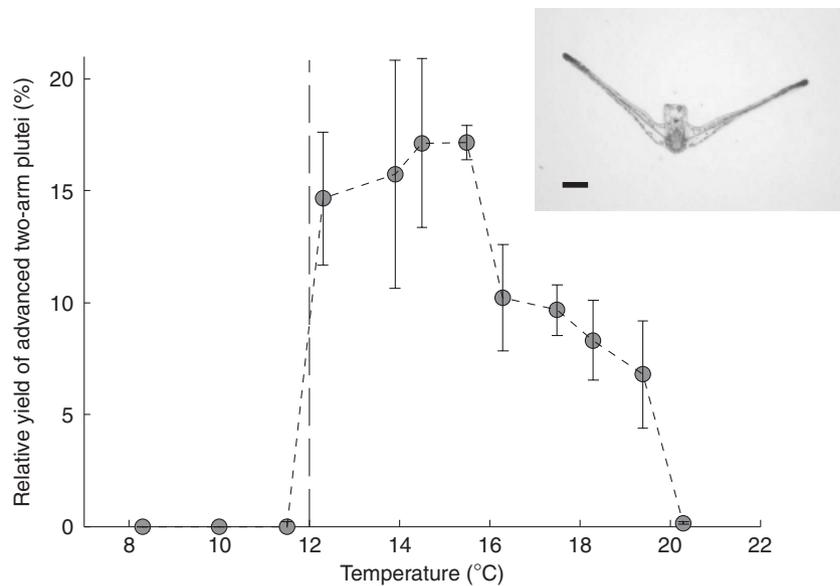
Fig. 5 Temperature-dependent yield of advanced two-arm plutei of Tasmanian *Centrostephanus rodgersii*. Data are relative yields of advanced two-arm plutei generated at each temperature treatment expressed as a percentage of the total number of advanced two-arm plutei produced per trial (means ± SE of $n = 3$ trials). Accompanying image is of a two-arm pluteus larva at 21 days postfertilization (scale bar = 200 μm).
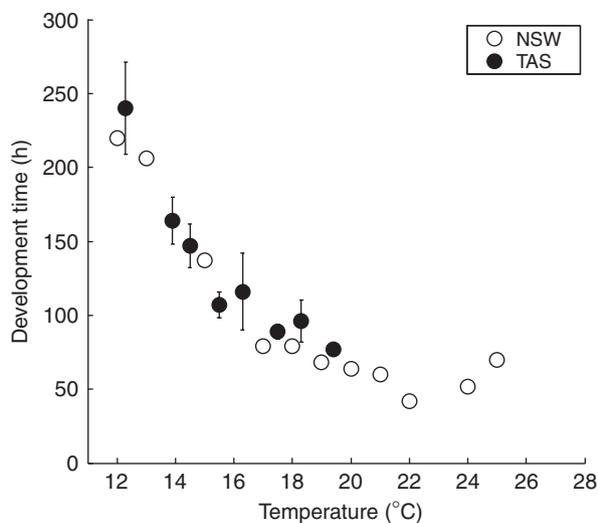

Fig. 6 Development time to early two-arm plutei vs. water temperature for Tasmanian and NSW-reared *Centrostephanus rodgersii*. Data for Tasmania are means derived from three trials (± SE); for NSW, data is means from King, 1992 (SE not available). Note: data from the 20.3 °C temperature for Tasmania has been omitted from this plot due to evidence of heat stress in this treatment. NSW, New South Wales.

Lack of adaptive shift in reproductive phenology

The observation that Tasmanian *C. rodgersii* undertook spawning in water temperature below 12 °C in 2004 (Fig. 2d) is intriguing given that gametes would have been released into a temperature environment unsuitable for successful larval development (Figs 4 and 5). Such a counter-productive strategy strongly suggests that *C. rodgersii* reproductive phenology has not undergone adaptive shift and is controlled by factors other than temperature. This contention is supported by research within the NSW range where consistencies in the timing of spawning of *C. rodgersii* occurred across 9° in latitude even though large temperature gradients were present over this range (Byrne *et al.*, 1998). Photoperiod coinciding with the winter solstice appears as a likely proximate factor cuing the onset of spawning across this broad geographic range (Byrne *et al.*, 1998 and references therein), as has been found in other closely related echinoid species (Kennedy & Pearse, 1975; Coppard & Campbell, 2005).

Mismatches between reproductive rhythms entrained by photoperiod and suitable temperatures for early development are predicted to become commonplace as accelerating climate change impacts on phenologies and ultimately the ranges of many species (e.g. Parmesan & Yohe, 2003). For species dispersed poleward by changing climate patterns, delay in establishment of reproductively viable populations is likely unless local climate is dually warmed above physiological thresholds or adaptive shifts in phenology and/or physiology is immediate. From an increasing number of examples of species undergoing adaptive shifts to climate change, these shifts are not immediate but require evolutionary time scales, and shifts in phenology are anticipated to

precede shifts in thermal optima or increased thermal tolerance (Bradshaw & Holzapfel, 2006).

Future trends in reproduction

Given that Tasmanian reared *C. rodgersii* displayed normal embryonic and larval development to the two-arm pluteus stage within 12–20 °C (Fig. 4), it is likely that the sea urchin successfully propagates larvae throughout its current Tasmanian range in years when the winter temperature during the major spawning period is ≥~12 °C. Hart & Scheibling (1988) report evidence of an analogous temperature threshold mechanism for *Strongylocentrotus droebachiensis* along the Atlantic coast of Nova Scotia where sea urchin population booms and associated overgrazing of kelp beds were correlated with a positive ocean temperature anomaly allowing optimal temperatures for larval development. Long-term monitoring of sea surface temperature in eastern Tasmania has revealed a 1.5 °C warming over the past 60 years, predominantly due to a greater influence of the EAC on this coast (Ridgway, 2007). Importantly, this warming trend is also apparent during winter months, such that temperatures above the 12 °C threshold for larval development are be-
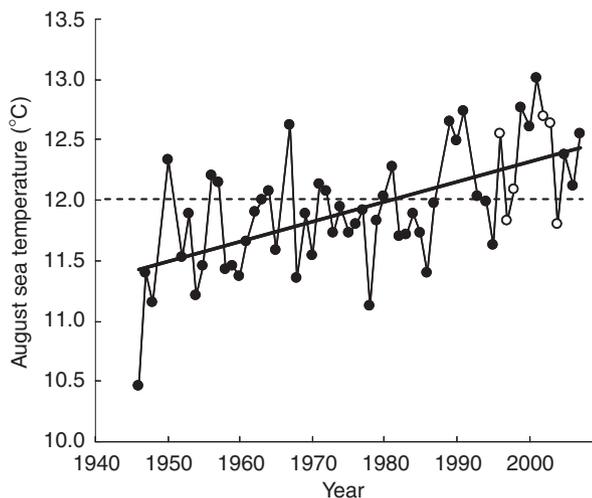
coming frequent during the major spawning period (Fig. 7) and are likely to arise with increasing frequency given anticipated ongoing coastal warming associated with global climate change (Cai et al., 2005). Continued coastal warming will also reduce larval development time (Figs 4 and 6) which may in turn enhance larval survival and increase the likelihood of self-recruitment of *C. rodgersii* within Tasmania due to decreased exposure to potentially hazardous planktonic conditions (e.g. Morgan, 1995). Thus, the long-term winter warming of eastern Tasmanian coastal waters and projected trend(s) under global climate change is leading to an environment more conducive for *C. rodgersii* development. Finally, by combining a trend of increasing population size with reproductive capability, this suggests that aided by a new thermal regime, *C. rodgersii* has established viable populations along the eastern Tasmanian coastline.

Acknowledgements

Fig. 7 Long-term winter-warming trend of coastal waters in eastern Tasmania, 1946–2007. Data are sea temperatures from the Maria Island coastal station (148°13′E, 42°36′S) averaged across depth (0–50 m) for August, i.e. the month of major spawning (data courtesy of CSIRO Marine & Atmospheric Research). Note that the water column is mixed across this depth range during August. Dashed horizontal line indicates the 12 °C larval development threshold for Tasmanian *Centrostephanus rodgersii*. Open symbols represent robust satellite derived estimates of sea surface temperature at the long-term station for recent years with missing *in situ* data (see Ridgway, 2007).

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