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# Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics

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**Abstract**

**Patterns of climate-forced range shift in the marine environment are informed by investigating the population dynamics of an ecologically important sea urchin (*Centrostephanus rodgersii* – Diadematidae) across its newly extended range in Tasmania (south-eastern Australia). A growth model of *C. rodgersii* is developed allowing estimation of a sea urchin age profile and, in combination with abundance data, we correlate the sea urchin population dynamic with respect to environmental signals across the range extension region. Growth patterns did not vary across the extension region; however, there was a strong pattern of decreasing sea urchin age with increasing distance from the historic range. The sequential poleward discovery of the sea urchin, a pattern of declining age and a general poleward reduction in abundance along the eastern Tasmanian coastline are consistent with a model of range extension driven by recent change in patterns of larval dispersal. We explore this hypothesis by correlating *C. rodgersii* population characteristics with respect to the East Australian Current (EAC), i.e. the chief vector for poleward larval dispersal, and reveal patterns of declining sea urchin age and abundance with increasing distance from this oceanic feature. Furthermore, *C. rodgersii* is generally limited to sites where average winter temperatures are warmer than the cold threshold for its larval development. Potential dispersal and physiological mechanisms defining the range extension appear to be strongly coupled to the EAC which has undergone recent poleward advance and resulted in coastal warming in eastern Tasmania. Predicted climate change conditions for this region will favour continued population expansion of *C. rodgersii* not only via atmospheric-forced ocean warming, but also via ongoing intensification of the EAC driving continued poleward supply of larvae and heat.**

*Keywords:* ageing, bioclimate envelope, *Centrostephanus rodgersii*, climate change, East Australian Current, growth, larval dispersal, sea surface temperature, spatial distribution, thermal tolerance

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## Introduction

Given the range of climate change projections (reviewed by Meehl *et al*., 2007), impacts on the distribution of marine species are likely to be profound. Anticipating responses of marine biota to climate change necessitates an understanding of how changed physical patterns will modify processes currently defining the distribution of marine populations. While species distributions are widely anticipated to shift poleward as a result of latitudinal shifts in bioclimate envelopes (e.g. Pearson & Dawson, 2003; Hijmans & Graham, 2006), the applicability of such models has been rarely assessed for marine environments (but see Lima *et al*., 2007). Given that redistribution of marine species is already occurring in response to recent climate change, generalized predictive models of marine biological responses are likely best informed by examining the physical and physiological context of marine populations already shifting (e.g. Barry *et al*., 1995; Holbrook *et al*., 1997; McGowan *et al*., 1998; Sagarin *et al*., 1999; Zacherl *et al*., 2003).

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In the southern hemisphere, the southeastern (SE) coast of Australia has been identified as a climate change hotspot (Poloczanska *et al*., 2007; Ridgway, 2007a). Here the East Australian Current (EAC) has strengthened resulting in greater poleward penetration of warm water over the past 60 years and an approximate quadrupling of ocean warming rates compared with the global ocean average (Ridgway, 2007a). This pronounced change in the physical oceanography of the region corroborates with a series of recent poleward range extensions (reviewed by Poloczanska *et al*., 2007) and is consistent with observations on other coasts where changed advective patterns and increased water temperature have been suggested as direct drivers of species range shifts (e.g. Fields *et al*., 1993; Gaylord & Gaines, 2000; Harley *et al*., 2006). The physical and biological expression of changes in the dynamics of the EAC is clearly evident on the east coast of Tasmania where oceanographic data reveal rising water temperature and salinity due to this feature (Ridgway, 2007a) and where species typical of warmer northern waters now occur (reviewed by Poloczanska *et al*., 2007).

Of those species recently established in Tasmania, the diadematid sea urchin *Centrostephanus rodgersii* (Agassiz) is arguably the most conspicuous and ecologically important due to its ability to catastrophically overgraze seaweed beds and maintain an alternative barrens habitat (Andrew & Byrne, 2001; Hill *et al*., 2003; Ling, 2008). Indeed, such is the impact of *C. rodgersii* on reef biodiversity that within the extended Tasmanian range, overgrazing by this species results in localized losses of $\sim$150 taxa that associate with seaweed beds (Ling, 2008). In SE Australia, *C. rodgersii* has historically been restricted to the coast of New South Wales (NSW; see Fig. 1), and while adult *C. rodgersii* remain highly localized on rocky reefs (reviewed by Andrew & Byrne, 2001), the sea urchin possesses a long-lived pelagic larval stage of $\sim$100 days (Huggett *et al*., 2005) that has considerable potential for long-distance dispersal via ocean currents. Thus, it has been suggested that the poleward range extension of *C. rodgersii* to Tasmania may have occurred due to increased larval dispersal (Andrew & Byrne, 2001; Johnson *et al*., 2005) driven by the poleward advance of the EAC by $\sim$350 km over the past 60 years (Ridgway, 2007a). Furthermore, *C. rodgersii* is now reproductively viable in eastern Tasmania, as coastal warming has led to a temperature regime warmer than the 12 °C cold limit for successful larval development in this species (Ling *et al*., 2008). Thus, the potential for population increase and widespread grazing impacts by *C. rodgersii* may be considerable, and thus poses a major threat to rocky reef biodiversity (Ling, 2008) and associated fisheries in Tasmania that depend on seaweed bed habitat (i.e. abalone and rock lobster fisheries worth $\sim$ AUS $150 M pa beach price, see Johnson *et al*., 2005).

Given the recent range extension of *C. rodgersii*, the aim of our study was to document the recent population dynamics of the sea urchin across the range extension region and to search for patterns that may inform future trends of this ecologically important species. Specifically, we develop a sea urchin growth model to determine the age dynamic across the extension region; then, in combination with patterns in sea urchin abundance, we use a correlative approach to examine the hypothesis that the population dynamics of the sea urchin reflects the new oceanographic regime of the extension region.

## Methods

### *Population structure of* Centrostephanus *across the newly extended range*

*Growth and age patterns.* A model of *C. rodgersii* growth was derived from annual growth increments of tagged individuals living in seaweed-dominated habitat on rocky reefs in northeastern (NE) (St Helens) and SE Tasmania (Tasman Peninsula) (Fig. 1). Individuals were tagged with tetracycline and growth increment data obtained from the change in length of jaw structures (demipyramids) (after Ebert, 2004; Pederson & Johnson, 2008). Jaws were used because they readily stain with fluorescent tetracycline and are widely accepted as the best structure to obtain highly precise measurement of sea urchin growth (Ebert, 2004; Pederson & Johnson, 2008). Annual growth in jaw length (JL) was obtained for *C. rodgersii* ranging from 61 to 133 mm test diameter (TD) (note that the relationship between JL and TD for Tasmanian *C. rodgersii* was described by the linear equation $TD = 4.12 \times JL$, $R^2 = 0.81$, $n = 1484$). During July–September 2004, approximately 300 *C. rodgersii* were obtained from each tagging site (see Table 1) by divers systematically collecting sea urchins from permanently marked plots ($\sim 8\,m \times 8\,m$) located within seaweed-dominated reef habitat. Sea urchins were measured for TD with knife-edge vernier callipers, tagged by injecting 2–4 mL (depending on size) of tetracycline HCl (concentration $20\,g\,L^{-1}$ seawater) through the peristomial membrane, and then returned to the marked plots. Tagged urchins were allowed to grow for at least 12 months *in situ* before recapture was attempted. As marked animals could not be identified in the field, recovery of tagged animals involved collecting all sea urchins from within the marked plots and to a distance of 5 m around the plots (Table 1). For each sea urchin collected, TD was measured and the Aristotles' lantern removed and placed in 12.5%

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sodium hypochlorite for 48 h to expose individual jaw structures. Jaws were then checked under UV light for the presence of a fluorescing tetracycline mark and, if present, the jaw growth increment ($\Delta L$) was measured to nearest 0.05 mm (after Pederson & Johnson, 2008).

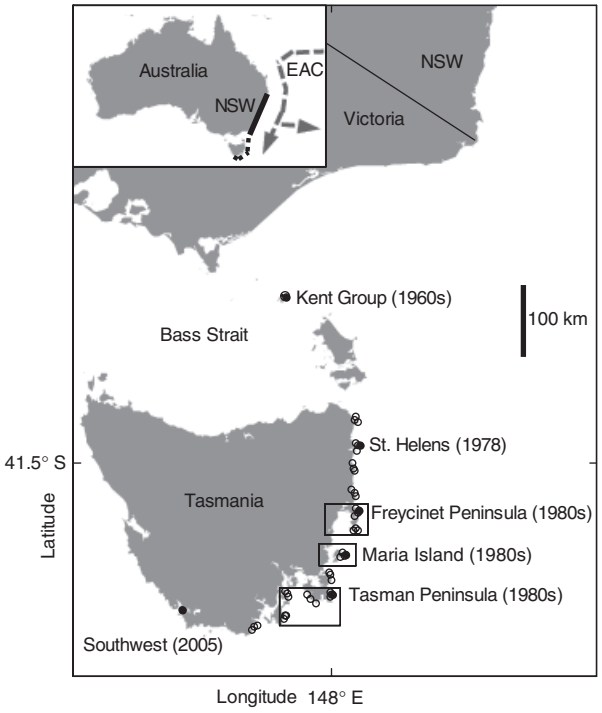


**Fig. 1** Map of southeastern Australia showing sites where *Centrostephanus rodgersii* age structure (filled circles) and density (open circles, data from Johnson *et al*., 2005) were determined in Tasmania. The timing of first sightings of *C. rodgersii* along the Tasmanian coastline is shown in parentheses (after Johnson *et al*., 2005). Inset displays mainland Australia and the direction of the East Australian Current (EAC); the 'native' distribution of *C. rodgersii* (solid line, after Andrew & Byrne, 2001); and the recent range expansion of the sea urchin (broken line). Boxes on eastern Tasmanian mainland indicate three locations where temperature was compared between headland (offshore) and inshore sites.

*Selection and fitting of growth model.* For tag-recaptured *C. rodgersii* in eastern Tasmania, the pattern of annual $\Delta L$ vs. initial jaw size at tagging ($L_t$) indicated an indeterminate growth pattern which was well described by an inverse logistic function (see Rodgers-Bennett *et al*., 2003; Haddon *et al*., 2008). Optimum fits for the inverse logistic functions were determined by minimizing the sum of the negative log-likelihoods for each of the observed jaw growth increments ($\Delta L$) and the expected jaw growth increments derived by the model. The expected variation around the growth increments was explicitly modelled as a power function of the expected length (after Haddon *et al*., 2008). The inverse logistic equation is written as

$$\Delta L = \frac{\mathrm{Max}\Delta L \times \Delta_t}{1 + e^{\mathrm{Ln}(19)\frac{\left(L_t - L_{50}^m\right)}{\left(L_{95}^m - L_{50}^m\right)}}} + \varepsilon_{L_t}, \qquad (1)$$

where Max$\Delta L$ is the hypothetical asymptotic maximum jaw growth increment at some initial jaw size that sets the exponential term to zero, $\Delta_t$ is the actual time increment between tagging and recovery, i.e. 1 year. $L_t$ is the JL when first tagged, $L_{50}^m$is the initial JL at which the mid-way point between the Max$\Delta L$ and zero growth increment is reached, $L_{95}^m$ denotes the initial JL at which 95% of the difference between zero and maximum increment is reached. The error term $\varepsilon_{L_t}$ is additive and normal, and assumed to have a mean of zero and standard deviation $\sigma_{L_t}$, which is also defined as a function of predicted length (see Haddon *et al*., 2008).

*Estimating age distributions from size distributions.* Size–frequency distributions of *C. rodgersii* were obtained by measuring JLs (and TDs) for a total of 1706 urchins from six locations spanning the Tasmanian range (Fig. 1). Age distributions for each location were then constructed by determining age at a given size for each individual from the logistic growth model. Given variability in the generalized growth model, there was relatively low confidence in the absolute nature (accuracy) of the

**Table 1** Summary of tetracycline tagging of *Centrostephanus rodgersii* in northeast (St Helens) and southeast (Tasman Peninsula) Tasmania. Growth models were generated from growth increment data standardized to 365 days growth. Size range of tagged urchins recovered was 61–133 mm test diameter (or 13.8–31 mm jaw length)

| Site | Number of tagged urchins | Date of tagging | Date of recovery | Days at liberty | Number of urchins collected | Number of tagged urchins recovered |
|---|---|---|---|---|---|---|
| St Helens | | | | | | |
| Site 1 | 341 | 28/07/2004 | 22/09/2005 | 421 | 731 | 153 |
| Site 2 | 383 | 17/08/2004 | 11/10/2005 | 420 | 660 | 89 |
| Tasman Peninsula | 250 | 12/09/2004 | 7/10/2005 | 390 | 289 | 189 |
| Total | 974 | | | | 1680 | 431 |

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predicted ages, e.g. from the model, an individual of 75 mm TD could be 6–10 years old, and a 100 mm TD individual could be 12–22 years old. Importantly, however, because growth patterns were consistent in NE and SE Tasmania (growth trajectories between sites were compared using likelihood ratio tests, after Haddon, 2001), the generation of age frequencies with this method provided an unbiased and precise tool for broad-scale examination of *C. rodgersii* age structure in eastern Tasmania. To allow for slight differences in collection times between sites, age was standardized to 22 December 2005.

### *Spatial distribution of* Centrostephanus *across the newly extended range*

The spatial distribution of *C. rodgersii* on the east coast of Tasmania was obtained from dive surveys conducted during 2001–2002 (Johnson *et al*., 2005). This survey involved a spatially hierarchical sampling design based on 13 eastern Tasmanian locations with three sites per location (Fig. 1). The density of *C. rodgersii* at each site was estimated from four replicate belt transects, each 2 m wide and extending from $\sim$ 6 m depth to the bottom edge of the reef or to a maximum depth of 18 m (for details, see Johnson *et al*., 2005). Data on *C. rodgersii* density additional to the primary survey was obtained for the Kent Group of Islands (2005), and southwest Tasmania (2005–2006), giving a total of 41 sites. For the six locations where age structure was estimable, the abundance of *C. rodgersii* was modelled as a function of average urchin age.

### *Patterns in the environment across the newly extended range*

*Proximity to source populations.* For the *C. rodgersii* population to have spread sequentially poleward from the historic NSW range across eastern Tasmania, then within the extension region, there should be a pattern of younger ages and lower population density with increasing distance from the native range. Alternatively, if the population has arisen and spread following a rare recruitment/anthropogenic translocation event to a particular Tasmanian site, then the expectation would be for a punctuated distribution of abundance and ages within the vicinity of a founding population. To examine patterns in age and abundance of *C. rodgersii* across the newly extended range, the edge of the native range was assigned to be the NSW–Victorian border (Fig. 1).

Because the EAC is the major current system in SE Australia and the chief mechanism enabling poleward transport of water mass and larvae from NSW to eastern Tasmania, we hypothesized that *C. rodgersii* populations should, on average, be more abundant and of older average age with closer proximity to this current system (based on the likelihood of cross-shore diffusion of larvae, e.g. Largier, 2003). Alternatively, if *C. rodgersii* populations in eastern Tasmania are not associated with this environmental signal, then it would suggest that other abiotic or biotic factors are more important in driving the observed range extension. Proximity to the EAC was determined by estimating the position of its western margin based on the distribution of isotherms generated from averaged sea surface temperature (SST) maps over the period 1992–2006 (SST Pathfinder, 4 km $\times$ 4 km interpolated pixels). Note that while the EAC extension is widely recognized as a predominantly summer phenomenon in SE Australia (Ridgway, 2007a, b), the western margin of this oceanographic feature from the NSW–Victorian border south was most strongly demarcated as the 12.9 °C isotherm during winter when atmospheric cooling of neighbouring water masses clearly revealed the proximal edge of this warm feature. Average age of *C. rodgersii* at each of the six locations where age was estimable was therefore regressed against proximity to NSW–Victorian border and proximity to the western edge of the EAC. Abundance of *C. rodgersii* was also regressed against distance to the NSW–Victorian border (native range) and proximity to the EAC.

*Winter climate across the newly extended range.* Species undergoing poleward range extension will be most physiologically challenged during cold winter conditions. Given that the cold water threshold for *C. rodgersii* larval development is 12 °C and that coastal water temperatures in eastern Tasmania during the winter spawning period (August) fluctuate about the 12 °C threshold (Ling *et al*., 2008), we examined the distribution of *C. rodgersii* abundance with respect to winter climate across Tasmania. We hypothesized that the abundance of *C. rodgersii* in eastern Tasmania should reflect this lower physiological limit of the sensitive larval phase, i.e. sites where winters are warmer should be more suitable habitat for *C. rodgersii* larvae to develop and settle, and thus adult populations should be larger. Using the population density of *C. rodgersii* as a proxy for recruitment, we correlated density of *C. rodgersii* with respect to the average August (coldest winter month) temperature obtained from remotely sensed SST imagery available for 1992–2006 (SST Pathfinder). Note that the average August SST for each site was interpolated from the surrounding 4 km $\times$ 4 km pixel, and to avoid distortion from coastal landmasses, sites were offset seaward by 4 km. Furthermore, because the SST was obscured on days of cloud cover, each daily temperature estimate was calculated as the running mean for $\pm$ 3 days about the day of interest.

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*Local-scale patterns: headlands vs. embayments.* Observations of the distribution of *C. rodgersii* in eastern Tasmania suggest an association of the sea urchin with headlands along this coastline (S. Ling, personal observation). This pattern contrasts with that observed within the native range of *C. rodgersii* where the sea urchin is found abundantly throughout headlands and embayments (Andrew & Byrne, 2001). We therefore compared interannual SST signals for rocky reef habitats at headlands and adjacent inshore reefs at three locations, where SST data and estimates of *C. rodgersii* density were available (see Fig. 1). The density of *C. rodgersii* was then examined with respect to the proportion of winters in which the temperature regime existed above the 12 °C cold threshold for *C. rodgersii* larval development. Additional sea temperature data were obtained at headlands and embayments from calibrated *in situ* loggers (Optic Stowaway WTA08-05 + 37 by Onset®, Onset Computer Corp., MA, USA, accuracy ± 0.2 °C) fixed to reef at a depth of 9 m.

## Results

### *Population structure of* Centrostephanus *across the newly extended range*

Growth patterns of *C. rodgersii* across sites in eastern Tasmania were highly similar (likelihood ratio test between St Helens and Tasman Peninsula sites indicated no difference, $P = 0.45$, with almost total overlap of the 99% bounds around the residuals). Thus, all growth increment data were pooled to derive a generalized growth model for *C. rodgersii* in eastern Tasmania. Annual growth of *C. rodgersii* jaws was best described by an inverse logistic model (indeterminate growth) (Fig. 2a). From this model, age at a given JL (Fig. 2b) and age at a given TD (Fig. 2c) were estimated. Estimation of age structure from size distributions for six locations spanning the Tasmanian range of *C. rodgersii* revealed a pattern of younger ages with increasing poleward (southward) extent. Northern locations contained populations represented by a broad range of predicted ages including many older individuals. Moving southward, age distribution became dominated by younger individuals with relatively few old individuals represented (Fig. 3). Across the extension region, the density of *C. rodgersii* was positively related to mean population age ($y = 0.031x + 0.2$, $R^2 = 0.70$).

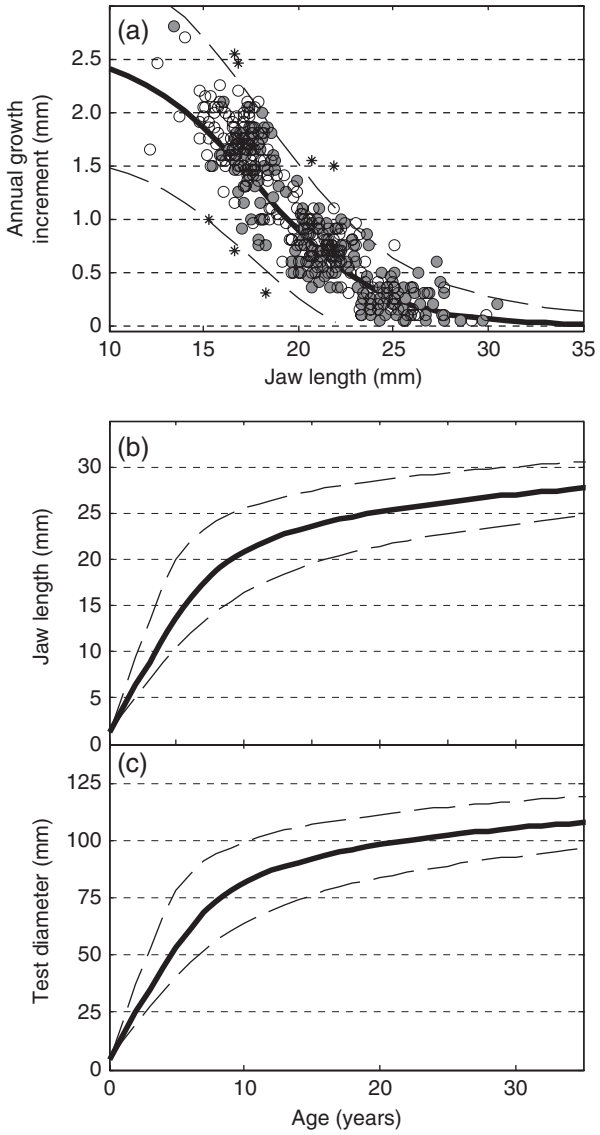


**Fig. 2** Growth of *Centrostephanus rodgersii* in macroalgal habitat in eastern Tasmania. (a) Generalized *C. rodgersii* growth model in macroalgal habitat in eastern Tasmania based on annual jaw growth. Closed circles are data for St Helens, while open circles are for Tasman Peninsula. The seven samples represented as stars in panel (a) were removed from the analysis after being identified as outliers from the spread of residuals. The optimal inverse logistic parameters for Eqn (1) were Max$\Delta L$ = 2.599 mm, $L_{50}^{m}$ = 17.994 mm, and $L_{95}^{m}$ = 27.290 mm. From this equation, jaw length (JL) at age (b) and test diameter (TD) at age (c) are predicted. TD is determined from the relationship between TD and JL: TD = 4.12 × JL, $R^2 = 0.81$. In all panels, solid lines represent the median model fit generated from 1000 bootstrap simulations and broken lines indicate 95% confidence intervals.

### *Correlative patterns across the newly extended range*

Mean SST patterns reveal the dominant influence of the EAC on coastal waters in SE Australia, including eastern Tasmania (Fig. 4a). Across the range extension region of *C. rodgersii*, mean population age of the sea urchin was negatively related to increasing distance from the southern limit of the sea urchins historical

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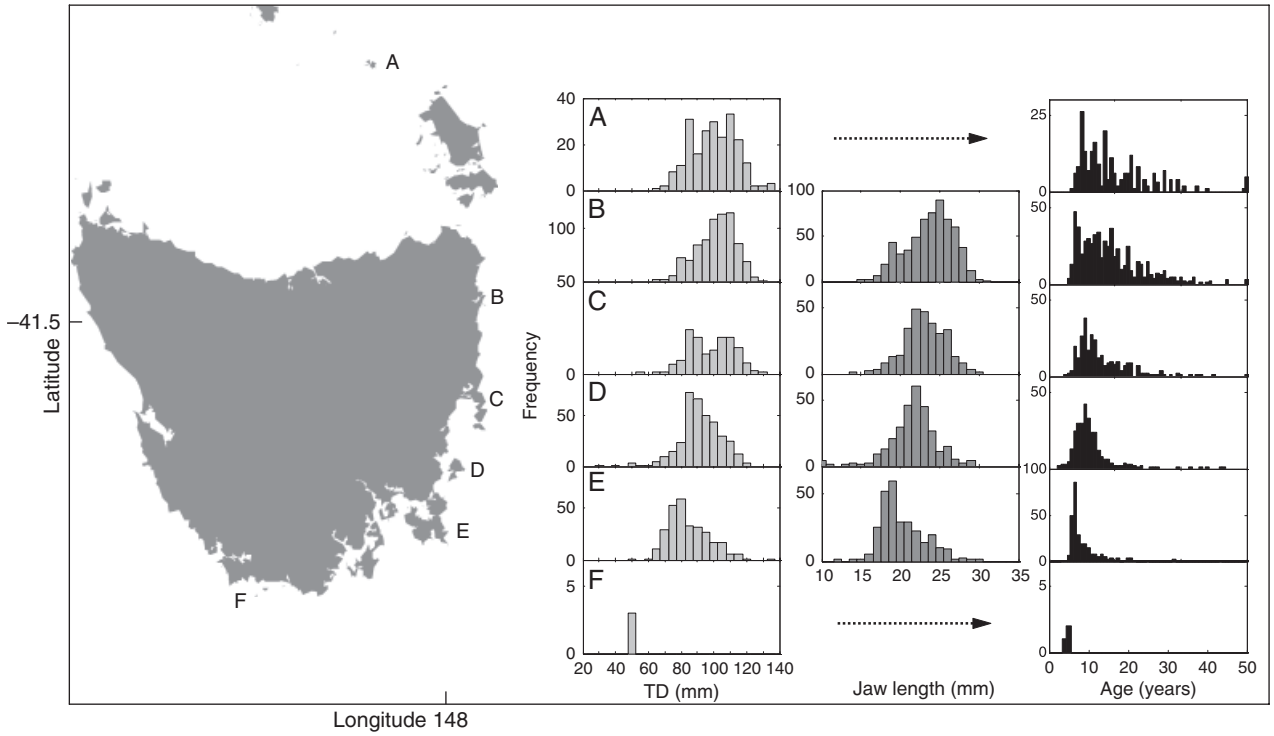


**Fig. 3** Spatial pattern of *Centrostephanus rodgersii* size and age structures in eastern Tasmania. A: Kent Group, $n = 222$; B: St Helens, $n = 600$; C: Freycinet Peninsula, $n = 300$; D: Maria Island, $n = 300$; E: Tasman Peninsula, $n = 281$; F: Southwest Tasmania, $n = 3$. Note that age frequencies for Kent Group and southwest Tasmania were generated by converting test diameters (TDs) to jaw lengths using the generalized allometric relationship for eastern Tasmania.

range (i.e. the NSW–Victorian border) (Fig. 4b); and evidence for an exponential decline in mean age was observed with increasing distance from the western edge of the EAC across eastern Tasmania, but not for Bass Strait where the Kent Group appeared anomalous to this pattern (Fig. 4c). The local abundance of *C. rodgersii* across the extension region (i.e. number of sea urchins $m^{-2}$ of rocky reef) vs. proximity to population sources also revealed evidence of negative, but noisy, correlations with distance from the historical range (Fig. 4d) and distance from the western edge of the EAC (Fig. 4e). Note that proximity of the historical range of *C. rodgersii* did not simply co-vary with proximity to the western edge of the EAC; for eastern Tasmania (NE to Tasman Peninsula, excluding the anomalous Kent Group), a slight negative correlation was observed (linear fit, $EAC_{prox.} = -0.037 \times historic_{prox.} + 43.75$, $R^2 = 0.46$); meanwhile, a strong positive relationship was described for sites in southern Tasmania where *C. rodgersii* was rare (linear fit, $EAC_{prox.} = 0.62 \times historic_{prox} - 356.48$, $R^2 = 0.42$).

Examination of mean SST for 41 eastern Tasmanian sites during the known *C. rodgersii* spawning period of August (winter) revealed that the sea urchin is generally limited to sites experiencing relatively warm winter temperatures in eastern Tasmania (Fig. 5a). Interannual SST profiles across eastern Tasmania (for the period 1993–2006) revealed a clear pattern of increasing local density of *C. rodgersii*, with an increasing proportion of winters experiencing temperatures warmer than the 12 °C cold water threshold for larval development (Fig. 5b). Examination of sea temperature profiles on headlands, where *C. rodgersii* was abundant, also revealed warmer winter temperatures at these sites and a greater proportion of winters >12 °C, relative to adjacent inshore sites where fewer or no *C. rodgersii* were established (Fig. 6a–c).

## Discussion

### *Poleward decrease in age*

Within the recently extended range of *C. rodgersii*, mean population age of the sea urchin became progressively younger towards the poleward range limit. This age dynamic is therefore consistent with the historical time course of sequential poleward discoveries and expansion of *C. rodgersii* populations across eastern Tasmania, which has occurred at a rate of $\sim 160\,km\,decade^{-1}$ over the past 40 years (see Fig. 1). Furthermore, the

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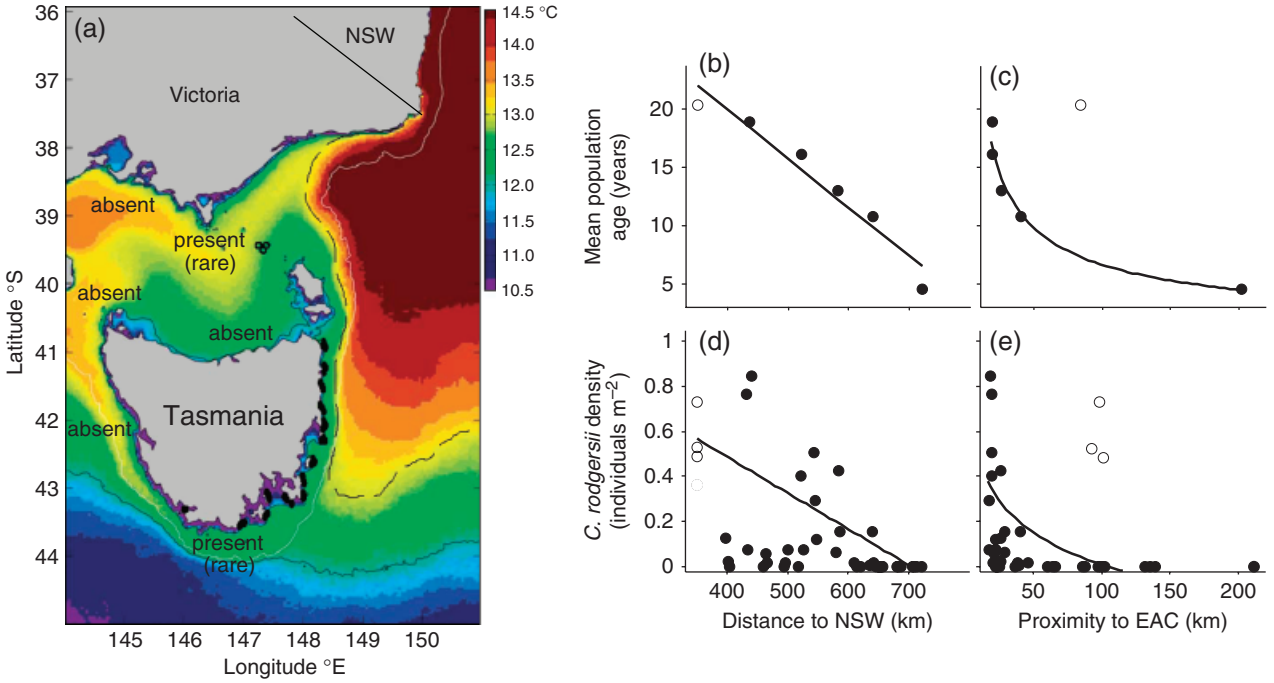


**Fig. 4** (a) Sea surface temperature map showing influence of the East Australian Current (EAC) in eastern Tasmania (data are means for August 1993–2007); western edge of the EAC is shown as broken line; also shown is the presence/absence of *Centrostephanus rodgersii* for locations west of New South Wales (NSW)/eastern Tasmania. (b) Regression of mean population age of *C. rodgersii* against proximity to native range, $y = -0.042x + 36.66$, $R^2 = 0.94$; filled symbols are for mainland Tasmania and open symbols are for the Kent Group. (c) Mean population age vs. distance to the mean position of the western margin of the EAC 1992–2006; data across mainland Tasmania (excluding Kent Group) displays a negative exponential, $y = 87.46x^{-0.56}$, $R^2 = 0.98$. (d) Density of *C. rodgersii* in eastern Tasmania vs. distance to native range; linear trend line represents 'ceiling' of the distribution obtained by regression of highest ranking sites within each location, $y = -0.0016x + 1.1276$, $R^2 = 0.41$. (e) Density of *C. rodgersii* in eastern Tasmania vs. proximity to the EAC; log trend line represents 'ceiling', as per (c), but excluding Kent Group, $y = -0.2036\,\mathrm{Ln}(x) + 0.95$, $R^2 = 0.41$.

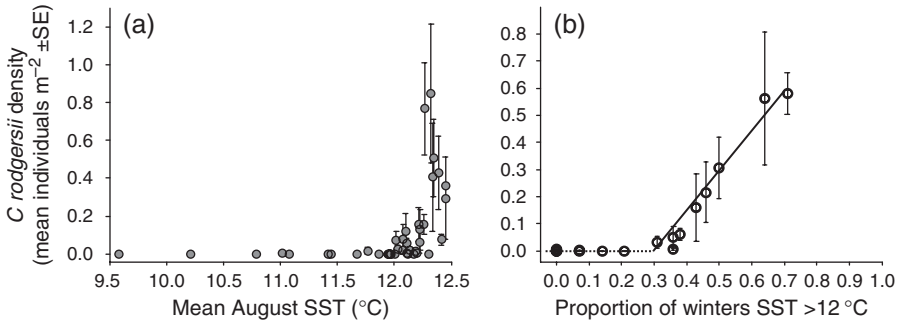


**Fig. 5** (a) Density of *Centrostephanus rodgersii* as a function of mean August temperature [mean sea surface temperature (SST) derived from satellite images for the period 1993–2006] for 41 sites in eastern Tasmania. (b) Density of *C. rodgersii* as a function of proportion of winters (July–August–September, 1993–2006) where mean temperature is greater than the 12 °C larval development threshold (after Ling *et al.*, 2008); linear trend line fitted to data where $x$ values $>0.3$, $y = 1.4044x - 0.4143$, $R^2 = 0.93$.

broad range of *C. rodgersii* ages in NE Tasmania indicates that the range extension has not occurred as the result of a single, massive recruitment event. Rather, there appears to have been multiple episodes of sea urchin recruitment with seemingly fewer and more recent recruitment events towards the southern limit of the extension region. Indeed, analyses of genetic diversity of *C. rodgersii* from within the extension region and historical regions of the species' range yield no evidence of a founder effect, suggesting continued

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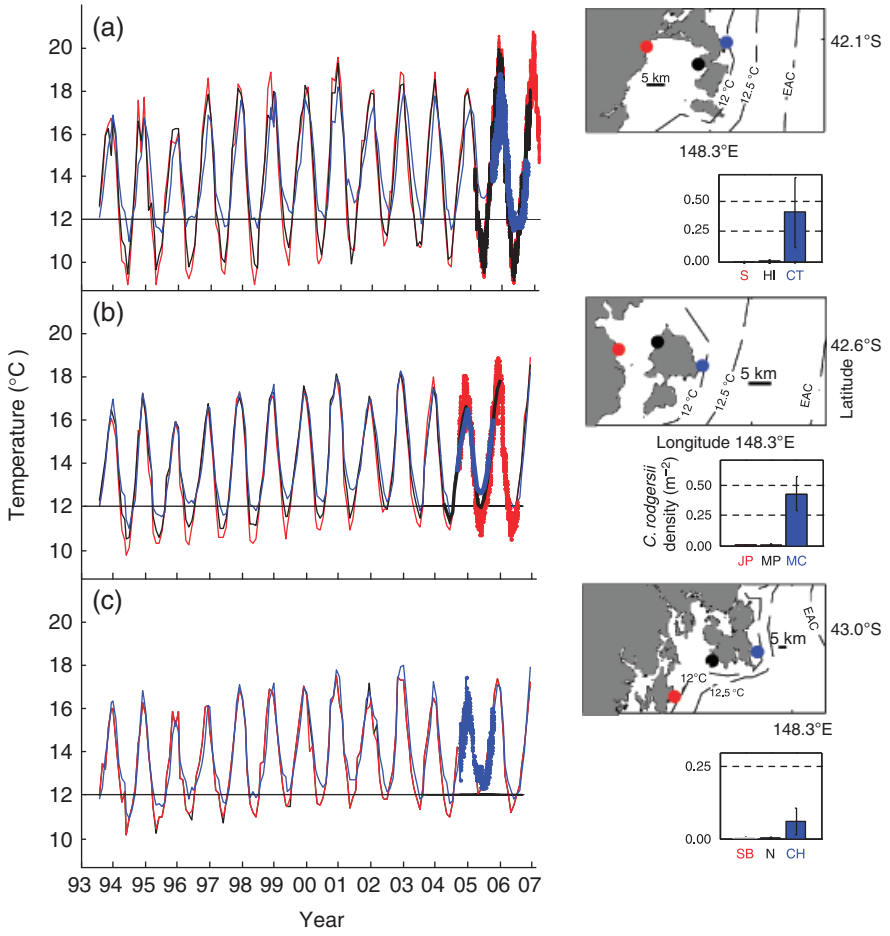


**Fig. 6** Seasonal temperature profiles and abundance of *Centrostephanus rodgersii* at 'headland' and adjacent inshore reefs. Data are sea surface temperature for 1993–2007; thickened lines are data obtained from *in situ* temperature loggers. Horizontal bar on temperature plots indicates the lower temperature threshold (12 °C) for *C. rodgersii* larval development (after Ling *et al.*, 2008); numbers in parentheses indicate proportion of winters >12 °C at each site for 1993–2007. (a) Freycinet Peninsula: CT, Cape Tourville (0.43); HI, Hazards Is. (0.00); S, Swansea (0.00). (b) Maria Island: MC, Mistaken Cape (0.46); MP, Magistrates Pt. (0.00); JP, Johnson's Pt. (0.00). (c) Tasman Peninsula: CH, Cape Huay (0.38); N, Nubeena (0.07); SB, South Bruny (0.07). For locations within Tasmania, refer to Fig. 1. On maps, isotherms and western EAC margin represent mean positions for winter 1993–2006. *C. rodgersii* abundance data for HI and S, in panel (a), courtesy of N. Barrett.

supply of individuals from within the historical range (Johnson *et al.*, 2005; Banks *et al.*, 2007). Given that the benthic phase of *C. rodgersii* is reef bound and because of a lack of contiguous reef habitat from the historic range to the range extension region (i.e. across Bass Strait, see Fig. 1), migration of the sea urchin to Tasmanian waters must have occurred, and most likely continually occurs via the sea urchins highly dispersive pelagic larval phase. The only alternative would be continual migration via direct anthropogenic translocation of adult individuals via vectors such as shipping; however, patterns in population spread, age structure, genetic signals (*op cit*) and port locations provide no evidence supporting the existence of such a mechanism.

The positive relationship observed between the abundance and age of *C. rodgersii* across the extension region is consistent with a population undergoing expansion (as documented by Johnson *et al.*, 2005) and suggests a mechanism(s) for continued recruitment of larvae to previously established populations. For *C. rodgersii* to undergo localized population expansion, its larvae must either actively seek sites with conspecific adults (e.g. Tegner & Dayton, 1977; Rowley, 1990), or local nearshore coastal hydrodynamics somehow determines larval supply, or there is differential habitat suitability such that particular sites accumulate cohorts to become abundant and old (e.g. Ebert & Russell, 1988; Morgan *et al.*, 2000; Wing *et al.*, 2003). Because of the long-lived planktotrophic larval phase of *C. rodgersii*, dispersal of larvae from parental sites is potentially great. Hence, the scale at which larvae could actively seek out adult populations is likely to be small relative to scales over

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which larvae are potentially dispersed. Therefore, differential exposure of coastal sites to larval supply would appear a plausible mechanism explaining the observed relationship between population abundance and age structure of *C. rodgersii* across the extension region in eastern Tasmania.

### *Proximity to larval sources*

Supporting a model of range extension based on larval supply, the proximity of eastern Tasmanian sites to putative population sources of *C. rodgersii* revealed that average age and abundance of the sea urchin not only declined with increasing distance from the southern boundary of NSW (i.e. across a latitudinal gradient), but sea urchin age and abundance were also negatively correlated with distance to the nearshore margin of the EAC in eastern Tasmania. While a decline in abundance with increasing distance (latitude) from a native range may be simply explained by gradual diffusion of the species from a population centre at lower latitude (e.g. Brown's principle), in the case of a benthic invertebrate with a highly dispersive larval phase, yet a nonmigratory reef-bound adult phase, such a distributional pattern is also likely to reflect opportunity for larval dispersal (e.g. Largier, 2003). With respect to the chief mechanism for poleward transport, the EAC, mean age and abundance of *C. rodgersii* were correlated with proximity to this oceanic feature across the range extension region. While this pattern held strongly across eastern Tasmania and while general proximity to the EAC provides a broad biogeographic description of the sea urchins presence throughout the SE Australian region (see Fig. 4a), the high densities and relatively old ages of *C. rodgersii* within the Kent Group of Islands (eastern Bass Strait) was an exception to this pattern. Intriguingly, the reef biota of the Kent Group, unlike adjacent island groups immediately north (Hogan Group) and south (Flinders Group), is typical of southern NSW and formally classified within the same bioregion (IMCRA, 2006). Clearly, some form of connectivity (perhaps relating to the proximity of the warm tongue of 13 °C water observable in NE Bass Strait in Fig. 4a, or perhaps dynamic interseasonal ocean patterns evident in this region, but not captured by our analysis) must be invoked to explain the presence of *C. rodgersii* in the Kent Group and the lack of genetic differentiation between this population and populations in NSW or eastern Tasmania (Johnson *et al*., 2005).

### *Winter climate and the cold physiological limit*

Because eastern Tasmania represents the southern range extent where coastal waters are cold (~ 10–18 °C) relative to NSW (~ 13–25 °C), the observed distribution of *C. rodgersii* in Tasmania may be due to the moderating influence of the warm EAC along this coast (Ridgway, 2007a, b; see Fig. 4a). Indeed, any limiting effects of cold water on the development and survival of the sea urchin in Tasmania would most likely be felt during winter. Examination of *C. rodgersii* distribution with respect to winter water temperature revealed that the sea urchin is most abundant at sites of relatively warm winter climate (Figs 4a, 5, 6). In eastern Tasmania, warmer sites generally supported higher abundances of *C. rodgersii* relative to nearby colder sites where its abundance was low or the sea urchin was absent altogether (see Fig. 4a). However, variability in *C. rodgersii* abundance across warmer winter sites suggests that factors other than temperature per se are important in determining patterns in abundance such as reef habitat quality (Johnson *et al*., 2005), or barriers against dispersal of sea urchin larvae (e.g. Gaylord & Gaines, 2000). Clearly, a model of *C. rodgersii* distribution in SE Australia based purely on a bioclimate envelope of suitable temperature for larval development (i.e. >12 °C) is inappropriate, as the suitable bioclimatic envelope would extend across most of southern Australia. However, *C. rodgersii* is not present on coastlines west of Bass Strait (Fig. 4a). Indeed, current-mediated dispersal barriers are known to define many biogeographical boundaries in coastal oceans, despite apparently suitable habitat occurring beyond dispersal barriers (e.g. Gaylord & Gaines, 2000 reviewed in Harley *et al*., 2006). Similar to our findings, Banks and co-workers (2007) conclude that the oceanographic influence on local genotypic structure of *C. rodgersii* relates to the temporal variability in sea temperature, as opposed to temperature per se or other factors that may vary purely across a latitudinal gradient.

The global extent of *C. rodgersii* further suggests that patterns in the EAC are important in determining the biogeography of the species as populations of the sea urchin occurring outside of Australian waters, i.e. in northern New Zealand including the Kermadec Islands (e.g. Schiel *et al*., 1986) occur where the EAC flows proximal to these sites (Ridgway & Dunn, 2003). Demonstrating population connectivity and larval dispersal capability across large scales (>1000s km), *C. rodgersii* populations in NZ also show weak genetic differentiation from SE Australian populations (Banks *et al*., 2007). Given that variability in SST for the SE Australian region is strongly influenced by southward movement of the EAC (Ridgway, 2007a, b; see Fig. 4a), it is plausible that patterns in local age structure of *C. rodgersii* across the range extension region reflect the supply of larvae driven by patterns of the EAC. Thus, variability in the EAC, as a mechanism for dispersal of

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*C. rodgersii* larvae, appears important in defining large-scale (>1000s km) and local-scale (1000s m) distribution of the sea urchin. However, the observed temperature dependency of *C. rodgersii* larvae strongly indicates the potential for a dual role played by the EAC across the range extension region by providing (1) a physical dispersal mechanism governing larval supply from within the historic range, and (2) poleward transport of heat maintaining localized reef habitats in Tasmania above the thermal threshold for early development. Because *C. rodgersii* populations in eastern Tasmania undergo normal seasonal reproductive activity and can produce viable larvae, it is likely that the sea urchin is capable of self-recruiting and undergoing population expansion within the extension region when winter temperatures, driven by EAC dynamics, are maintained above the threshold for successful larval development (Ling *et al*., 2008).

### *Local-scale patterns: headlands vs. embayments*

Examination of local-scale patchiness in seasonal climate revealed that headland sites, where *C. rodgersii* was abundant, expressed milder winter climates relative to inshore areas where seasonal temperature fluctuated with greater amplitude. Furthermore, headland sites were also closer to the EAC, and they more likely project further beyond potential coastal boundary layers and so may more frequently sample offshore currents (e.g. Shanks, 1995; Largier, 2003). Thus, the EAC appears to drive milder winter temperature regimes at such headland sites as well as greater larval supply to these sites, whereas the thermal regime of inshore areas appears more influenced by atmospheric forcing as evidenced by higher summer maxima and lower winter minima (Fig. 6a–c; also see Ridgway, 2007a, b).

The pattern of greater apparent recruitment of *C. rodgersii* to headlands across eastern Tasmania contrasts with the findings of Ebert & Russell (1988) on the west coast of North America, where a negative association between inferred recruitment rates of sea urchins (*Strongylocentrotus franciscanus*) and headlands was reported. In their study, enhanced upwelling of cold water containing fewer urchin larvae was more prevalent at headlands, leading to variable recruitment at these sites relative to more uniform coastline and embayments where upwelling was unpredictable and size frequencies indicated a more consistent annual recruitment (see also Morgan *et al*., 2000). In reconciling differences between our study and those of others (i.e. Ebert & Russell, 1988; Morgan *et al*., 2000), it would appear that the presence of headlands per se does not determine sea urchin recruitment. Rather, it is the interaction of these coastal features with the prevailing oceanic features that appears important in influencing larval dispersal and determining local recruitment patterns for planktotrophic sea urchins (see also Banks *et al*., 2007). Clearly, finer scale resolution of oceanic influences on *C. rodgersii* distribution and demographics would necessitate the sampling of sea urchin settlement (0+ year class) across multiple sites over several years to determine the nature of putative fine-scale links between sea urchin recruitment and environmental signals.

### *Latitudinal trends in adult performance?*

While the positive relationship observed between *C. rodgersii* abundance and age across the range extension region is consistent with a population undergoing expansion (and corroborates with the observed discovery and expansion of the urchin in Tasmania documented by Johnson & co-workers, 2005), alternatively, this pattern may reflect a gradient in adult performance (e.g. Brown's principle, Brown, 1984; Brown *et al*., 1995). Assuming homogenous recruitment of juveniles across the study locations, natural mortality rates would have to be at least four times greater in SE as opposed to NE Tasmania, and up to 25 times greater in southern Tasmania compared with the NE Tasmanian locations, in order to sufficiently account for the observed patterns in age structure (Fig. 7a). However, in contrast to poor larval performance, adult *C. rodgersii* in Tasmania are observed to grow to large size at reef sites where sea temperatures readily fall below 12 °C during winter (see Figs 5 and 6). While such reefs contain few *C. rodgersii* (see Fig. 6), sea temperature alone would appear insufficient to drive such large discrepancies in rates of adult mortality, given low latitudinal variability in temperature, particularly across exposed coastal sites in eastern Tasmania (see Fig. 7a and b). Furthermore, patterns in adult growth rates (Fig. 2), dietary composition (S. Ling, unpublished results) and reproductive output of *C. rodgersii* (Ling *et al*., 2008) across eastern Tasmania indicate no evidence of declining adult performance with increasing latitude (also see Byrne *et al*., 1998; Ebert *et al*., 1999; Gilman, 2005; Lester *et al*., 2007).

Another possible explanation is that the pattern of younger ages towards the edge of the extension region is driven by potential latitudinal trends in mortality rates due to either disease or predation. While disease outbreaks and predators can have major impacts on sea urchin populations (reviewed by Steneck *et al*., 2002), moribund *C. rodgersii* have not been observed in Tasmania (during observations over >8 years; S. Ling, personal observation), and the principal predators capable of consuming *C. rodgersii* in Tasmania, i.e. large

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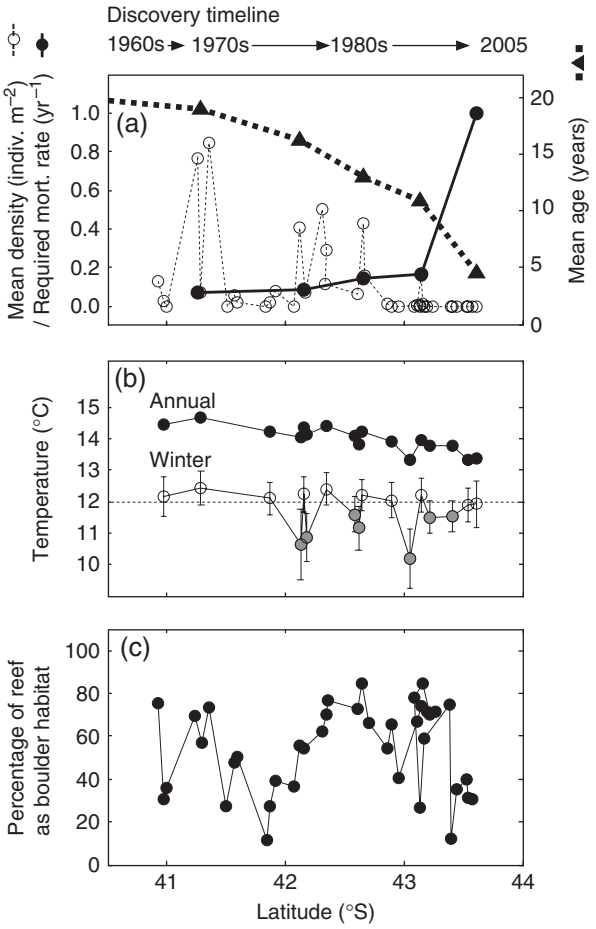


**Fig. 7** Latitudinal patterns in (a) density of *Centrostephanus rodgersii* (data from Johnson *et al*., 2005), age, and adult mortality rate (*Z* estimate) required to generate the observed age profile across the range extension region, assuming equal larval settlement across locations; (b) mean annual and mean winter sea temperature, note that mean winter temperature consistently exceeds the cold 12 °C physiological threshold for larval development for exposed eastern Tasmanian sites north of Tasman Peninsula 43°S); and (c) availability of preferred boulder habitat for *C. rodgersii* (data from Johnson *et al*., 2005). For (a), *Z* was estimated as the negative slope of the natural log of frequencies across age classes (for age classes 7 + ), after Haddon, 2001; note that *Z* refers to natural mortality only as *C. rodgersii* is not currently harvested in Tasmania. Further note that, for winter temperatures, i.e. plot (b), filled symbols represent 'embayment' sites, whereas open symbols are exposed coastal locations.

spiny lobsters (*Jasus edwardsii*) >140 mm carapace length (S. D. Ling *et al*., unpublished results), have been heavily fished across eastern Tasmania and were rarely observed across all sites from which age frequencies were obtained. Nonetheless, because predation risk is highly size specific among sea urchins (e.g. Shears & Babcock, 2002; Pederson *et al*., 2006; S. D. Ling *et al*., unpublished results), younger (i.e. smaller) individuals are more vulnerable to lobster predation; hence, expectations for urchin populations experiencing heavy rates of predation would be a bias towards older, not younger individuals. Furthermore, because *C. rodgersii* prefers boulder habitat where it can seek shelter from predators (Andrew, 1993; reviewed by Andrew & Byrne, 2001), predation risk will be influenced by the availability of this preferred habitat type; however, the proportion of boulder habitat across the eastern Tasmanian study sites did not reveal a latitudinal gradient (Fig. 7c).

### *Future trends*

Typical of benthic marine invertebrates, the chief mechanisms defining the SE Australian range of *C. rodgersii* appear to be dispersal barriers and physiological limits of early life history stages (e.g. Zacherl *et al*., 2003). That is, a poleward advance of the EAC of ~350 km over the past 60 years (Ridgway, 2007a) appears to have dually created opportunity for *C. rodgersii* to undergo range extension by facilitating greater southward transport of larvae and promoting a warming local temperature regime that is now suitable for successful development of the sea urchin within eastern Tasmania. While it was not our goal to explicitly test the contribution of 'temperature' vs. 'transport' (e.g. Gaylord & Gaines, 2000), the relative importance of each mechanism in defining the range extension/expansion of *C. rodgersii* in Tasmania may have varied historically and may vary in the future. More importantly, in highlighting links between *C. rodgersii* population trends and the physical environment across the extension region, our results suggest that ongoing climate change is poised to have further effects on *C. rodgersii* distribution in eastern Tasmania by (1) increasing the extent of thermally suitable reef habitat as a direct result of atmospheric forced ocean warming, and (2) by driving further poleward supply of larvae and accelerating a warmer coastal regime as a result of ongoing intensification of the EAC (as predicted by Cai *et al*., 2005; Cai, 2006). Finally, our results strongly indicate that any generalized prediction of species range shifts in the marine environment must not only account for shift in bioclimate envelopes, but that the spatial and temporal extent of bio-climate envelopes must themselves be defined within the bounds of current-driven dispersal potential.

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## References

Andrew NL (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. *Ecology*, **74**, 292–302.

Andrew NL, Byrne M (2001) The ecology of *Centrostephanus rodgersii*. In: *Edible Sea Urchins: Biology and Ecology* (ed. Lawrence JM), pp. 149–160. Elsevier Science, Amsterdam, the Netherlands.

Banks SC, Piggot MP, Williamson JE, Bové U, Holbrook NJ, Beheregaray LB (2007) Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. *Ecology*, **88**, 3055–3064.

Barry JP, Baxter CH, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science*, **267**, 672–675.

Brown JH (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Byrne M, Andrew NL, Worthington DG, Brett PA (1998) Reproduction in the diadematoid sea urchin *Centrostephanus rodgersii* in contrasting habitats along the coast of New South Wales, Australia. *Marine Biology*, **132**, 305–318.

Cai W (2006) Antarctic ozone depletion causes an intensification of the Southern Ocean super-gyre circulation. *Geophysical Research Letters*, **33**, L03712, doi: 10.1029/2005GL024911.

Cai WJ, Shi G, Cowan T, Bi D, Ribbe J (2005) The response of southern annular mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. *Geophysical Research Letters*, **32**, L23706, doi: 10.1029/2005GL024701.

Ebert TA (2004) Shrinking sea urchins and the problems of measurement. In: *Echinoderms: München: Proceedings of the 11th International Conference* (eds Heinzeller T, Nebelsick JH), pp. 321–325. Taylor & Francis Group, London.

Ebert TA, Dixon JD, Schroeter SC, Kalvass PE, Richmond NT, Bradbury WA, Woodby DA (1999) Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. *Marine Ecology Progress Series*, **190**, 189–209.

Ebert TA, Russell MP (1988) Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnology and Oceanography*, **33**, 286–294.

Fields PA, Graham JB, Rosenblatt RH, Somero GN (1993) Effects of expected global climate change on marine faunas. *Trends in Ecology and Evolution*, **8**, 361–367.

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist*, **155**, 769–789.

Gilman S (2005) A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846). *Journal of Biogeography*, **32**, 1583–1589.

Haddon M (2001) *Modelling and Quantitative Methods in Fisheries*. Chapman & Hall/CRC, Boca Raton, FL, USA.

Haddon M, Mundy C, Tarbath D (2008) Using an inverse-logistic model to describe Tasmanian blacklip abalone (*Halitotis rubra*) growth increments. *Fishery Bulletin*, **106**, 58–71.

Harley CDG, Hughes RA, Hultgren KM *et al*. (2006) The impact of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.

Hill NA, Blount C, Poore AGB, Worthington D, Steinberg P (2003) Grazing effects of the sea urchin *Centrostephanus rodgersii* in two contrasting rocky reef habitats: effects of urchin density and its implications for the fishery. *Marine and Freshwater Research*, **54**, 691–700.

Holbrook SJ, Schmitt RJ, Stephens JA (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications*, **7**, 1299–1310.

Huggett MJ, King CK, Williamson JE, Steinberg PD (2005) Larval development and metamorphosis of the Australian diadematid sea urchin *Centrostephanus rodgersii*. *Invertebrate Reproduction and Development*, **47**, 197–204.

IMCRA (2006) *The Integrated Marine and Coastal Regionalisation of Australia, Version 4.0: Meso-scale Bioregions*. Department of the Environment and Heritage, Australian Government http://www.environment.gov.au/coasts/mbp/publications/imcra/pubs/map2-msb.pdf.

Johnson CR, Ling SD, Ross J, Shepherd S, Miller K (2005) *Establishment of the long-spined sea urchin (Centrostephanus rodgersii) in Tasmania: first assessment of potential threats to fisheries*. FRDC Final Report, Project No. 2001/044. School of Zoology and Tasmanian Aquaculture and Fisheries Institute, University of Tasmania.

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications*, **13**, S71–S89.

Lester SE, Gaines SD, Kinlan BP (2007) Reproduction on the edge: large-scale patterns of individual performance in a marine invertebrate. *Ecology*, **88**, 2229–2239.

Lima FP, Ribeiro PA, Queiroz N, Xavier R, Tattoso P, Hawkins SJ, Santos AM (2007) Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. *Global Change Biology*, **13**, 2065–2077.

Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia*, **156**, 883–894.

Ling SD, Johnson CR, Frusher S, King CK (2008) Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology*, **14**, 907–915.

McGowan JA, Cayan DR, Dorman LM (1998) Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science*, **281**, 210–217.

Meehl GA, Stocker TF, Collins WD *et al*. (2007) Global climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S,

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Qin D, Manning M *et al*.), Cambridge University Press, Cambridge, UK and New York, NY, USA.

Morgan LE, Wing SR, Botsford LW, Lundquist CJ, Diehl JM (2000) Spatial variability in red sea urchin (*Strongylocentrotus franciscanus*) recruitment in northern California. *Fisheries Oceanography*, **9**, 83–98.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography*, **12**, 361–371.

Pederson HG, Johnson CR (2006) Predation of the sea urchin *Hellocidaris erythrogramma* by rock lobsters *(Jasus edwardsii)* in no-take marine reserves. *Journal of Experimental Marine Biology and Ecology*, **336**, 120–134.

Pederson HG, Johnson CR (2008) Growth and age structure of sea urchins (*Heliocidaris erythrogramma*) in complex barrens and native macroalgal beds in eastern Tasmania. *ICES Journal of Marine Science*, **65**, 1–11.

Poloczanska ES, Babcock RC, Butler A *et al*. (2007) Climate change and Australian marine life. *Oceanography and Marine Biology: An Annual Review*, **45**, 407–478.

Ridgway KR, Dunn JR (2003) Mesoscale structure of the mean East Australian Current system and its relationship with topography. *Progess in Oceanography*, **56**, 189–222.

Ridgway KR (2007a) Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters*, **34**, L13613, doi: 10.1029/2007GL030393.

Ridgway KR (2007b) Seasonal circulation around Tasmania: an interface between eastern and western boundary dynamics. *Journal of Geophysical Research*, **112**, C10016, doi: 10.1029/2006JC003898.

Rodgers-Bennett L, Rodgers DW, Bennett WA, Ebert TA (2003) Modeling red sea urchin (*Strongylocentrotus franciscanus*) growth using six growth functions. *Fisheries Bulletin*, **101**, 614–626.

Rowley RJ (1990) Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. *Marine Ecology Progress Series*, **62**, 229–240.

Sagarin R, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an intertidal community over short and long term time scales. *Ecological Monographs*, **69**, 465–490.

Schiel DR, Kingsford MJ, Choat JH (1986) Depth distribution and abundance of benthic organisms and fishes at the subtropical Kermadec islands. *New Zealand of Marine and Freshwater Research*, **20**, 521–535.

Shanks AL (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: *Ecology of Marine Invertebrate Larvae* (ed. McEdward L), pp. 323–367. CRC Marine Science Series, Boca Raton, FL, USA.

Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, **132**, 131–142.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estos JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, **29**, 436–459.

Tegner MJ, Dayton PK (1977) Sea urchin recruitment patterns and implications of commercial fishing. *Science*, **196**, 324–326.

Wing SR, Lamare MD, Gibbs MT (2003) Reproductive sources and sinks within a sea urchin, *Evechinus chloroticus*, population of a New Zealand fjord. *Marine Ecology Progress Series*, **248**, 109–123.

Zacherl D, Gaines SD, Lonhart SI (2003) The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). *Journal of Biogeography*, **30**, 913–924.

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