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Sea urchin development in a global change hotspot, potential for southerly migration of thermotolerant propagules

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ABSTRACT

The distribution of the sea urchin *Heliocidaris erythrogramma* coincides with the southeast Australia global change hot spot where marine ecosystems are warming significantly due to changes in ocean circulation. To address questions on future vulnerabilities, the thermotolerance of the planktonic life phase of *H. erythrogramma* was investigated in the climate and regionally relevant setting of projected near-future (2100) ocean warming. Experimental treatments ranged from 18 to 26 °C, with 26 °C representing +3–4 °C above recent ambient sea-surface temperatures. Developmental success across all stages (gastrula, 24 h; larva, 72 h; juvenile, 120 h) decreased with increasing temperature. Development was tolerant to a +1–2 °C increase above ambient, but significant deleterious effects were evident at +3–4 °C. However, larvae that developed through the early bottleneck of normal development at 26 °C metamorphosed successfully. The inverse relationship between temperature and planktonic larval duration (PLD) was seen in a 25% decrease in the PLD of *H. erythrogramma* at 24 and 26°C. Ocean warming may be advantageous to a subset of larvae through early settlement and reduction of the vulnerable planktonic period. This positive effect of temperature may help buffer the negative effects of ocean warming. In parallel studies with progeny derived from northern (Coffs Harbour) and southern (Sydney) *H. erythrogramma*, northern embryos had significantly higher thermotolerance. This provides the possibility that *H. erythrogramma* populations might keep up with a warming world through poleward migration of thermotolerant propagules, facilitated by the strong southward flow of the East Australian Current. It is uncertain whether *H. erythrogramma* populations at the northern range of this species, with no source of immigrants, will have the capacity to persist in a warm ocean. Due to its extensive latitudinal distribution, its potential developmental thermotolerance and independence of its lecithotrophic larvae from exogenous food and the need to make a functional skeleton, *H. erythrogramma* may be particularly robust to ocean change.

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1. Introduction

As the planet warms due to increased atmospheric CO_2, so does the ocean. Ocean warming, through direct absorption of heat and changes in ocean circulation, is a major stressor to marine ecosystems (Harley et al., 2006; Poloczanska et al., 2007; Przeslawski et al., 2008; Brierley and Kingsford, 2009; Mueter and Litzow, 2009).

Temperature is the most pervasive factor affecting all biological processes and exerts a major influence on marine distributions (Somero, 2002; Brown et al., 2004; Pörtner and Knust, 2007; O'Connor et al., 2009). The long established link between thermal gradients and marine biogeography, 'Orton's Rule' (Orton, 1920, Thorson, 1950; Vernberg, 1962; Pechenik, 1987), has received renewed focus with respect to range shifts and local extinctions (Harley et al., 2006; O'Connor et al., 2007, 2009; Booth et al., 2007; Przeslawski et al., 2008; Brierley and Kingsford, 2009; Figueira and Booth, 2010; Jones et al., 2009; Mueter and Litzow, 2009). To survive in a changing ocean, species will need to acclimatize or adapt to altered local habitat conditions or migrate. The pelagic larval phase of benthic marine invertebrates provides a mechanism to drive range expansions with propagules migrating along latitudinal and thermal gradients, as opportunities and favourable conditions arise.

The influence of temperature on the planktonic phase of marine invertebrates has been investigated in a plethora of studies investigating the pace of embryogenesis, developmental constraints, swimming performance, planktonic larval duration and recruitment dynamics (Rupp, 1973; Andronikov, 1975; Pechenik, 1987; Chen and Chen, 1992; Roller and Stickle, 1993; Hoegh-Guldberg and Pearse, 1995; Sewell and Young, 1999; Gillooly et al., 2002; Staver and Strathmann, 2002; McDonald, 2004; O'Connor et al., 2007; Putnam et al., 2008). This wealth of data shows that temperature is the major environmental factor controlling development. The hypothesis that thermotolerance of the planktonic phase limits the geographical distribution of

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marine invertebrates (Andronikov, 1975) is supported by the correlation between spawning temperatures and successful development of many species (Andronikov, 1975; Fujisawa, 1989, 1995; Roller and Stickle, 1993; Davis, 2000; Negri et al., 2007). However, development in some species is thermotolerant well above (and below) ambient temperature (review Byrne, 2010). An in-built flexibility (polytopy) of life history to environmental stressors is noted for many marine invertebrates and is suggested to increase the probably of species persistence in geological time (Palmer, 1994; Hadfield and Strathmann, 1996; Davis, 2000). This may also influence comparative vulnerability of species to contemporary climate change. An understanding of the thermal thresholds of life histories is crucial as we attempt to predict how marine species may respond to ocean warming.

We investigated the thermotolerance of the planktonic stages of *Heliocidaris erythrogramma*, the most common and widely distributed sea urchin in temperate Australia (Rowe and Gates, 1995). This species, an ecologically important member of intertidal and shallow water marine communities (Laegdsgaard et al., 1991; Keesing, 2007), occurs from southern Queensland around the south coast to Shark Bay, Western Australia (Fig. 1), a range covering ca. 12,300 km of coast (Short, pers. comm.). In southeast Australia, the distribution of *H. erythrogramma* coincides with an ocean warming hot spot where, due to strengthening of the East Australian Current (EAC), the ocean has been warming for decades (Poloczanska et al., 2007; Ridgeway, 2007). Sea-surface temperatures (SST) have increased ca. 2.3 °C in 60 years, with a further rise of 2–3 °C projected by 2070 (Poloczanska et al., 2007). Due to the fast southerly flow of the EAC, range expansion of warm adapted species has occurred, as seen in migration of tropical fishes to temperate latitudes (ca. 175 km decade^{-1}) (Booth et al., 2007; Figueira and Booth, 2010) and migration of the sea urchin *Centrostephanus rodgersii* from New South Wales to Tasmania (Ling et al., 2009).

Although temperature is just one of many climate change stressors confronting marine biota, with factors such as ocean acidification and sea-level rise also being of concern (Poloczanska et al., 2007; Przeslawski et al., 2008; Doney et al., 2009; Brierly and Kingsford, 2009; Byrne, 2010), ocean warming is of immediate concern for southeast Australia. Indeed, a recent study of development in *H. erythrogramma* shows that ocean warming is the most serious contemporary climate-change stressor to the embryos of this species (Byrne et al., 2009).

Here we addressed questions on future vulnerabilities of the planktonic phase of *H. erythrogramma* within the climate and regionally relevant setting of near-future ocean warming (IPCC, 2007; Poloczanska et al., 2007). *Heliocidaris erythrogramma* has abbreviated development (4–5 d) to the juvenile, providing an opportunity to investigate thermotolerance across planktonic and benthic life stages. The extensive distribution of *H. erythrogramma* (Fig. 1) and its planktonic life stage provide a mechanism to keep up with a warming world through dispersal of thermotolerant larvae poleward in the EAC. To assess this possibility we compared the thermotolerance of progeny from northern (Coffs Harbor) and southern (Sydney) *H. erythrogramma*. We expected that, although increased temperature would impair larval success, the extensive distribution of *H. erythrogramma* might provide scope for population maintenance through dispersal in a changing EAC.

2. Methods

2.1. Specimen collection, spawning and temperature data

Data for SST (1993–2003) were used to document the thermal regimes that *H. erythrogramma* experiences along the east coast during the spawning season (ca. November to March) (Fig. 1). The data were collected from the CSIRO live access server (http://www.marine.csiro.au/las/servlets/dataset) for each week. Each point in Fig. 1 represents an average of three AVHRR NOAA satellite readings taken near each coastal city. The server provides SST values every 0.042 degrees of latitude (4 km) and 0.036 degrees of longitude (see Griffin et al., 2005). These data are given in 2-day intervals composited over 10 days to account for atmospheric effects and to determine the “best” temperature. Representative SST is determined by taking the 65th percentile of the cumulative frequency distribution of the satellite values (Griffin et al., 2005). Temperature accuracy is limited to a half of a degree by the AVHRR instrument and is subject to an additional degree due to atmospheric effects. Spatial error is <1 km. Ambient SST was monitored from a local reference station (www.mhl.nsw.gov.au) and NASA Physical Oceanography DAAC Ocean ESIP Tool (POET) (http://poet.jpl.nasa.gov/).

Heliocidaris erythrogramma was collected from their rocky intertidal habitat in Sydney and Coffs Harbour, New South Wales (NSW). For experiments on the influence of temperature on development to the juvenile, urchins were collected in Sydney. These urchins had experienced SSTs of 22–23 °C for the month prior to collection. To compare thermotolerance of progeny from northern (Coffs Harbour) and southern (Sydney) *H. erythrogramma*, urchins that had experienced a recent SST ca. 20 °C were used. Adult acclimatization influences the thermotolerance of development (O'Conner and Mulley, 1977) and so for this comparison, adults with a similar recent thermal history were used to reduce this potentially confounding factor.

The urchins were placed in aquaria maintained at ambient SST in a temperature controlled room and were used for experiments within a day of collection. They were induced to spawn by injection of 1–2 ml of 0.5 M KCl. For each experiment gametes were pooled from 2 to 6 females and 2 to 4 males. All experiments were conducted with freshly collected filtered seawater (FSW, 1.0 μm), pH 8.2, salinity 35–37 ppt and dissolved oxygen $\geq 90\%$. Seawater variables were monitored using a WTW Multiline F/Set-3 multimeter.

The eggs were placed in FSW and sperm were collected dry. The total number of eggs for each experiment was measured from a 50-ml suspension determined through counts of 100-μl aliquots. For each fertilisation the eggs were placed in a 500-ml beaker at a density of 3–4 eggs ml^{-1}. The sperm concentration used in all experiments, 10^4 sperm ml^{-1}, determined in haemocytometer counts, resulted in $\geq 90\%$ fertilisation and high rates of normal development ($\geq 75\%$) in procedural controls.

Water baths were used to maintain constant temperature. Temperature treatments were switched between water baths after each trial to reduce the likelihood that inherent differences between water baths would confound the effects of temperature. All experiments were repeated three times with embryos each derived from an independent source of gametes.

2.2. Influence of temperature on early development

To investigate the thermal sensitivity of early embryos (first 24 h) and potential for a thermal threshold in early development, 50 fertilised eggs were placed into replicate beakers (100 ml) containing experimental FSW (18, 20, 24, 26 °C). These temperatures reflect the SST range experienced by local populations during the spawning season (ca. 19–25 °C, Fig. 1). With respect to recent SST (22–23 °C), the 26 °C treatment represented a +3–4 °C warming. A previous study determined that ≥ 28 °C is lethal to *H. erythrogramma* embryos (Nguyen, 2007).

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