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How does embryonic and larval thermal tolerance contribute to the distribution of the sea urchin *Centrostephanus rodgersii* (Diadematidae) in New Zealand?

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ABSTRACT

Sea surface temperature (SST) influences the physiology of marine invertebrates, and, in turn, their geographical distribution. The Diadematidae sea urchin *Centrostephanus rodgersii* has expanded its range in Eastern Australia as a result of increased winter sea temperatures, and there is interest in the potential for the species to increase its range and abundance in New Zealand. We investigated the extent to which embryonic and larval thermal tolerance of fertilization, cleavage, hatching, gastrulation and appearance of plutei may control the distribution of the adult populations in New Zealand. We also compared these individuals with an Australian population in northern New South Wales at Coffs Harbour from a region just north of where the Eastern Australian Current gives rise to the Tasman Front current to New Zealand. The aim of the present study was to find evidence for adaptation in fertilization and the developmental stages to New Zealand winter sea temperatures. Fertilization was not affected by temperature over a broad thermal range (12.0 °C–26.4 °C and 12.8 °C–29.5 °C for the New Zealand and the Coffs Harbour population respectively). The first cleavage, hatching, gastrulation and appearance of plutei were more sensitive to temperature and occurred within a well-defined thermal window (17.2 °C–23.5 °C in New Zealand and 17.3 °C–24.5 °C in Coffs Harbour). The sites where *C. rodgersii* adults have been reported in New Zealand lie on the 15 °C winter isotherm, consistent with our findings with regard to the lower temperature for pluteal development for the New Zealand population. We found evidence for a shift in thermal tolerance between the two populations of *C. rodgersii* examined, with fertilization and each developmental stage showing an upper thermal limit consistently shifted by ≈1 °C towards lower temperatures in New Zealand individuals. Our findings indicate that the thermal window for larval development of *C. rodgersii* may contribute to its present distribution in New Zealand. In addition, given that larval development in New Zealand presently occurs at the colder limit of the thermal window of *C. rodgersii*, there may be the potential for a future expansion of its distributional range under future ocean warming scenarios.

1. Introduction

Temperature is one of the major factors influencing the physiology and distribution of marine invertebrate species (Andronikov, 1975; Brown et al., 2004; Gunter, 1957; Hoegh-Guldberg and Pearse, 1995; Kinne, 1970; O'Connor et al., 2007; Orton, 1920; Pechenik, 1987; Somero, 2002). Through a general effect on metabolic rate (Allen et al., 2006; Brown et al., 2004; Enquist et al., 2003), it positively affects the speed at which biochemical reactions take place until a thermal threshold of proteins are reached (Hofmann and Todgham, 2010; Somero, 2002, 2010; Tomanek, 2010). Temperature may control the geographical distribution of the species within the spatial and temporal thermal range potentially encountered (Pörtner and Farrell, 2008). Importantly, the effects of temperature on physiology can vary across key life-history stages, such as fertilization and early development, and that can influence the distribution of adults.

This process was proposed by Andronikov (1975) who concluded that the thermal tolerance of gametes of marine invertebrates is mostly fixed within each species, and that temperatures found throughout a whole year in the environment determine the time of spawning and sets a limit to the geographical distribution of such species. This principle became known as “Andronikov's hypothesis” and more concisely states that ‘*temperature at the time of spawning is a factor limiting geographical distribution of species*’.

Andronikov (1975) explored thermal tolerances of spermatozoa and ova in a range of marine invertebrates, but mainly echinoderms and molluscs. The author recorded the maximum temperature at

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which spermatozoa remained mobile and fertilized eggs cleaved, and subsequently found a relationship between such limits with temperatures at which successful reproduction occurs in the field.

A subsequent study by Reitzel et al. (2004) further analyzed the relationship between temperature, timing of spawning and larval development for 139 invertebrate species comprising a total of 11 phyla. The authors reported that temperature plays a major role in determining spawning time of marine invertebrates and that they spawn at times of the year that minimize development time of their offspring. Reitzel et al. (2004) also noted, however, that factors such as predation or benthic recruitment might be a greater selection pressure for individual fitness and ultimately life history evolution.

Under global warming scenarios, the effects of temperature in determining the distributional range of marine species have become even more relevant. A change in species ranges has been recorded as temperature rises and larvae are transported further along thermal gradients (Figueira and Booth, 2010; Hoegh-Guldberg and Bruno, 2010; Ling et al., 2009b). Provided that there are no obstacles to dispersion, as new regions are included in the area of thermal tolerance of a species, a range extension may take place. For example Barry et al. (1995) compared the abundance and distribution of the invertebrate fauna along a rocky shore in Monterey Bay (California, USA) with data collected 60 years earlier. They found that over the 60 years the abundance of southern species had increased while the abundance of northern species had decreased. During the same period the average winter and summer SST had warmed by 0.5 °C and 2.2 °C respectively. In their study, cosmopolitan species showed no change in abundance. The authors interpreted these findings as evidence for a shift northward in the geographical range of regional fauna, consistent with the predicted change in distributions as a result of warming.

Even more relevant to the present study is the range expansion of the sea urchin *Centrostephanus rodgersii* in southeastern Australia (Ling et al., 2009b). Following the strengthening of the Eastern Australian Current along the eastern coast of Australia, sea surface temperatures along eastern Tasmania have progressively increased above the 12 °C threshold for larval development in the local populations of *C. rodgersii* (Ling et al., 2008). This has caused an expansion of the geographical range of *C. rodgersii* southward along the Tasmanian coastline, where younger individuals were recorded at sites that were included later within the boundaries of the 12 °C isotherm (Ling et al., 2009b).

According to the Andronikov (1975) hypothesis, sea surface temperature increases may trigger responses in particular life-history stages of marine invertebrates, potentially creating bottlenecks at specific developmental phases. For echinoderms, several stages of reproduction and larval development have been examined in terms of thermal tolerance. Fertilization has been found to be relatively insensitive to temperature change (review Byrne, 2011) within a 2–4 °C temperature increase associated with climate change (IPCC, 2007). For all echinoderms examined, such tolerance at fertilization encompasses a broad spectrum of temperatures far beyond those predicted for near future scenarios (review Byrne, 2011; Nguyen et al., 2012). In contrast, developmental responses to temperature at first cleavage, hatching, gastrulation and in larvae tend to be species-specific and, in the case of species with broad latitudinal distributions, site-dependent. (Byrne, 2011; Byrne et al., 2009, 2011; Sewell and Young, 1999).

For example, Sewell and Young (1999) showed that the sea urchin *Echinometra lucunter* is able to reach the echinopluteus stage at temperatures well outside the range of temperatures occurring throughout a year on the Caribbean reef flat, while Byrne et al. (2011) found that, for the warm-temperate species *Heliocidaris erythrogramma*, an increase of 3–4 °C was enough to cause significant deleterious effects on larval development. Rahman et al. (2009) also highlighted that thermal tolerance in *Tripneustes gratilla* is stage dependent, and that early larvae can survive acute thermal stress for short periods of time (a few hours), an ability that has an adaptive role in larvae that may be exposed to heated superficial waters.

Here we examine the thermal tolerance of pre-settlement processes in the Diadematidae sea urchin *C. rodgersii* in two populations, one in Australia (Coffs Harbour, New South Wales) and one in New Zealand (Mokohinau Islands, north east of the North Island). This species is a strong grazer capable of causing phase-shifts from kelp habitats to barren grounds (Ling, 2008; Ling et al., 2009a). *C. rodgersii* has long-lived (≈4 months) *Echinopluteus transversus* larvae (Huggett et al., 2005; Soars et al., 2009) and therefore a high capacity to expand its distribution into suitable regions through larval transport. It is an ecologically important species able to overgraze macroalgal beds and maintain alternative and stable barren habitats (review Byrne and Andrew, 2013). A geographic expansion of *C. rodgersii* from its historical range on the Australian mainland to Tasmania has been linked to the increased sea surface temperatures that resulted from greater flow southward of the Eastern Australian Current (EAC) (Ling et al., 2009b). Ling et al. (2008) showed that the larvae of the Tasmanian population do not develop at winter sea temperatures below 12 °C and that following the shift southward of the 12 °C sea surface isotherm, populations established further south in a process likely limited by the thermal tolerance of the pre-settlement life stages of the local population of *C. rodgersii*.

The eastern branch of the EAC, the Tasman Front (Godfrey et al., 1980) influences northern New Zealand. It is the only major vector at present available for transporting larvae (such as from *C. rodgersii*) from Australia to New Zealand and appears to connect New Zealand and Australian populations. This is apparent in the lack of genetic differentiation between the New Zealand and Australian populations (Banks et al., 2007). Two recent studies on a New Zealand population has shown that these *C. rodgersii* are similar in their ecology and grow at a similar pace and to a similar size as the Tasmanian individuals (Pecorino et al., 2012a), undergo a typical annual reproductive cycle, and can produce viable gametes that can develop to the early pluteus stage (Pecorino et al., 2012b).

No information on the thermal tolerance of pre-settlement processes is available for any New Zealand *C. rodgersii* populations. This is significant as sea temperatures are predicted to increase ≈3 °C (IPCC, 2007) globally and therefore there is a potential for range expansion of *C. rodgersii* in northern New Zealand, if population distribution is temperature-limited during pre-settlement processes as shown for Tasmania. With this in mind, we determined the thermal tolerance and threshold for fertilization, first cleavage, hatching, gastrulation and appearance of early plutei of *C. rodgersii* in New Zealand. To assess intraspecific differences and acclimation processes, we also conducted the same study on an Australian population of *C. rodgersii* from Coffs Harbour in northern New South Wales. This allowed us to evaluate the degree to which this species can acclimate to new environmental conditions, specifically sea temperature. A population from Coffs Harbour was chosen as it is close to the latitude (≈32°S; Godfrey et al., 1980) at which the Eastern Australian Current splits and the eastern branch (the Tasman Front) flows towards New Zealand, making it most likely to be the area where larvae reaching New Zealand originate. In light of our observation of thermal tolerances in pre-settlement stages, knowing *C. rodgersii* occurrence and winter sea surface temperatures in New Zealand are compared.

2. Methods

2.1. Specimens collections and spawning

New Zealand *C. rodgersii* were collected from the Mokohinau Islands (35°55′ S, 175°07′ E) during August 2011 (Fig. 1). The Australian population of *C. rodgersii* was sampled in July 2011 from Coffs Harbour, New South Wales (30° 27′ S, 153° 14′ E) (Fig. 1), at the northern subtropical limit of the species, just North of the divergence of the EAC creating the Tasman Front to New Zealand. At both sites, individuals were collected by snorkelling from a depth of 5 m.