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The effects of temperature on embryonic development and larval survival in two scleractinian corals

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ABSTRACT: Increased temperatures are deleterious to early life stages in many organisms; however, the biological effects of decreased temperatures are rarely explored. For example, the tolerance of marine invertebrate larvae to temperatures lower than ambient might affect the capacity of species to disperse from tropical to subtropical locations. In addition, reduced rates of development are likely to affect the proportion of larvae retained on natal reefs. Here, we explore the relationship between temperature, embryonic development and larval survival over an 8°C temperature range (–4 to +4°C around the ambient temperature at the time of spawning of 24°C) in 2 reef-building corals, *Goniastrea favulus* and *Acropora spathulata* from One Tree Island in the southern Great Barrier Reef. Rates of development were generally slower at lower temperatures: embryos of both species took longer to complete gastrulation and to become motile at temperatures below ambient. In contrast, temperatures below ambient did not affect larval survivorship in either species. *A. spathulata* larvae were more sensitive to increased temperatures than *G. favulus*, which also had higher survivorship than *A. spathulata* at all temperatures except 20°C. These results suggest that fluctuations in temperature at the time of spawning will influence patterns of coral larval dispersal. Furthermore, cold water is unlikely to prevent the dispersal of tropical corals to subtropical locations.

KEY WORDS: Coral reefs · Larval ecology · Thermal tolerance · Dispersal · Development · Cold tolerance

INTRODUCTION

The Earth's environment is changing rapidly as a consequence of climate change. Increasing temperatures are affecting terrestrial, marine and freshwater populations by altering processes such as growth and reproduction (Parmesan & Yohe 2003, Root et al. 2003, Poloczanska et al. 2007). However, climate change will not necessarily result in all locations becoming hotter. For example, the effects of climate change are expected to alter ocean currents, including the East Australian Current, which delivers warm waters from the tropics to higher latitudes in eastern Australia (Poloczanska et al. 2007). Such changes in circulation patterns may result in some subtropical locations, such as Lord Howe Island, becoming colder than at present. Consequently, it is important to investigate the effects of both increased and decreased temperatures to accurately predict the consequences of climate change (Addo-Bediako et al. 2000, Pörtner 2001).

The effects of increased temperature on coral larval biology are well known. Deleterious effects, such as an increase in the proportion of abnormal embryos

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and a decrease in larval survivorship, are evident at as little as 2°C above ambient temperature (Bassim et al. 2002). Increased temperatures also increase rates of coral larval development (Chua et al. 2013) and coral larvae become competent to settle more quickly at higher temperatures (Nozawa & Harrison 2007, Heyward & Negri 2010). Given a strong association between rates of development and levels of self-recruitment in corals (Figueiredo et al. 2013), increasing sea surface temperatures are likely to affect patterns of dispersal by reducing the levels of connectivity among populations (O'Connor et al. 2007). The effects of colder temperatures on coral larval biology are less well known. Edmondson (1946) demonstrated that coral larvae were robust to short-term exposures to temperatures as low as 0.5°C. In contrast, metamorphosis to crustose coralline algae by *Stylophora pistillata* was 5 times lower at 2°C below ambient temperature (Putnam et al. 2008). Similarly, settlement was approximately 50% lower in *Acropora solitaryensis* larvae at 3°C below ambient temperature (Nozawa & Harrison 2007).

Climate-driven changes in ocean circulation are altering dispersal patterns in many marine organisms (O'Connor et al. 2007, Przeslawski et al. 2008). For example, the mussel *Mytilus edulis* (Jones et al. 2009), many reef fish species (Feary et al. 2013) and some corals (Yamano et al. 2011, Baird et al. 2012) have recently shifted their ranges poleward. Similarly, the fossil record indicates that scleractinian corals have been tracking climate on geological timescales (Veron 1992, Precht & Aronson 2004, Greenstein & Pandolfi 2008). This tendency of marine organisms to track changing climates strongly suggests that there are environmental barriers to dispersal, although geographical ranges could also be limited indirectly, e.g. by changes in competitive interactions among species (Cahill et al. 2013). Nonetheless, one potential factor limiting the dispersal of corals south from the Great Barrier Reef into subtropical areas may be the capacity of coral larvae to withstand the colder waters they encounter en route.

In this study, we compared the response of the early life history stages of 2 species of scleractinian corals, *Goniastrea favulus* and *Acropora spathulata*, to an 8°C temperature range from −4 to +4°C around the ambient temperature experienced at the natal location, One Tree Island, around the time of spawning. In addition to comparing the temperature response, we aimed to test whether cool water is a barrier to the dispersal of larvae of these species to higher latitudes from this location. Both *G. favulus* and *A. spathulata* are common at One Tree Island; however, while One Tree Island is the southern latitudinal limit for *A. spathulata* (Wallace 1999), *G. favulus* occurs as far south as Lord Howe Island (Veron 1993).

MATERIALS AND METHODS

Coral collection and culture of propagules

A total of 6 colonies of *Acropora spathulata* and 5 colonies of *Goniastrea favulus* were collected from the reef flat of the first lagoon at One Tree Island (23° 30′ S, 152° 05′ E) in the southern Great Barrier Reef, a few days before the predicted spawning period in 2010. Colonies were maintained in flow-through filtered seawater (FSW) in shaded outdoor aquaria. Just before spawning, species were placed in separate aquaria and water flow was stopped to prevent gametes being washed away. *G. favulus* spawned on the afternoon of 26 November 2010 and *A. spathulata* spawned on the night of 30 November 2010. *A. spathulata* egg and sperm bundles were collected and broken apart with gentle agitation and the density of sperm diluted to ~10^6 sperm ml^{-1} to maximize the fertilization success (Oliver & Babcock 1992). Once cleavage was observed approximately 2 h post-fertilization (hpf), embryos were washed 3 times in 0.2 µm FSW to remove excess sperm, which can cause cultures to deteriorate. In contrast to the positively buoyant egg and sperm bundles released by *A. spathulata*, *G. favulus* releases eggs and sperm separately, with the negatively buoyant eggs released ~30 min before sperm. Consequently, the eggs of *G. favulus* were collected from the base of parent colonies ~30 min after spawning was complete. The time that eggs were spawned was considered to be the time of fertilization in *G. favulus*.

Experimental design

To test for the effects of increased and decreased temperature on larval development and survivorship, water baths were set up in a temperature-controlled room at 5 temperatures: 20, 22, 24, 26 and 28°C (i.e. −4°C, −2°C, ambient, +2°C, +4°C). Aquarium heaters, coolers and pumps kept treatment baths stable and within 0.5°C of the target temperatures (monitored with HOBO data loggers). Ambient average sea surface temperature for the month before spawning (24.2°C) was determined from on-reef sensors (Australian Institute of Marine Sciences 2012a).

Effect of temperature on embryonic development

To test the effect of temperature on embryonic development, washed embryos were transferred to 20 ml glass vials filled with 0.2 µm FSW and distributed among temperature treatments at 2 hpf (~30 embryos per vial, 3 vials per treatment). The stage of development of the first 20 embryos in each vial was assessed at 8 or 9 time points depending on the species: 18, 24, 30, 36, 48, 72, 96, 120 and 144 hpf (6 d). The following 5 development stages were identified (following Ball et al. 2002): 4-cell blastula, multiple cell blastula, early gastrula, gastrula and planulae (motile stage). To test for differences in development time between treatments, the average time for propagules to reach gastrulation and motility $\bar{X}$ was estimated following Chua et al. (2013):

$$\bar{X} = \Sigma(\text{Time (h)} \times \text{No. of propagules to reach stage}) / \text{Total no. of propagules} \quad (1)$$

Effect of temperature on larval survival

To test the effect of temperature on coral larval survival, 50 washed embryos were placed in 50 ml glass vials filled with 0.2 µm FSW and distributed among temperature treatments at 2 hpf (50 embryos × 3 vials per treatment). Survival was measured by counting the number of embryos remaining at each of the above time points. Coral larvae lyse within 24 h of death (Baird et al. 2006), so all larvae counted were considered to be alive at the time of census.

Data analysis

Differences in mean time to complete gastrulation and to reach the planula stage (for *Goniastrea favulus* only) among temperature treatments (fixed, 5 levels: 20, 22, 24, 26 and 28°C) were tested using a 1-way ANOVA for each species separately. Data were log-transformed and homogeneity of variance was confirmed by Levene's test. Tukey's honestly significant difference post-hoc tests were used to identify which treatment levels differed. Non-parametric Kaplan-Meier product limit analyses were used to test for differences in median survivorship among temperatures for each species separately. Median survivorship (in hours) was considered significantly different when the 95% confidence intervals did not overlap. All analyses were performed using SPSS v19®.

RESULTS

Temperature had a significant effect on rates of propagule development in both species. In general, the slowest rates of development occurred at the lowest temperatures (Figs. 1 & 2). Temperature had a significant effect on the mean (±SE) time to complete gastrulation in both *Acropora spathulata* ($F_{4,10}$ = 71.53, p < 0.001) and *Goniastrea favulus* ($F_{4,10}$ = 11.84, p = 0.001) (Fig. 1). *A. spathulata* embryos at 28°C took 23.1 ± 0.9 h to complete gastrulation compared with 37.7 ± 2.1 h at 20°C. Similarly, *G. favulus* embryos required 30.4 ± 4.0 h to complete gastrulation at 20°C compared with 20 ± 1.0 h at 28°C. In addition, *G. favulus* developed more rapidly than *A. spathulata* at all temperatures (Fig. 1). Over all temperatures pooled, the mean time to complete gastrulation was 21.6 ± 1.4 h in *G. favulus* and 28.4 ± 1.3 h in *A. spathulata*. Similarly, temperature had a significant effect on the mean time to reach the planula

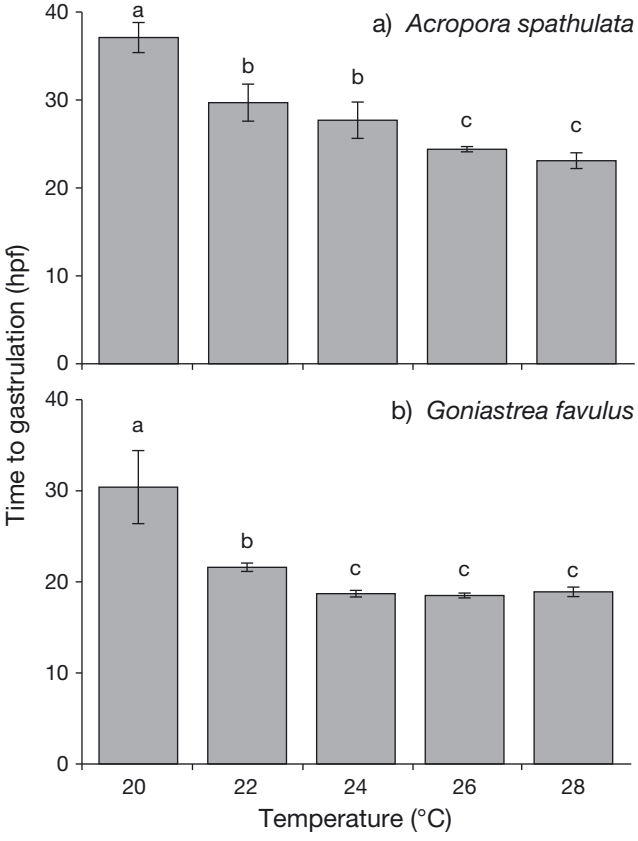

Fig. 1. Mean (±1 SE) time to gastrulation (h post-fertilization, hpf) of (a) *Acropora spathulata* and (b) *Goniastrea favulus* at 5 temperatures (n = 60, ambient = 24°C). Letters above the error bars indicate homogenous groups identified by Tukey's honestly significant difference post-hoc analysis (p < 0.05)

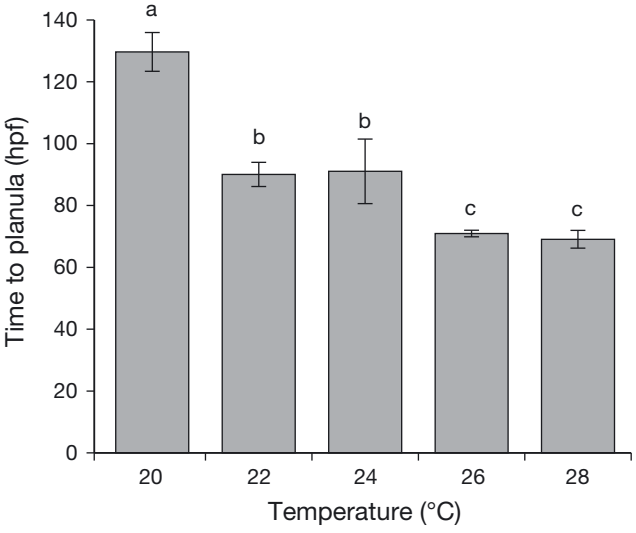

Fig. 2. Mean (± 1 SE) time to the planula stage (h post-fertilization, hpf) in *Goniastrea favulus* at 5 temperatures (n = 60, ambient = 24°C). Letters above the error bars indicate homogenous groups identified by Tukey's honestly significant difference post-hoc analysis ($p < 0.05$)

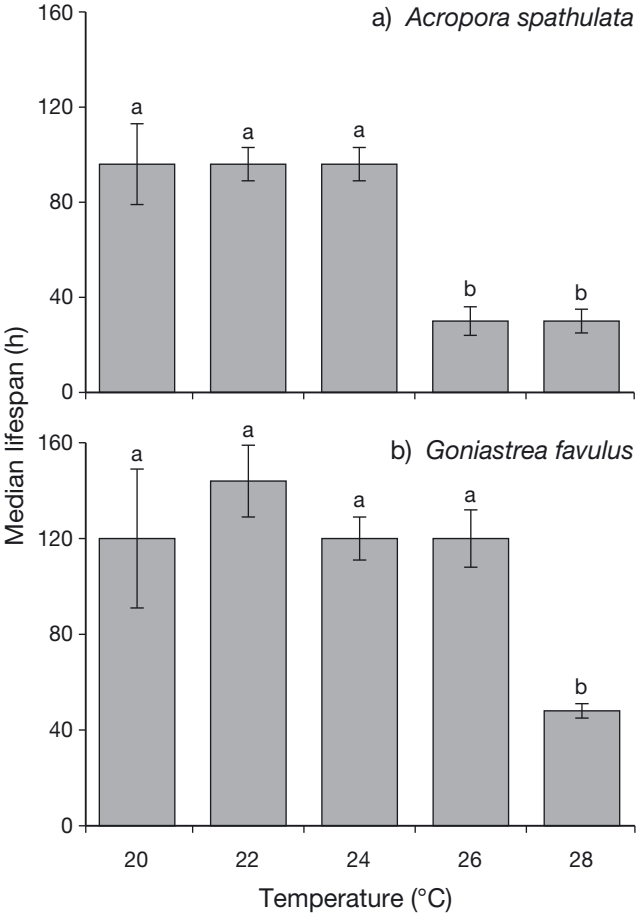

Fig. 3. Kaplan-Meier median (±95% CI) survivorship estimates for (a) *Acropora spathulata* and (b) *Goniastrea favulus* at 5 temperatures (n = 150, ambient = 24°C). Letters indicate homogenous groups determined by the overlap of confidence intervals

stage in *G. favulus* ($F_{4,0} = 15.62$, $p < 0.001$; Fig. 2). The mean time to reach the planula stage was greatest at 20°C (129.7 ± 6.3 h) and lowest at 26°C and 28°C (Fig. 2).

Only increased temperatures had a significant effect on larval survival (Fig. 3). In *Acropora spathulata,* survival was reduced at both temperatures above ambient (Fig. 3a). In contrast, *Goniastrea favulus* survival was reduced only at the highest temperature (Fig. 3b). In addition, *G. favulus* larval had higher survivorship than *A. spathulata* larvae at all temperatures, with the exception of 20°C (Fig. 3).

DISCUSSION

Embryonic development was strongly affected by temperature. In general, the lower the temperature, the longer it took to complete gastrulation and for larvae to become motile. In contrast, larval survival was only reduced at temperatures above ambient. While the response of both species to temperature was broadly similar, there were, nonetheless, differences between the species in development rate, larval survivorship and thermal tolerance.

The effect of temperature on development rates in these coral embryos is typical of most marine invertebrates (Pechenik 1987). For example, embryos of *Goniastrea australensis* in the Solitary Islands (30° S) developed more slowly at 22°C than at 26 and 28°C (Wilson & Harrison 1998). This suggests that rates of embryonic development are likely to depend on the temperature conditions prevailing shortly after the time of spawning. Given that rates of self-recruitment are typically higher in larvae that develop more rapidly (Figueiredo et al. 2013), patterns of dispersal are likely to vary among years if ambient temperatures vary. In addition, patterns of dispersal might vary predictably among locations at different latitudes. In particular, high-latitude locations are likely to have lower levels of self-recruitment than tropical locations because larvae take longer to develop. In addition, rates of predation are likely to increase the longer larvae remain in the plankton. For example, reduced levels of self-recruitment might help explain low numbers of juvenile corals at Lord Howe Island (31.5° S) compared with many tropical locations (Hoey et al. 2011). However, the effect of low temper-

atures on rates of recruitment cannot be discounted (Putnam et al. 2008).

Rates of embryonic development were also influenced by the size of the propagules. Across all temperatures, *Goniastrea favulus* embryos (mean diameter of 320 µm) developed more rapidly than *Acropora spathulata* embryos (mean diameter of 500 µm; Fig. 1), which can most likely be attributed to faster rates of cell division in species with smaller eggs (Berrill 1935, Marshall & Keough 2008). Similarly, in 18 species of broadcast spawning corals, egg size was strongly and positively correlated with time to motility (Figueiredo et al. 2013). The more rapid rate of development in *G. favulus* embryos did not come at the cost of reduced larval survival: *G. favulus* larvae survived longer than *A. spathulata* at all temperatures, except at 20°C where there was no difference between the species (Fig. 3).

In contrast to the relationship between development and temperature, larval survival was only reduced at temperatures 2 to 4°C above ambient (Fig. 3). These upper thermal limits appear to be consistent over a very large geographical scale and among many different species (Bassim et al. 2002, Randall & Szmant 2009, Heyward & Negri 2010), supporting the hypothesis that many corals live close to their upper thermal limits. In contrast, temperatures up to 4°C below ambient had no effect on larval survival (Fig. 3). Projections based on the speed and direction of the East Australia Current suggest that the time taken to disperse from One Tree Island in the southern Great Barrier Reef to Lord Howe Island takes approximately 16 to 33 d. Given that spawning occurs at One Tree Island in November, larvae will arrive at Lord Howe Island between late November and early January. In the course of this journey, water temperatures can be as low as 19°C (Australian Institute of Marine Science 2012b). Consequently, it is unlikely that temperature is a barrier to dispersal from the southern Great Barrier Reef to higher latitudes for either of these species and therefore other factors must determine why *Acropora spathulata* is not found on Lord Howe Island.

Thermal tolerance differed between the species. In particular, larval survival was reduced at 26°C in *Acropora spathulata* and at 28°C in *Goniastrea favulus* (Fig. 3). A similar difference in thermal tolerance was also observed between acroporid and merulinid embryos by Negri et al. (2007). Consistent differences in stress tolerance are also apparent between adult colonies of these 2 families: adult acroporids are much more susceptible to bleaching and disease when compared with adult merulinids (Hughes & Connell 1999, Marshall & Baird 2000, Diaz & Madin 2011).

In conclusion, temperature has important effects on many aspects of coral larval biology. In particular, development rates varied predictably with temperature, suggesting that patterns of dispersal are likely to change in response to climate change. In addition, coral larvae appear to be tolerant of temperatures 2 to 4°C below ambient, suggesting that cold water is unlikely to limit the dispersal of tropical species to subtropical locations.

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