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REPORT

Latitudinal variation in thermal tolerance thresholds of early life stages of corals

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Abstract Organisms living in habitats characterized by a marked seasonal temperature variation often have a greater thermal tolerance than those living in more stable habitats. To determine the extent to which this hypothesis applies to reef corals, we compared thermal tolerance of the early life stages of five scleractinian species from three locations spanning 17° of latitude along the east coast of Australia. Embryos were exposed to an 8 °C temperature range around the local ambient temperature at the time of spawning. Upper thermal thresholds, defined as the temperature treatment at which the proportion of abnormal embryos or median life span was significantly different to ambient controls, varied predictably among locations. At Lizard Island, the northern-most site with the least annual variation in temperature, the proportion of abnormal embryos increased and life span decreased 2 °C above ambient in the two species tested. At two southern sites, One Tree Island and Lord Howe Island, where annual temperature variation was greater, upper temperature thresholds were generally 4 °C or greater above ambient for both variables in the four species tested. The absolute upper thermal threshold temperature also varied among locations: 30 °C at Lizard Island; 28 °C at One Tree Island; 26 °C at Lord Howe Island. These results support previous work on adult corals demonstrating predictable differences in upper thermal thresholds with latitude. With projected ocean warming, these temperature thresholds will be exceeded in northern locations in the near future, adding to a growing body of evidence indicating that climate change is likely to be more detrimental to low latitude than high latitude corals.

Keywords Coral reefs · Larval ecology · Biogeography · Dispersal

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Introduction

Rising temperatures, as a result of climate change, are altering species distributions and causing reductions in global biodiversity (Thomas et al. 2004; Pereira et al. 2010). Although proximate causes of local extinction vary (Cahill et al. 2012), thermal tolerance is often a good predictor of the potential of a population to persist as temperatures increase (Sorte et al. 2011). Consequently, it is important to consider the thermal tolerance of species when projecting the potential effects of increased temperatures on biodiversity.

At the global scale, temperatures are more stable throughout the year in tropical regions compared to

temperate regions (Spencer and Christy 1990), and consequently, the thermal tolerance of organisms is generally greater at higher latitudes (Janzen 1967; Stevens 1989; Chown et al. 2004; Bozinovic et al. 2011). This phenomenon is especially relevant in ectotherms because these organisms rely on the environment to regulate internal temperatures. Indeed, many tropical ectotherms (e.g., insects, lizards) are already living close to their upper thermal limits and are thus more likely to be adversely affected by projected temperature rises as a consequence of climate change (Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009).

Similar systematic differences in temperature thresholds have been observed for adult corals. The temperature at which bleaching is induced varies predictably among regions (Coles et al. 1976; Goreau and Hayes 1994), although the correlation between bleaching thresholds and latitude can be complicated by the type of algal symbiont hosted by the coral (Ulstrup et al. 2006). For example, during the 1998 mass bleaching on the Great Barrier Reef (GBR), the temperature threshold at which bleaching was induced varied predictably with latitude: 30.0 °C in the northern GBR, 29.2 °C in the central GBR, and 28.3 °C in the southern GBR (Hoegh-Guldberg 1999). These thermal thresholds are reasonably well understood for adult corals; however, there is a paucity of data on temperature thresholds on crucial stages in the early life history of corals.

Here, we compare thermal tolerance among latitudes by quantitatively establishing the upper thermal threshold at each location and then qualitatively comparing these thresholds. We exposed developing gametes of five species of scleractinian corals to a temperature range of 8 °C around the ambient at the time of spawning for each of three locations. Locations spanned 17° of latitude along the east coast of Australia, from Lizard Island in the north to Lord Howe Island, the world's southernmost coral reef. Specifically, larvae from higher latitude reefs were predicted to have a greater upper thermal tolerance limit relative to ambient than those from lower latitude reefs.

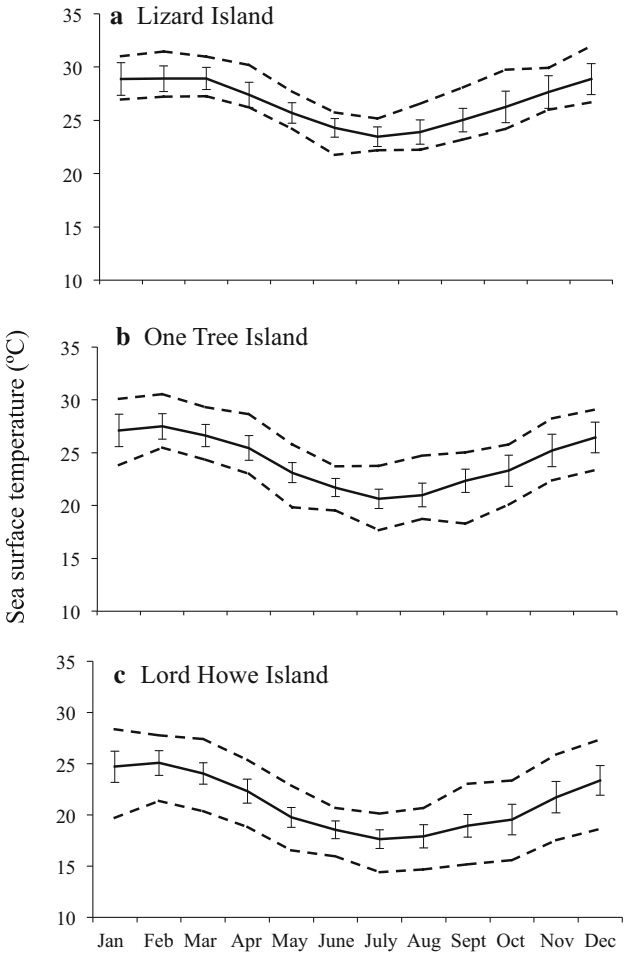

Fig. 1 Lagoonal sea surface temperatures (SST) 2010–2013 at **a** Lizard Island (14.7°S), **b** One Tree Island (23.5°S) and **c** Lord Howe Island (31.5°S). *Solid lines* represent average SST for each month, 2010–2013. *Vertical bars* show SD. *Dashed upper lines* represent average maximum SST for each month. *Dashed lower lines* represent average minimum SST for each month. Monthly differences between average maximum and average minimum ranged from approximately 3–5 °C at Lizard Island, 4–7 °C at One Tree Island and 5–9 °C at Lord Howe Island. Data were collected from the Australian Institute of Marine Science (AIMS) and Great Barrier Reef Ocean Observing System (GBROOS) Web sites. The spawning months at each location, and the months in which experiments were conducted, were November at Lizard Island and One Tree Island, and January at Lord Howe Island

Materials and methods

Collection of adult coral colonies and larvae

The effects of temperature on the early life stages of coral were tested at three locations in eastern Australia: Lizard Island (LI, 14.7°S), One Tree Island (OTI, 23.5°S), and Lord Howe Island (LHI, 31.5°S). Data collected at One Tree Island have been used in a previous publication (Woolsey et al. 2013). Six colonies each of *Acropora millepora*, *Acropora spathulata*, and *Goniastrea favulus* were collected from LI lagoon in November 2011. Six colonies of *A. spathulata* and five colonies of *G. favulus* were collected from OTI lagoon in November 2010. Five colonies of *Goniastrea australensis* and six colonies of *Cyphastrea microphthalma* were collected from LHI lagoon in January 2012. It was not possible to use the same coral species at each location because of differences in the distribution and abundance of species among these widely separated locations. All species that were used are abundant at their respective locations and are therefore likely to be of ecological significance. Colonies were maintained in

Table 1 ANOVA results testing for differences among temperatures in the proportion of abnormal embryos 18 h post-fertilization at Lizard Island (LI), One Tree Island (OTI), and Lord Howe Island (LHI)

Location	Species	*df*	*F*	*p*	Treatment order (°C)
LI	*Acropora millepora*	4	11.48	0.001	24 = 26 = 28 < 30 = 32 (−4 = −2 = ambient < +2 = +4)
LI	*Acropora spathulata*	4	10.98	0.001	24 = 26 = 28 < 30 = 32 (−4 = −2 = ambient <+2 = +4)
LI	*Goniastrea favulus*	4	4.15	0.031	24 = 26 = 28 < 30 = 32 (−4 = −2 = ambient <+2 = +4)
OTI	*Acropora spathulata*	4	27.60	<0.001	20 = 22 = 24 = 26 < 28 (−4 = −2 = ambient = +2 < +4)
OTI	*Goniastrea favulus*	4	0.99	0.458	NS
LHI	*Goniastrea australensis*	4	6.04	0.010	18 = 20 = 22 = 24 < 26 (−4 = −2 = ambient = +2 < +4)
LHI	*Cyphastrea microphthalma*	4	4.98	0.018	18 = 20 = 22 = 24 < 26 (−4 = −2 = ambient = +2 < +4)

Data were arcsine transformed. Treatment order from Tukey's HSD post hoc test ($p = 0.05$)

flow-through filtered seawater (FSW) in shaded outdoor aquaria at all locations except LHI, where colonies were kept below a pier in the lagoon for a maximum of 3 d. Immediately prior to spawning, colonies were placed in separate aquaria with no water flow to capture the gametes. At LI, *G. favulus, A. spathulata*, and *A. millepora* spawned on the night of November 15, 2011. At OTI, *G. favulus* spawned on November 26, 2010 and *A. spathulata* spawned on November 30, 2010. At LHI, *G. australensis* and *C. microphthalma* spawned on January 20, 2012.

Egg and sperm bundles were collected and broken apart with gentle agitation. Sperm was diluted to a density of approximately 10^6 sperm ml^{-1} by eye, a technique that regularly results in close to 100 % fertilization success (Baird pers obs). Eggs were mixed with the sperm stock at the local ambient temperature. Once cleavage was observed, approximately 2 h post-fertilization (hpf), embryos were washed three times in 0.2 μm FSW to remove excess sperm and placed in the experimental treatments. The reproductive ecology of *G. favulus* necessitated a different collection method. *G. favulus* releases clusters of negatively buoyant eggs followed by sperm. The eggs of *G. favulus* were collected with a pipette from the base of parent colonies approximately 30 min after sperm was released.

Temperature treatments and temperature profiles for each location

To investigate the effects of temperature on embryonic development and survivorship, water baths were set up in a temperature-controlled room at five temperatures (−4, −2 °C, ambient, +2, and +4 °C). Ambient temperatures (Table 2) were defined as the mean temperature in the month prior to spawning obtained from the on-reef sensor network of the GBR Ocean Observing System and the Australian Institute of Marine Science (AIMS 2013; GBROOS 2013). Aquarium heaters, coolers, and pumps kept treatment baths within ca. 0.5 °C of the target temperatures (Electronic Supplementary Materials, ESM Table 1). Temperature profiles for each location are presented in Fig. 1. Temperature regimes were predictably more variable at higher latitudes. For example, the average difference between average monthly maximum sea surface temperature (SST) and average monthly minimum SST for each month between 2010 and 2013 was 4.2 ± 0.21 °C (mean ± SE) at Lizard Island, 5.7 ± 0.20 °C at One Tree Island, and 7.0 ± 0.36 °C at Lord Howe Island (Table 2). Similarly, the temperature range (i.e., the difference between the average monthly maximum and average monthly minimum SST, from 2010 to 2013) during the month of spawning was greater at higher latitudes: 3.9 °C (26.0–29.9 °C) at Lizard Island, 5.9 °C (22.4–28.3 °C) at One Tree Island, and 8.7 °C (19.7–28.4 °C) at Lord Howe Island (Table 2).

The effect of temperature on embryonic development

To investigate the effect of temperature on development, embryos raised at ambient temperature were transferred to 20-ml glass vials containing UV-C treated, 0.2 μm FSW and distributed among temperature treatments (ca. 30 embryos per vial; three vials per treatment) following Chua et al. (2013a, b) and Woolsey et al. (2013). The proportion of abnormal embryos was counted at 18 hpf. Abnormal embryos are easily identified because they deviate strongly from the regular and predictable pattern of development described by Ball et al. (2002).

The effect of temperature on survival

To test the effect of temperature on survival, 50 embryos were placed in 50-ml glass vials containing UV-C treated, 0.2 μm FSW and distributed among temperature treatments (three vials per treatment) following Chua et al. (2013a, b) and Woolsey et al. (2013). Survival was measured by counting the number of embryos or larvae remaining at 8 or 9 time points depending on the species: 18, 24, 30, 36, 48, 72, 96, 120, and 144 hpf. Coral embryos and larvae typically lyse within 24 h of death (Baird et al. 2006), so all propagules present were counted as alive at the time of census. Water in the vials was changed daily after being heated or cooled to the appropriate temperature.

Statistical analysis

Differences in the mean proportion of abnormal embryos among treatments were tested using one-way ANOVA with temperature as a fixed factor (five levels: −4, −2 °C, ambient, +2, +4 °C). Proportional data were arcsine transformed, and homogeneity of variance was confirmed

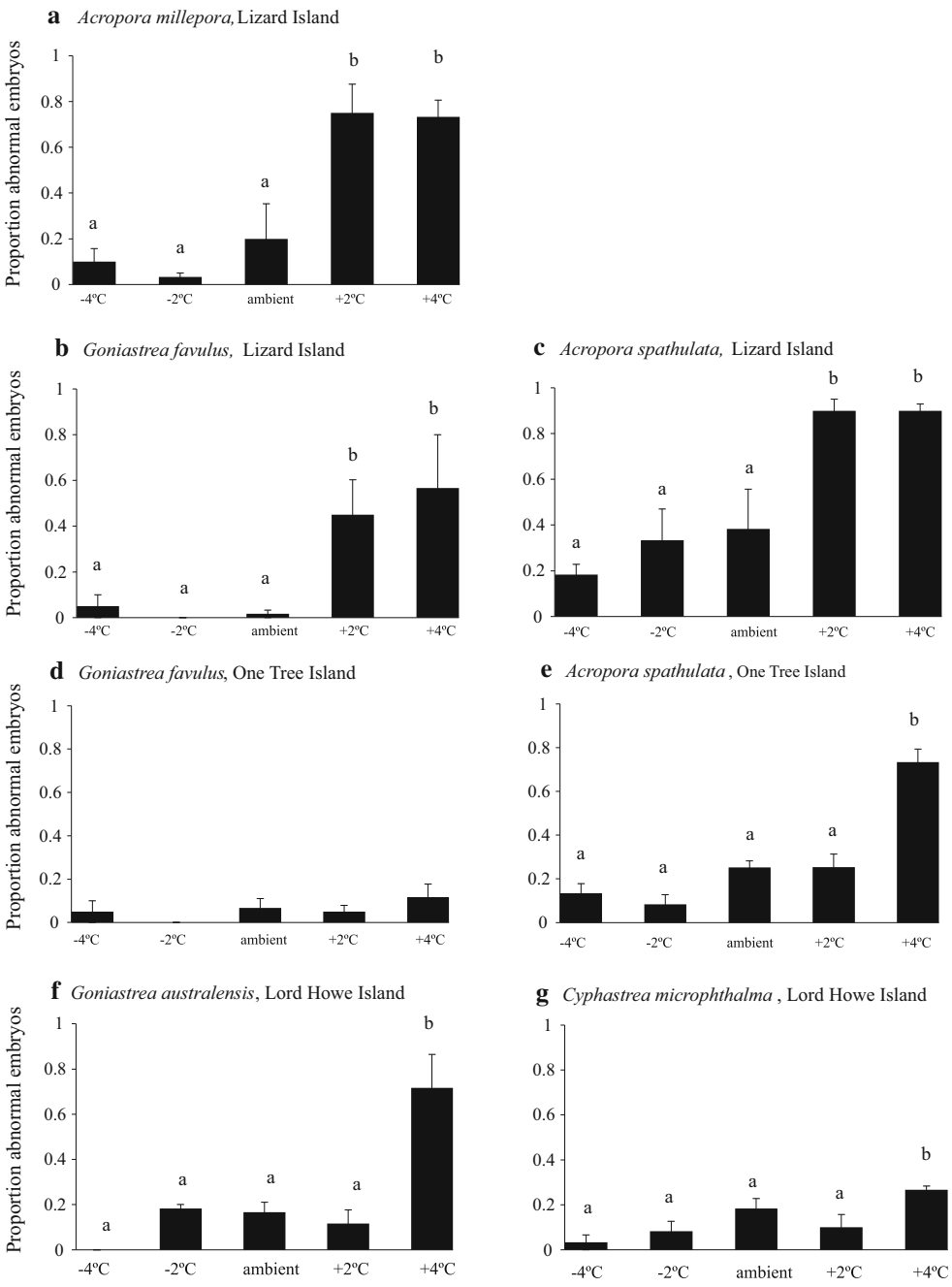

Fig. 2 Proportion of abnormal embryos (±1 SE) 1 h post-fertilization of **a** *A. millepora*, **b**, **d** *G. favulus*, **c**, **e** *A. spathulata*, **f** *G. australensis*, and **g** *C. microphthalma* in treatments 2–4 °C above and below the ambient temperature: 28 °C at Lizard Island, 24 °C at One Tree Island, and 22 °C at Lord Howe Island. *Letters* above the *error bars* indicate groups identified by Tukey's HSD post hoc test

Table 2 The upper thermal threshold temperature for each species at each location and ambient temperature at each location in the month prior to experiments

Location (latitude)	Ambient	Average monthly SST range (±SE)	SST range during spawning month	Species	Threshold for normal development (treatment)	Threshold for normal development (temperature)	Threshold for survival (treatment)	Threshold for survival (temperature)
Lizard Island (14.7°S)	28 °C	4.2 ± 0.21 °C	3.9 °C	*Acropora millepora*	+2 °C	30 °C	+2 °C	30 °C
			(26.0–29.9 °C)	*Acropora spathulata*	+2 °C	30 °C	+2 °C	30 °C
				Goniastrea favulus	+2 °C	30 °C	+2 °C	30 °C
One Tree Island (23.5°S)	24 °C	5.7 ± 0.20 °C	5.9 °C	*Acropora spathulata*	+4 °C	28 °C	+2 °C	26 °C
			(22.4–28.3 °C)	*Goniastrea favulus*	> +4 °C	>28 °C	+4 °C	28 °C
Lord Howe Island (31.5°S)	22 °C	7.0 ± 0.36 °C	8.7	*Goniastrea australensis*	+4 °C	26 °C	> +4 °C	>26 °C
			(19.7–28.4 °C)	*Cyphastrea microphthalma*	+4 °C	26 °C	> +4 °C	>26 °C

The threshold temperature was defined as the temperature at which median larval life span was significantly lower and the proportion of abnormal embryos significantly higher than at ambient. Monthly sea surface temperature (SST) ranges were calculated by subtracting average minimum SST from average maximum SST of that month, collected from on-reef AIMS and GBROOS sensors, 2010–2013 (ESM). Spawning months were November at Lizard and One Tree Islands, and January at Lord Howe Island

by Levene's test. Tukey's HSD post hoc tests were used to identify which treatment levels differed. Nonparametric Kaplan–Meier product limit analyses were used to test for differences in median survivorship among temperatures for each species separately. Median survivorship (in h) was considered significantly different when the 95 % confidence intervals did not overlap. Analyses were performed using SPSS v19® (IBM Corp. 2010). Threshold temperatures were defined as the temperature relative to ambient at which the response variable differed significantly to the control temperature (i.e., ambient). Finally, to estimate the potential effects of projected increase in SST as a result of global warming on the embryonic development and survival, we compared the experimentally determined temperature thresholds to projected average annual maximum SST at these locations in 2100, taken from Lough (2008).

Results

The effect of temperature on larval development

The proportion of abnormal embryos was high (50–90 %) in elevated temperature treatments in all assays (Table 1; Fig. 2), with the exception of *G. favulus* at OTI where there was no effect of temperature (Table 1; Fig. 2d). Temperatures below ambient had no effect on the proportion of abnormal embryos in any assays (Table 1; Fig. 2). Threshold temperatures for normal development varied predictably among locations (Table 2). At LI, the proportion of abnormal embryos increased significantly at +2 °C above ambient in all three species (Table 2; Fig. 2). At OTI and LHI, the threshold temperature was +4 °C or greater in all assays (Table 2; Fig. 2).

The effect of temperature on life spans

Life span was reduced by temperatures above ambient except for the two species from LHI where there was no effect of temperature (Fig. 3). Temperatures below ambient did not affect life span, with the exception of *A. millepora* at LI where life span was reduced at −4 °C (Fig. 3 a). Threshold temperatures for larval life span varied predictably among locations (Table 2). At LI, life span was significantly reduced at +2 °C above ambient in all three species (Table 2; Fig. 3 a–c). At OTI and LHI, the threshold temperatures were +2, +4 °C, or not observed over the 8 °C experimental range (Table 2; Fig. 3).

The effects of projected changes in sea temperatures on embryonic development and survival

Average annual SST in 2100 is projected to exceed the upper thresholds for normal development and survival in *Acropora* and *Goniastrea* at LI (Table 3). Similarly, projected average annual SST in 2100 will exceed the upper

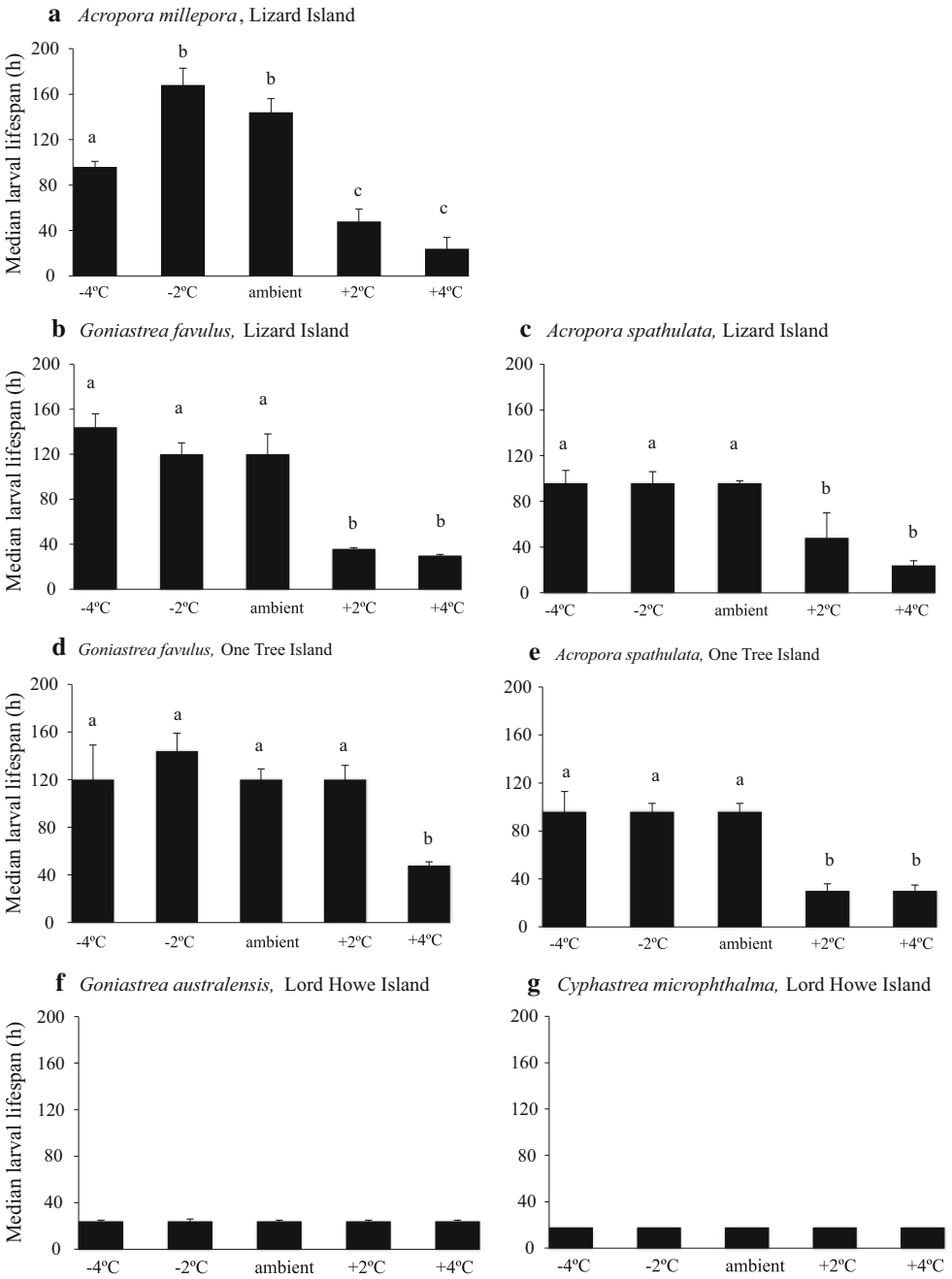

Fig. 3 Larval life span (**h**) of **a** *A. millepora*, **b**, **d** *G. favulus*, **c**, **e** *A. spathulata*, **f** *G. australensis*, and **g** *C. microphthalma* in treatments 2–4 °C above and below the local ambient temperature: 28 °C at Lizard Island, 24 °C at One Tree Island, and 22 °C at Lord Howe Island. *Error bars* show 95 % confidence intervals, and *letters* indicate homogenous groups determined by the overlap of confidence intervals

threshold for survival in *Acropora* and *Goniastrea* at OTI (Table 3). In contrast, at LHI, thermal thresholds are not projected to be exceeded within this time frame (Table 3).

Discussion

Temperatures above ambient increased the percentage of abnormal development and reduced survival. Moreover, as predicted, the temperature at which the effects were evident varied among locations. At LI, the lowest latitude location, thresholds were generally 2 °C above the local ambient in all species, whereas at the higher latitude locations, OTI and LHI, thresholds were 2–4 °C above ambient in most species (Table 2). In addition, the absolute threshold temperature varied as expected among locations: 30 °C at LI, 28 °C at OTI, and 26 °C at LHI, with higher absolute thresholds in warmer regions (Table 2).

The temperature thresholds for embryos and larvae differed predictably among locations (Table 2). For

Table 3 Current (1950–2007) and projected (2100) average annual sea surface temperatures (SST) and average annual maximum SST, after Lough (2008)

Location	Current (1950–2007)		Projected by 2100		Observed threshold of early life stages of *Goniastrea* spp (°C)		Observed threshold of early life stages of *Acropora* spp (°C)	
	Average annual SST (°C)	Average annual maximum (°C)	Average annual SST (°C)	Average annual maximum (°C)	Normal development	Survival	Normal development	Survival
Northern GBR (14.5°S)	28.8	30.0	29.5	30.4	30	30	30	30
Southern GBR (23.5°S)	24.0	26.6	25.4	27.9	–	28	28	26
High latitude (29.5°S)	21.2	23.2	22.5	24.6	26	–	na	na

Thresholds of early life stages in *Goniastrea* and *Acropora* spp are the temperature treatments at which there was a significant increase in the proportion of abnormal embryos or decrease in larval life span. Dashes indicate that a threshold was not observed over the 8 °C experimental range

Na no data

instance, in *G. favulus* temperatures 2 °C above ambient reduced the life span for lower latitude Lizard Island populations, whereas at the higher latitude One Tree Island temperatures 4 °C above ambient were required to produce an effect. These results are consistent with work on adult corals indicating that thermal thresholds for bleaching vary predictably among locations (Hoegh-Guldberg 1999) and suggest that thermal tolerance breadth might be greater at locations that experience greater fluctuations in temperature (McClanahan et al. 2007). In addition, absolute thermal thresholds identified by Hoegh-Guldberg (1999) and Ulstrup et al. (2006) produce relative thresholds that support the fact that corals at high latitudes have a greater upper thermal threshold than those at lower latitudes. These data add to a growing body of evidence suggesting that low latitude corals are living close to the upper thermal limit for many critical life history stages. Therefore, in the absence of acclimatization or adaptation, projected temperature rises are likely to be more detrimental to tropical corals than those at higher latitudes.

Thermal thresholds did not vary greatly among species within locations. However, at OTI, embryos and larvae of the acroporid *A. spathulata* were more sensitive to temperature increase than the merulinid *G. favulus*. Similarly, temperatures 4 °C above ambient increased the proportion of abnormal embryos in *A. millepora* but not in the merulinids *Favites chinensis* and *Mycedium elephantotus* (Negri et al. 2007). These findings are consistent with previous observations that adult acroporids are less thermally tolerant than merulinids (Loya et al. 2001; Baird and Marshall 2002) and suggest that acroporids are therefore at greater risk than merulinids from increased ocean temperatures caused by climate change.

Larval life spans were uniformly low at LHI, with a median life span of 24 ± 2 h compared to >80 h at ambient in all species at the other locations (Fig. 3), suggesting that the gametes of these subtropical corals were either highly sensitive to handling or of poor quality. Indeed, the marginal conditions for coral growth, for example, winter temperatures as low as 14.4 °C (AIMS 2013), might have a detrimental effect on gamete quality. Low larval survivorship is consistent with low rates of recruitment at LHI (Noreen et al. 2009; Hoey et al. 2011) and suggests that isolated margin habitats, such as LHI, will be highly susceptible to disturbance.

Climate change is likely to have profound effects on patterns of dispersal and population dynamics of reef corals. Our results suggest that coral populations in tropical regions are likely to be more seriously affected by increased sea temperatures than those in the subtropics because they are living at temperatures closer to the maximum values that various life history stages can tolerate.

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