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Temperature affects the early life history stages of corals more than near future ocean acidification

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ABSTRACT: Climate change is projected to increase ocean temperatures by at least 2°C, and levels of pH by ~0.2 units (ocean acidification, OA) by the end of this century. While the effects of these stressors on marine organisms have been relatively well explored in isolation, possible interactions between temperature and OA have yet to be thoroughly investigated. OA at levels projected to occur within this century has few direct ecological effects on the early life history stages of corals. In contrast, temperature has pronounced effects on many stages in the early life history of corals. Here, we test whether temperature might act in combination with OA to produce a measurable ecological effect on fertilization, development, larval survivorship or metamorphosis of 2 broadcast spawning species, *Acropora millepora* and *A. tenuis*, from the Great Barrier Reef. We used 4 treatments: control, high temperature (+2°C), high partial pressure of CO_2 (pCO_2) (700 µatm) and a combination of high temperature and high pCO_2, corresponding to the current levels of these variables and the projected values for the end of this century under the IPCC A2 scenario. We found no consistent effect of elevated pCO_2 on fertilization, development, survivorship or metamorphosis, neither alone nor in combination with temperature. In contrast, a 2°C rise in temperature increased rates of development, but otherwise had no consistent effect on fertilization, survivorship or metamorphosis. We conclude that OA is unlikely to be a direct threat to the early life history stages of corals, at least in the near future. In contrast, rising sea temperatures are likely to affect coral population dynamics by increasing the rate of larval development with resulting changes in patterns of connectivity.

KEY WORDS: Coral reefs · Climate change · Connectivity · Development · Larval ecology · Survivorship · Settlement

INTRODUCTION

Increasing carbon dioxide (CO_2) concentrations in the atmosphere are causing the oceans to warm. Sea surface temperatures have risen by a global average of 0.7°C since the industrial revolution (Feely et al. 2009) and are predicted to rise by a further 2 to 3°C by the end of the century under the IPCC A2 scenario (Bindoff et al. 2007). In addition, the absorption of atmospheric CO_2 is changing ocean chemistry, decreasing seawater pH and reducing the availability of carbonate ions (CO_3^{2-}). Ocean pH has decreased by 0.1 units since the 1950s and is projected to decrease by a further 0.2 to 0.3 units by the end of the century (Feely et al. 2009).

The effects of rising sea surface temperature on marine organisms are well documented. Symbiotic organisms, such as corals, seem particularly sensitive to elevated temperatures (Baird et al. 2009), and the resulting coral bleaching has a range of ecological effects from reductions in growth, reproduction and competitive ability to high mortality of individuals over large spatial scales (see review in McClanahan et al. 2009). In contrast, the effects of ocean acidi-

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fication (OA) are less obvious, in part because the effects are often sub-lethal (Fabricius et al. 2011). Early experiments suggested a linear decline in calcification in response to a declining aragonite saturation state (Langdon & Atkinson 2005); however, more recent work indicates that the response is highly variable among species and dependent upon experimental techniques (see review in Pandolfi et al. 2011).

The effects of temperature on the early life history stages of coral are also well documented. For example, temperature increases of 1 to 2°C above ambient levels result in high numbers of abnormally developed larvae (Bassim et al. 2002, Negri et al. 2007). Similarly, high temperatures reduce larval survivorship (Baird et al. 2006), particularly in larvae that contain symbiotic algae (Yakovleva et al. 2009, Nesa et al. 2012). In contrast, the effects of OA on coral larval ecology are much more variable and direct effects are only evident at very high partial pressure of CO_2 (pCO_2) levels or when gametes and larvae are past their peak (see review in Dufault et al. 2012).

In the wild, these 2 stressors clearly act on organisms simultaneously; however, there have been very few experiments that explore the combined effects of high pCO_2 and temperature. The general assumption is that the effect of OA and temperature will be additive. Indeed, high pCO_2 in combination with high temperature lowers thermal bleaching thresholds in corals and crustose coralline algae (Anthony et al. 2008). Similarly, growth rates of *Porites panamensis* juveniles were lowest in a combined high pCO_2 and high temperature treatment (Anlauf et al. 2011). However, the interaction could be antagonistic because temperature increases metabolism (O'Connor et al. 2009), and high pCO_2 reduces it (Pörtner et al. 2004). In another example, high temperatures can compensate for dwarfism that would otherwise eventuate due to reduced calcification in acidified sea water, as in *Tripneustes gratilla* larvae (Sheppard Brennand et al. 2010).

In this study, we tested the combined effects of elevated temperature and elevated pCO_2 on the early life history stages of 2 common spawning acroporids of the northern Great Barrier Reef region.

MATERIALS AND METHODS

Collection of mature colonies

Six mature colonies of *Acropora tenuis* and *A. millepora* were collected at Magnetic Island (19° 9′ S, 146° 50′ E) and a second batch of 6 *A. millepora* colonies were collected from Orpheus Island (18° 35′ S, 146° 29′ E), a few days prior to the predicted spawning period in 2010. They were transported to James Cook University and maintained in outdoor aquaria (GBRMPA permit: G10/33174.1). *A. tenuis* spawned on the night of 28 October 2010; *A. millepora* from Magnetic Island spawned on the nights of 1 and 2 November 2010. *A. millepora* colonies from Orpheus Island spawned on 22 and 30 November 2010. Consequently, 6 cohorts of larvae were available for the experiments: *A. tenuis*, *A. millepora* Nov_1, *A. millepora* Nov_2, *A. millepora* Nov_22 and *A. millepora* Nov_30. However, not all response variables were tested in each of these cohorts.

Experiments on ocean acidification and warming

The CO_2 tanks were located in a temperature controlled room (27°C). Two levels of CO_2 concentration (ambient and elevated pCO_2) and 2 levels of temperature (ambient 27°C and 29°C) were selected as recommended by the European Project on Ocean Acidification (EPOCA) protocol (Barry et al. 2010). The 4 treatments were (1) ambient temperature + ambient pCO2, (2) ambient temperature + high pCO2, (3) high temperature + ambient pCO2, (4) high temperature + high pCO2 (see Table 1 for mean values of each level of each factor used in the experiments).

Experimental temperatures were maintained using aquarium heaters (Eheim Jäger 300W placed in water baths and bath temperatures were measured twice daily. The desired pCO_2 level in the sea water was produced using a CO_2 mixing system developed by Munday et al. (2009) and the pCO_2 concentration was measured in ppm units using a CO_2 gas probe (Vaisala®). The mixed gases were bubbled through 250 l sump tanks and water chemistry parameters and corresponding total alkalinity (TA) were measured for each treatment throughout the experiment (Table 1) by using a fixed end point titration method. Experimental calcite (Ω_{calc}) and aragonite saturations (Ω_{arag}), as well as actual pCO_2 (µatm) were calculated from average total alkalinity data (TA), salinity, temperature and pHNBS using CO2SYS with dissociation constants of Mehrbach et al. (1973) as refitted by Dickson & Millero (1987) (Pierrot et al. 2006). Dissolved oxygen (DO% saturated) was measured daily to ensure sufficient oxygen flow in the treatment tanks.

The effect of temperature and pCO_2 on fertilization

Egg and sperm bundles were collected from individual colonies, mixed and then gently agitated to

Table 1. Water chemistry parameters (means ± SE) for experiments with (1) *Acropora tenuis, A. millepora* Nov_01 and *A. millepora* Nov_02, and (2) with *A. millepora* Nov_22 and *A. millepora* Nov_30. Saturation values of aragonite (Ω_{arag}) and calcite (Ω_{calc}) and actual saturated values of pCO_2 in treatments tanks calculated using CO2SYS (Pierrot et al. 2006)

Treatment	pH	Total alkalinity (µmol kg^{-1} as $CaCO_3$)	Temp (°C)	Ω_{calc}	Ω_{arag}	pCO_2 calculated (µatm)
(1) *A. tenuis, A. millepora* Nov_01 and *A. millepora* Nov_02						
Ambient temp + Ambient pCO_2	8.17 ± 0.01	2205 ± 19	25.7 ± 0.13	4.8 ± 0.1	3.2 ± 0.1	421 ± 10
High temp + Ambient pCO_2	8.18 ± 0.01	2232 ± 9	28.5 ± 0.10	4.7 ± 0.1	3.2 ± 0.1	499 ± 9
Ambient temp + High pCO_2	8.06 ± 0.02	2111 ± 44	25.6 ± 0.12	3.3 ± 0.1	2.2 ± 0.1	655 ± 41
High temp + High pCO_2	8.06 ± 0.01	2162 ± 54	28.9 ± 0.01	2.8 ± 0.3	1.9 ± 0.2	663 ± 20
(2) *A. millepora* Nov_22 and *A. millepora* Nov_30						
Ambient temp + Ambient pCO_2	8.12 ± 0.01	1947 ± 14	26.5 ± 0.11	3.7 ± 0.2	2.4 ± 0.1	474 ± 34
High temp + Ambient pCO_2	8.12 ± 0.01	1955 ± 21	28.9 ± 0.03	3.7 ± 0.2	2.5 ± 0.1	521 ± 43
Ambient temp + High pCO_2	7.98 ± 0.02	1920 ± 25	26.7 ± 0.09	2.7 ± 0.2	1.8 ± 0.1	699 ± 34
High temp + High pCO_2	8.01 ± 0.01	1911 ± 22	29.2 ± 0.11	2.8 ± 0.3	1.9 ± 0.2	759 ± 70

break up the bundles. Buoyant eggs were then separated from the sperm and a stock of sperm solution was prepared. We counted 20 eggs into each of 12 replicates of 25 ml glass jars (6 with high pCO_2 and 6 with ambient pCO_2 seawater) and an equal quantity of sperm was introduced into each jar to produce a final concentration of 10^6 sperm ml^{-1} to maximize the fertilization rate (Oliver & Babcock 1992). Gametes were mixed within 30 min of spawning. The volume of sperm solution added was <1 ml and, therefore, unlikely to have influenced the pH levels in the jars. Then, 3 jars were placed in each of the 2 water baths containing heated water and 6 were kept at ambient temperature, resulting in 3 replicate jars in each of the 4 treatments. The number of cleaved embryos was quantified 2 h after the gametes were mixed to estimate fertilization rates. The cohorts used in these experiments are listed in the legend of Fig. 1.

Effect of temperature and pCO_2 on development

Once cleavage was observed, embryos were washed 3 times in 0.2 µm filtered sea water to remove excess sperm, which can cause cultures to deteriorate. Then, ~1000 embryos were placed in each of 12 replicate 3.5 l plastic jars, 3 jars per treatment, with 0.2 µm filtered seawater at a flow rate of 1.5 to 2 l h^{-1}. At 12, 18, 24, 36, 48, 72 and 96 h after the gametes were mixed, 20 propagules were pipetted from each jar and the number of propagules in each of the following 5 development stages were identified (following Ball et al. 2002): (1) 4-cell blastula, (2) multiple cell blastula, (3) early gastrula, (4) gastrula and (5) planulae (motile stage). The cohorts used in these experiments are listed in the legend to Fig. 2.

To test for differences in development time between treatments, the average time ($\overline{X}$) for propagules to reach a certain stage of development was estimated as follows:

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

Effect of temperature and pCO_2 on larval survival

Fifty motile larvae (4 d old) were placed in each of 3 replicate jars with plankton mesh lids and immersed in the treatment tanks. Surviving larvae were counted every 4 h. This period is sufficient for dead larvae to lyse and disappear from the jars (Baird et al. 2006). Larval survival was followed for up to 14 d in each treatment. The cohorts used in these experiments are listed in the legend of Fig. 4.

Effect of temperature and pCO_2 on metamorphosis

Metamorphosis of *Acropora* larvae typically peaks between 6 and 10 d after spawning (Connolly & Baird 2010). Consequently, 7 d old larvae were used to test for differences in metamorphosis between treatments. Ten to 20 larvae were pipetted from each of the 12 replicate plastic jars and placed into each well of a 6-well cell culture plate. Consequently, there were 3 replicate 6-well plates in each treatment with a total of 180 or 360 larvae per treatment. A 2 × 2 mm chip of live crustose coralline algae (CCA) (*Titanoderma* sp.) was placed in each well to induce metamorphosis (Harrington et al. 2004) and the plates were then immersed in the treatments. The lids of the

6-well plates were modified with plankton mesh to allow treated seawater to mix with the water in the wells. The number of larvae that completed metamorphosis was assessed after 24 h under a dissecting microscope (10×). Metamorphosis was defined as the deposition of a basal disc, which is generally visible through the juvenile coral tissue (Babcock et al. 2003, Baird & Babcock 2000). The cohorts used in these experiments are listed in the legend of Fig. 5.

Data analysis

Mean differences among the 4 treatments in the proportion of eggs fertilized, time to complete gastrulation, time to motility, and the number of larvae completing metamorphosis were tested with a fully orthogonal 2-way ANOVA. The factors were Temperature (fixed, 2 levels: 27 and 29°C) and pCO_2 (fixed, 2 levels: ambient and elevated pCO_2). Each assay was analyzed independently (i.e. 2 to 4 assays representing the different cohorts of larvae depending on the response variable). A Bonferroni correction was used to adjust the probability of type I error (i.e. probability was considered significant when beta < alpha/n, where beta equals the Bonferoni corrected probability, alpha = 0.05 and n = the number of assays run for the specific response variable). Any bias in these data was explored by residual analysis. Response variables were transformed as follows: percent fertilization – no transformation necessary; time to gastrulation and motility – $\log_{10}$ transformed; proportion metamorphosis – arcsine transformed. Differences in the median survival time among treatments for each assay were tested using Kaplan-Meier survival analysis. All statistical analyses were performed using SPSS 16®.

RESULTS

The mean proportion of eggs completing fertilization was not affected by either temperature or pCO_2 in 3 of the 4 assays. In all these assays, fertilization success was uniformly high (Fig 1A–C). In the *Acropora millepora* Nov_22 assay, the proportion (mean ± SE) of eggs fertilized was significantly lower at high temperatures ($F_{(1,20)}$ = 10.376, p = 0.005): 100% fertilized eggs at 27°C versus 89.5 ± 3.8 at 29°C (Fig. 1D).

The effects of temperature and pCO_2 on time to complete gastrulation were variable. In all but one cohort, *Acropora millepora* Nov_22, embryos completed gastrulation more rapidly at high temperature

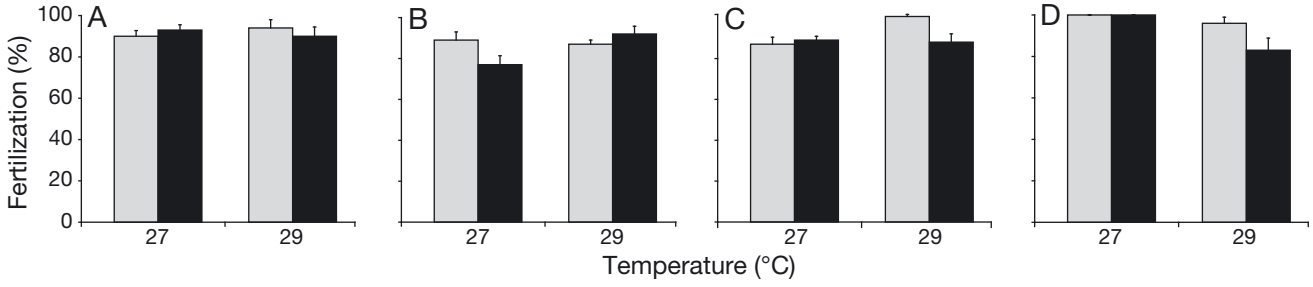

Fig. 1. Fertilization (mean percent +1 SE) in 4 combinations of temperature and pCO_2. (A) *Acropora tenuis*, (B) *A. millepora* Nov_01, (C) *A. millepora* Nov_02, (D) *A. millepora* Nov_22. Bars: grey: ambient pCO_2, black: high pCO_2 (values for the levels of each factor are listed in Table 1)

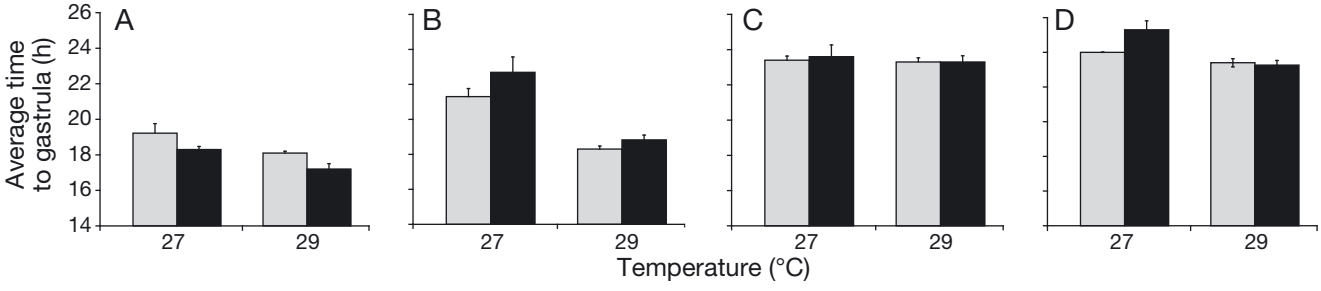

Fig. 2. Time to gastrula stage (mean +1 SE) in 4 combinations of temperature and pCO_2. (A) *Acropora tenuis*, (B) *A. millepora* Nov_01, (C) *A. millepora* Nov_22, (D) *A. millepora* Nov_30. For details, see Fig. 1 legend

Table 2. Two-way ANOVA testing for difference among treatments in the mean time for embryos to develop to the gastrula stage. Data were $\log_{10}$ transformed. Bonferroni corrected probability = 0.013

Cohorts	n	df	*F*	p
A. tenuis	238			
Temp		1	14.475	<0.001
pCO_2		1	10.067	0.002
Temp × pCO_2		1	0.696	0.405
***A. millepora* Nov_01**	232			
Temp		1	50.353	<0.001
pCO_2		1	2.525	0.113
Temp × pCO_2		1	0.157	0.692
***A. millepora* Nov_22**	240			
Temp		1	0.090	0.765
pCO_2		1	0.050	0.823
Temp × pCO_2		1	0.090	0.765
***A. millepora* Nov_30**	237			
Temp		1	18.846	<0.001
pCO_2		1	2.143	0.145
Temp × pCO_2		1	3.993	0.047

Table 3. Two-way ANOVA testing for difference among treatments in the mean time for embryos to reach motility. Data were $\log_{10}$ transformed. Bonferroni corrected probability = 0.013

Cohorts	n	df	*F*	p
A. tenuis	142			
Temp		1	323.125	<0.001
pCO_2		1	4.935	0.028
Temp × pCO_2		1	44.796	<0.001
***A. millepora* Nov_01**	218			
Temp		1	53.519	<0.001
pCO_2		1	10.597	0.001
Temp × pCO_2		1	17.654	<0.001
***A. millepora* Nov_22**	142			
Temp		1	3.015	0.085
pCO_2		1	10.101	0.002
Temp × pCO_2		1	3.622	0.059
***A. millepora* Nov_30**	210			
Temp		1	13.202	<0.001
pCO_2		1	0.070	0.792
Temp × pCO_2		1	0.587	0.444

(Fig. 2, Table 2). For example, the average time to complete gastrulation in *A. millepora* Nov_01 was 22.0 ± 0.49 h at 27°C, compared to 18.6 ± 0.16 h at 29°C. In the *A. tenuis* cohort pCO_2 also had an effect, with embryos in high pCO_2 completing gastrulation more quickly (17.8 ± 0.18 h) than those at ambient pCO_2 (18.7 ± 0.28 h) (Fig. 2A, Table 2). No cohort showed any interaction between temperature and pCO_2 (Table 2). Similarly, the effects of temperature and pCO_2 on time to motility were variable. In all but one cohort, *A. millepora* Nov_22, motility was achieved more rapidly at higher temperatures (Fig. 3, Table 3); however, 2 cohorts showed an interaction between temperature and pCO_2. In *A. tenuis*, there was no difference between the pCO_2 treatments at 27°C; however, at 29°C motility was reached more rapidly in the high pCO_2 treatment (Fig. 3A). In *A. millepora* Nov_01, there was no difference between the pCO_2 treatments at 29°C; however, at 27°C, embryos in the high pCO_2 treatment became motile more quickly (Fig. 3B). In only one instance there was an effect of just pCO_2. In *A. millepora* Nov_22 motility was reached more rapidly at high pCO_2 (Fig. 3C, Table 3) than at ambient pCO_2 (59.2 ± 1.7 h vs. 66.8 ± 2.84 h) (Fig. 3C, Table 3).

The effects of temperature and pCO_2 on larval survivorship were also variable. In *Acropora tenuis*, median survivorship was significantly lower in the high temperature + ambient pCO_2 treatment, but did not vary among the other 3 treatments as indicated by the overlap in the 95% CIs (Fig. 4A). In *A. millepora* Nov_22, median survivorship was lower in the high temperature and the combined high temperature high pCO_2 treatment when compared to ambient temperature + ambient pCO_2 (Fig. 4B); however, there was no significant difference in median survivorship between the high pCO_2 treatment and any other treatment (Fig. 4B).

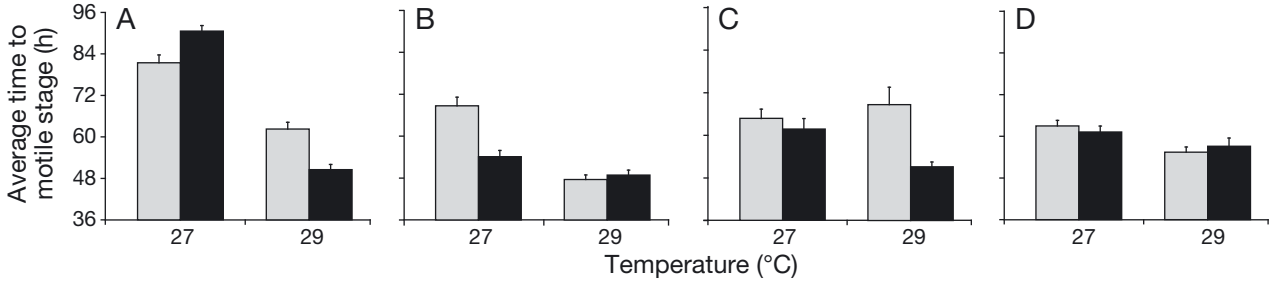

Fig. 3. Time to motile stage (mean +1 SE) in 4 combinations of temperature and pCO_2. (A) *Acropora tenuis*, (B) *A. millepora* Nov_01, (C) *A. millepora* Nov_22, (D) *A. millepora* Nov_30. For details, see Fig. 1 legend

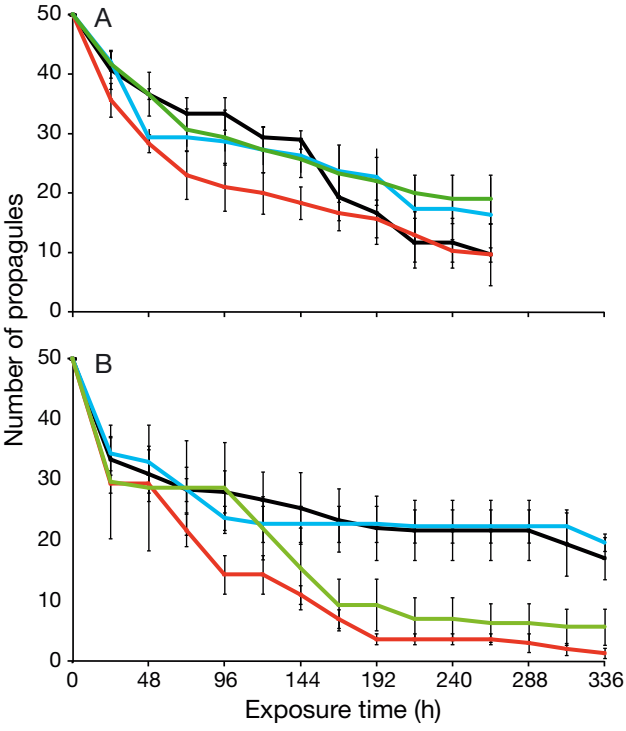

Fig. 4. Number of surviving propagules (median ± 95% CI) estimated using Kaplan-Meier analysis in 4 combinations of temperature and pCO_2. (A) *Acropora tenuis*, (B) *A. millepora* Nov_22. Black lines: ambient temperature + ambient pCO_2; red lines: high temperature + ambient pCO_2; blue lines: high pCO_2 + ambient temperature; green lines: high temperature + high pCO_2 (details on experimental parameters in Table 1)

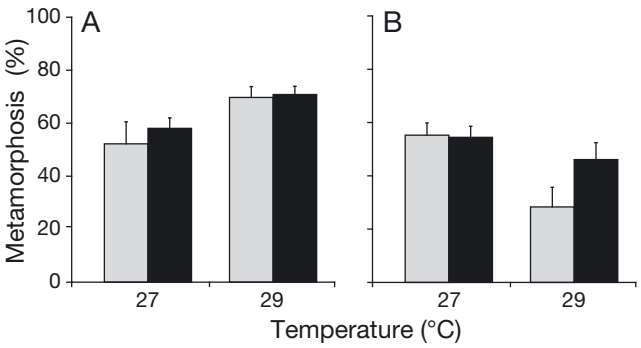

Fig. 5. Percentage of metamorphosis (mean +1 SE) in 4 combinations of temperature and pCO_2. (A) *Acropora tenuis*, (B) *A. millepora* Nov_22. For details, see Fig. 1 legend

The effects of temperature and pCO_2 on larval metamorphosis were also variable. In *A. tenuis*, metamorphosis was significantly higher at 29°C (55.1 ± 4.5% vs. 70.3 ± 2.5%) ($F_{(1,72)}$ = 7.30, p = 0.009; Fig. 5A). In contrast, metamorphosis was lower at 29°C in *Acropora millepora* Nov_22 (54.9% ± 3.0 vs. 40.2% ± 4.5) ($F_{(1,72)}$ = 7.24, p = 0.009; Fig. 5B). pCO_2 did not have any effect on metamorphosis, either on its own, or in combination with high temperature.

DISCUSSION

Increased temperature (by +2°C) more consistently affected the early life stages of corals in comparison to elevated pCO_2 (~215 µatm above ambient). In general, rates of development were faster at high temperature, as predicted by metabolic theory (Gillooly et al. 2001). In contrast, elevated pCO_2 rarely affected development and, with one exception, only in combination with temperature. However, the effect was contrary to what is generally predicted. In both assays where an interaction was detected (Fig. 3A,B, Table 3), high pCO_2 decreased the time to motility, whereas elevated pCO_2 would be expected to slow rates of development (Pörtner et al. 2004). Similarly, in the only assay where elevated pCO_2 had a significant effect on development rates, time to motility was faster in high pCO_2 treatments. Neither temperature, elevated pCO_2 nor the combination of these variables affected fertilization, larval survivorship or metamorphosis in any consistent or predictable way. We conclude that the changes in temperature and elevated pCO_2 projected for this century are unlikely to have major ecological effects on the early life history of corals, either alone or in combination, except that temperature will speed up rates of larval development.

Fertilization was robust to both elevated pCO_2 and temperature within the range of variables used in the experiments. This result is in good agreement with most previous work with marine invertebrate larvae (reviewed in Byrne 2011), the exception being Albright et al. (2010) who reported a 64% decrease in fertilization rates at similar levels of OA, but only when sperm concentration was low. In general, fertilization rates in corals are only reduced at +4°C (e.g. Negri et al. 2007). Similarly, sea urchin fertilization is robust to these levels of elevated pCO_2 and temperature (Sheppard Brennand et al. 2010, Byrne 2011). Indeed, marine invertebrate fertilization is generally robust to acidity and minor increases in temperature because the propagules are often equipped with cellular defense mechanisms. These are present in the egg before fertilization (Hamdoun & Epel 2007, Portune et al. 2010), probably because the gametes are regularly exposed to fluctuating temperature and pCO_2 in the water column (Gagliano et al. 2010).

Consistent with the literature (Byrne 2011, Chua 2012), and to be expected on the basis of metabolic theory, rates of development were predictably in-

creased by temperature. However, it was surprising that elevated pCO_2 also on occasion increased rates of development, both on its own and in combination with high temperature, in contrast to a prediction of reduced metabolism from hypercapnia.

Metamorphosis was affected by temperature but not elevated pCO_2; however, the temperature effect was inconsistent. Again, these results are generally consistent with the literature (see Chua 2012). Temperatures of +2°C above ambient levels have little effect on metamorphosis, and both increases (Coles 1985) or decreases (Randall & Szmant 2009) are evident at temperature elevations >+2°C. Metamorphosis is rarely directly affected by elevated pCO_2 (Albright et al. 2010, 2011); indeed, Nakamura et al. (2011) reported a direct effect only for larvae that have passed peak metamorphosis. The effect of elevated pCO_2 on metamorphosis, if any, is indirect and mediated through elevated pCO_2 induced changes in the composition of the substratum, in particular the health of crustose coralline algae that are often required to induce metamorphosis in coral (Albright et al. 2010, Doropoulos et al. 2012). In the only other study on a synergistic effect between these stressors, metamorphosis was not affected (Anlauf et al. 2011).

Survivorship was not consistently affected by elevated pCO_2 or temperature. The temperature result is perhaps surprising because most previous experiments report an affect for an elevation of +2°C (e.g. Coles 1985, Bassim & Sammarco 2003, but see Yakovleva et al. 2009). In contrast, larval survivorship is rarely affected by elevated pCO_2 (Suwa et al. 2010, Nakamura et al. 2011). This suggests that some coral species are more susceptible to temperature and elevated pCO_2 stress than others (Fabricius et al. 2011).

In conclusion, the effects of a +2°C increase in temperature were relatively minor and had no effect on fertilization, and mixed effects on larval survivorship and metamorphosis. The only consistent effect was on rates of development, which were typically more rapid at high temperature. The effects of increased rates of development on coral demography are difficult to predict. If larvae develop competence more quickly, average dispersal distance should decrease which is, therefore, likely to reduce levels of reef connectivity (Heyward & Negri 2010). However, greater levels of retention are also likely to increase the rates of recruitment. Consequently, the effect of more rapid rates of development in response to increasing temperatures are likely to be highly dependent on local conditions such as reef density and hydrodynamics. In contrast to temperature, elevated pCO_2 had no predictable or consistent effect, either alone, or in combination with temperature. We conclude, that temperature increases associated with global warming are more likely to have ecological consequences than OA at least in the near-future (see also Cooper et al. 2012).

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