Vol. 486: 143–151, 2013
doi: 10.3354/meps10318

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 12

Near-future reductions in pH will have no consistent ecological effects on the early life-history stages of reef corals

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ABSTRACT: Until recently, research into the consequences of oceanic uptake of CO_2 for corals focused on its effect on physiological processes, in particular, calcification. However, events early in the life history of corals are also likely to be vulnerable to changes in ocean chemistry caused by increases in the atmospheric concentration of CO_2 (ocean acidification). We tested the effect of reduced pH on embryonic development, larval survivorship and metamorphosis of 3 common scleractinian corals from the Great Barrier Reef. We used 4 treatment levels of pH, corresponding to the current level of ocean pH and 3 values projected to occur later this century. None of the early life-history stages we studied were consistently affected by reduced pH. Our results suggest that there will be no direct ecological effects of ocean acidification on the early life-history stages of reef corals, at least in the near future.

KEY WORDS: *Acropora* · Climate change · Coral reefs · Development · Dispersal · Recruitment · Survivorship

INTRODUCTION

Global climate change has the potential to detrimentally affect coral reefs in many ways. In particular, increasing ocean acidity is predicted to be a severe threat to marine ecosystems before the end of this century (Kleypas et al. 1999, Orr et al. 2005). Ocean acidification (OA) is caused by the alteration of water chemistry through CO_2 absorption from the atmosphere, in particular, increased uptake of CO_2 by seawater will result in a decrease in pH, carbonate ion concentration (CO_3^{2-}) and the saturation state of aragonite. Recent changes in ocean chemistry, for example a decrease in pH of 0.1 units since the beginning of the Industrial Revolution (Caldeira & Wickett 2003), have already had pronounced effects on many calcifying marine organisms (Kroeker et al. 2011). Decreases in aragonite saturation projected to occur within this century are predicted to result in the net dissolution of calcium carbonate on coral reefs (Silverman et al. 2009).

To date, much of the research into OA has focused on its effects on adult marine organisms and, in particular, the process of calcification. However, the early life-history stages of marine organisms are also likely to be sensitive to changes in ocean chemistry (Pörtner et al. 2004, Albright 2011, Byrne 2011, Kroeker et al. 2011). Hypercapnia, defined as an increase in the partial pressure of CO_2 (pCO2) in the respiratory fluids, is well known to affect acid-base regulation, oxygen transport and metabolic function (Pörtner et al. 2004). Similarly, high CO_2 concentration in sea water has a narcotic effect on sperm, reducing motility (Havenhand et al. 2008, Morita et al. 2010). While hypercapnia and CO_2 narcosis may not necessarily be detrimental to the organism,

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responding to changes in pCO_2 will be energetically costly; therefore, OA has the potential to affect growth and reproductive output following prolonged exposure (Pörtner et al. 2004) in the absence of acclimatization. In addition, OA can lower metabolic rates, reducing rates of development in critical life-history stages of organisms, such as larvae (Kurihara & Shirayama 2004). Reduced rates of larval development are likely to extend pelagic durations with possible increases in rates of mortality and reduced recruitment success (Connolly & Baird 2010). Such changes are also likely to reduce levels of connectivity among affected organisms and therefore have the potential to affect rates of recovery from disturbance (Munday et al. 2009).

The effects of decreased pH on the early life-history stages of corals are highly variable (Table 1). For example, fertilization success in *Acropora palmata*

Table 1. A summary of previous research on the effects of ocean acidification on the early life-history stages of corals. Value of CO_2-related variables are from projections based on the Intergovernmental Panel on Climate Change A2S2 scenario (Bindoff et al. 2007, Barry et al. 2010). Percentage values are the increase or decrease (–) in the response variable when compared with controls. 'ns' means no significant differences were evident between the treatment level and controls. 'z' indicates larvae that contain *Symbiodinium*

Scenario parameters:	Year:		2050	2100	2100+
	pCO_2 atmosphere (ppm):		450–700	700–1000	1000+
	pH ocean:		7.9–8.0	7.7–7.9	<7.7
	Aragonite saturation state:		2.2–3.2	1.2–2.2	<1.5
Response variable and study	Special conditions	Species	Change in response variable (%) Scenario: 2050	2100	2100+
Sperm motility					
Morita et al. (2010)		*Acropora digitifera*		–30	–60
Fertilization					
Albright et al. (2010)	3.2×10^6 sperm ml^{-1}	*Acropora palmata*	ns	ns	
	1.6×10^6 sperm ml^{-1}	*Acropora palmata*	ns	ns	
	6.4×10^5 sperm ml^{-1}	*Acropora palmata*	–64	–63	
	3.2×10^5 sperm ml^{-1}	*Acropora palmata*	–29	–15	
Chua et al. (2013)		*Acropora millepora*		ns	
		Acropora tenuis		ns	
Embryonic development	Time to gastrulation	*Acropora millepora*		ns	
Chua et al. (2013)		*Acropora tenuis*		–12	
	Time to motility	*Acropora millepora*		–30	
		Acropora tenuis		10	
Larval respiration					
Albright & Langdon (2011)		*Porites astreoides* (z)		–27	–63
Cumbo et al. (2013)		*Pocillopora damicornis* (z)		ns	
Nakamura et al. (2011)		*Acropora digitifera*	ns	ns	ns
Larval survivorship					
Cumbo et al. (2013)		*Pocillopora damicornis* (z)		–25	
Nakamura et al. (2011)		*Acropora digitifera*			ns
Suwa et al. (2010)		*Acropora digitifera*			ns
		Acropora tenuis			ns
Chua et al. (2013)	1.0×10^6 sperm ml^{-1}	*Acropora millepora*		ns	
		Acropora tenuis		ns	
Metamorphosis					
Albright et al. (2008)		*Porites astreoides* (z)	ns	ns	
Albright et al. (2010)		*Acropora palmata*	–45	–65	
Albright & Langdon (2011)	Larvae treated	*Porites astreoides* (z)	ns	ns	
	Settlement tiles treated	*Porites astreoides* (z)	–45	–55	
Nakamura et al. (2011)	2 d exposure	*Acropora digitifera*		–20	–20
	7 d exposure	*Acropora digitifera*		–80	–80
Doropoulos et al. (2012)	Settlement tiles treated	*Acropora millepora*		–82	ns
	Larvae treated	*Acropora millepora*		–58	–75
	Larvae and tiles treated	*Acropora millepora*		ns	–60
Chua et al. (2013)		*Acropora millepora*		ns	
		Acropora tenuis		ns	

was reduced at low sperm densities at pH 7.85 and 7.72 (Albright et al. 2010), possibly because of reduced sperm motility (Morita et al. 2010). However, these levels of pH had no effect on fertilization success when experimental sperm concentrations (Albright et al. 2010) were similar to those in the field in the hour immediately following spawning, which is when most fertilization is likely to occur (i.e. approximately 10^6 sperm ml^{-1}; Oliver & Babcock 1992). In addition, gametes in the experiment were mixed 3 h after spawning and fertilization was scored 1 h later (Albright et al. 2010), therefore these gametes were likely to have dramatically reduced vitality (Oliver & Babcock 1992). In contrast, increased pCO_2 had no effect on fertilization rates of *A. millepora* or *A. tenuis* (Chua et al. 2013).

Larval survivorship differed among pH treatments in *Acropora tenuis*, but not in *A. digitifera* (Suwa et al. 2010). However, the difference in survivorship among treatments was not a dose-dependent or threshold effect, which would be expected if pH was toxic. Indeed, there was no difference between either pH treatment and the control in *A. tenuis*, rather the difference was between the 7.6 and 7.3 pH treatments, with survivorship significantly higher in the lower pH treatment (Suwa et al. 2010; Table 1). Similarly, larval survivorship was not affected by high pCO_2 in either *A. tenuis* or *A. millepora* (Chua et al. 2013). In contrast, survivorship of *Pocillopora damicornis* larvae was 25% lower at high pCO_2 (Cumbo et al. 2013). The respiration of *A. digitifera* larvae was not affected by pH as low as 7.3 (Nakamura et al. 2011). Similarly, high pCO_2 had no effect on larval respiration in *P. damicornis* (Cumbo et al. 2013). In contrast, respiration rates of *Porites asteroides* larvae declined as pH decreased (Albright & Langdon 2011).

The effects of decreased pH on larval metamorphosis are also variable (Table 1). Albright et al. (2008) found no effect of pH on the metamorphosis of *Porites asteroides*. Similarly, metamorphosis of *Acropora digitifera* was unaffected by a 2 d exposure to pH values of 7.6 and 7.3 (Nakamura et al. 2011). However, after 7 d of larval exposure, metamorphosis was 80% lower in the reduced pH treatments (Nakamura et al. 2011). In contrast, high pCO_2 had no effect on larval metamorphosis in either *A. tenuis* or *A. millepora* (Chua et al. 2013). The effects of pH on coral larval metamorphosis may be indirect and mediated through a change in the settlement substratum (Albright et al. 2010). Metamorphosis is often reduced when settlement substratum have been conditioned in treated seawater, suggesting that low pH affects organisms, such as crustose coralline algae, that induce larval metamorphosis, or interferes with the ability of coral larvae to sense the cues provided by crustose coralline algae (Albright et al. 2010, Albright & Langdon 2011). However, even in this situation, the results are highly variable and do not always follow the response expected if pH was to have either a dose-dependent or threshold effect. For example, metamorphosis of *A. millepora* larvae was reduced by 82% on settlement substrata that had been treated at a pCO_2 of 1300 ppm for 6 wk, but there was no effect of metamorphosis on substrata treated at 800 ppm (Doropoulos et al. 2012; Table 1). Similarly, while metamorphosis was lower when either the larvae or the substrate were treated at a pCO_2 of 800 ppm, there was no effect when both larvae and substrata were treated at this pCO_2 (Doropoulos et al. 2012; Table 1). Clearly, there is an urgent need to examine the response to pH in the larvae of a greater range of coral species to see if any general patterns emerge.

In this study, we manipulated pH levels to produce seawater with a range of pH values projected to occur at various stages later this century. The effects of these levels of pH were then tested on a number of processes crucial to successful coral recruitment: (1) embryonic development, (2) larval survivorship and (3) metamorphosis.

MATERIALS AND METHODS

Collection of gravid colonies

Gametes of *Acropora tenuis* and *A. hyacinthus* were collected at Magnetic Island (19° 9′ S, 146° 50′ E) in October 2009 and gametes of *A. millepora* collected at Orpheus Island (18° 35′ S, 146° 29′ E) in November and December 2009. Adult colonies were collected a few days before the predicted spawning date, and maintained in outdoor aquaria. *A. tenuis* and *A. hyacinthus* spawned at night on 9 October and 13 October, respectively. *A. millepora* colonies spawned on 10 November and 10 December (these assays are referred to as *A. millepora* Nov and *A. millepora* Dec).

Experimental manipulation of pH

The experiments were performed in a temperature-controlled room (between 26 and 27°C) under fluorescent lights on a 12:12 h light:dark regime. A CO_2 mixing system, developed by Munday et al. (2009), was used to bubble CO_2 through seawater at 3 concentrations chosen to match the projections of

Table 2. Mean pH and total alkalinity measurements (±SE) for the 4 pCO_2 levels averaged over all the assays

pCO_2 atmosphere (ppm)	pH	Total alkalinity (µmol kg^{-1})	Temperature (°C)	Calcite saturation state	Aragonite saturation state	pCO_2 seawater (µatm)
380	8.16 ± 0.01	2028.8 ± 51	27.5 ± 0.15	4.33 ± 0.13	2.87 ± 0.08	414.2 ± 21
550	8.08 ± 0.01	2065.6 ± 95	27.6 ± 0.16	3.41 ± 0.19	2.26 ± 0.13	618.6 ± 36
750	7.96 ± 0.01	1876.7 ± 44	28.0 ± 0.13	2.71 ± 0.07	1.80 ± 0.05	669.2 ± 21
1000	7.86 ± 0.01	1867.7 ± 30	27.8 ± 0.13	2.14 ± 0.09	1.42 ± 0.06	916.9 ± 30

the Intergovernmental Panel on Climate Change (2007) over the next 80 yr. pH was measured on the National Bureau of Standards (NBS) scale with a portable meter (Hach HQ11D), calibrated daily with pH 4 and pH 7 buffers. Temperature, pH, oxygen concentration and total alkalinity were monitored daily at 11:00 h (Moya et al. 2012). Experimental calcite and aragonite saturations, as well as actual pCO2 (µatm) were calculated from average total alkalinity data (TA), salinity, temperature and pH NBS using CO2SYS with dissociation constants of Mehrbach et al. (1973), as refitted by Dickson & Millero (1987) (Pierrot et al. 2006). Average pCO_2 (seawater) for the 4 treatments was estimated to be 414, 618, 669 and 917 µatm (Table 2; Moya et al. 2012).

Effect of pH on embryonic development

Embryos were cultured following Babcock et al. (2003). Sperm and egg bundles were collected from between 4 and 6 colonies of each species on each occasion and mixed in a bucket. Once cleavage was observed, approximately 1000 embryos were placed in each of 3 replicate 3.5 l plastic jars, modified to allow 0.2 µm filtered CO_2 treated seawater to flow through at the rate of 1.5 to 2.0 l h^{-1}. At 12, 18, 24 and 36 h after the gametes were mixed, 20 embryos were removed from each jar for *Acropora tenuis* and *A. hyacinthus* and 10 embryos for *A. millepora*, and the number that had completed gastrulation was scored. To test for differences in development time among treatments, the average time for embryos to complete gastrulation was estimated following Chua et al. (2013):

Average time to reach stage, $\bar{x} = \Sigma$ [time (h) × number of propagules to reach stage]/[number of propagules to reach stage]

Effect of pH on larval survivorship

To test whether reduced pH had a direct effect on larval survivorship, 50 motile larvae (4 days old) were introduced into 3 replicate 200 ml plastic jars with mesh lids for water exchange, which were then immersed in the CO_2 enriched seawater treatments. The number of surviving larvae was counted every 24 h, at which point the enriched seawater in the jars was completely replaced. This period is sufficient for dead larvae to lyse and disappear (Baird et al. 2006). Larvae were followed for between 5 and 7 d.

Effect of pH on metamorphosis

Metamorphosis of *Acropora* larvae typically peaks between 6 and 10 d after spawning (Connolly & Baird 2010). Therefore, the ages of larvae used to test for effects of pH on larval metamorphosis were as follows: *A. hyacinthus*, 8 d old; *A. millepora* Nov, 6 d old; *A. millepora* Dec, 9 d old. From each of the 3.5 l jars, 10 larvae of *A. hyacinthus* or 20 larvae of *A. millepora* Nov *and A. millepora* Dec were taken and placed in each well of a 6-well Iwaki cell culture plate with a modified meshed lid. A 2 × 2 mm crustose coralline algae (CCA) chip (*Neogolithion* sp. for the *A. hyacinthus* assay and *Titanaderma* sp. for *A. millepora*) was also placed in each well to induce metamorphosis (following Heyward & Negri 1999) and the wells, covered by plankton mesh to retain the larvae, were immersed in the CO_2 treated seawater. The number of larvae completing metamorphosis was assessed 24 h later. Larvae were defined as metamorphosed once a basal disc had been deposited (Baird & Babcock 2000).

Data analysis

Mean differences in the time to gastrulation were tested with 1-way ANOVA: the treatment factor was pH with 4 levels that differed slightly among assays (Table 2). Mean differences in the number of larva completing metamorphosis were tested with 2-way ANOVA: the first factor was pH (fixed) with 4 levels;

the second factor, plate (random, n = 3), was nested within treatment. There were 6 replicate wells in each plate. Each species on each occasion was analyzed independently (i.e. 3 to 4 separate assays depending on the response variable) because the pH values were slightly different in each assay (Table 2). Bonferroni correction was used to adjust the probability of type I error (i.e. probability was considered significant when $p < 0.05$ per number of assays). Tukey's honestly significant difference multiple comparison tests were conducted when ANOVAs detected significant differences among the main factors. Any bias in these data was explored by residual analysis. Only the *Acropora millepora* Nov data for metamorphosis required a $\log_{10}(x + 1)$ transformation. Differences in the median survival time in days among treatments were compared using Kaplan-Meier survival analysis. All analyses were performed in SPSS version 20.

RESULTS

Effect of pH on embryonic development

The mean time to gastrulation did not vary consistently among species as a function of pH (Fig. 1). *Acropora tenuis* larvae developed more slowly at the lowest pH (Fig. 1A) ($F_{(3,225)} = 4.27$; $p = 0.006$) as did *A. millepora* Dec (Fig 1D) ($F_{(3,116)} = 3.13$; $p = 0.029$). In contrast, *A. hyacinthus* larvae developed more quickly in the 2 lowest pH treatments (Fig. 1B) ($F_{(3,225)} = 4.31$; $p = 0.006$). In the *A. millepora* Nov assay there was no significant difference in development times among the pH treatments (Fig. 1C) ($F_{(3,116)} = 2.5$; $p = 0.06$).

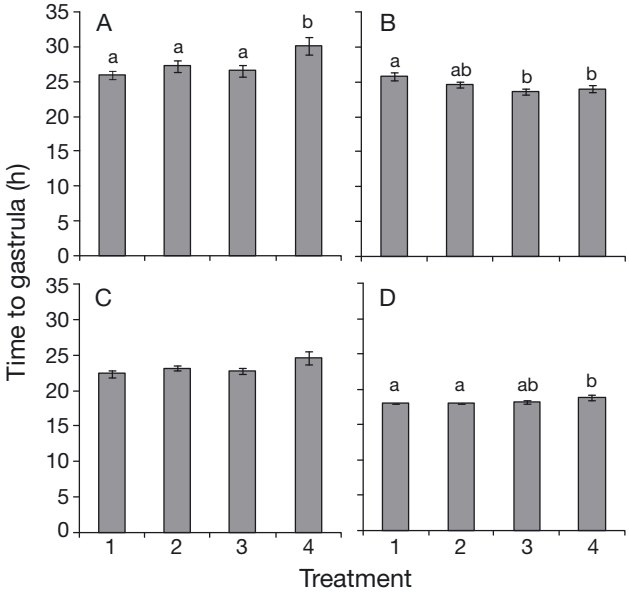

Fig. 1. Time in hours to complete gastrulation (mean ± SE) in 4 separate assays (A: *Acropora tenuis*; B: *A. hyacinthus*; C: *A. millepora* Nov; D: *A. millepora* Dec) under 4 acidity treatments (1 = pH 8.2; 2 = 8.1; 3 = 8.0; 4 = 7.9). Tukey's groups indicated by lower case letters

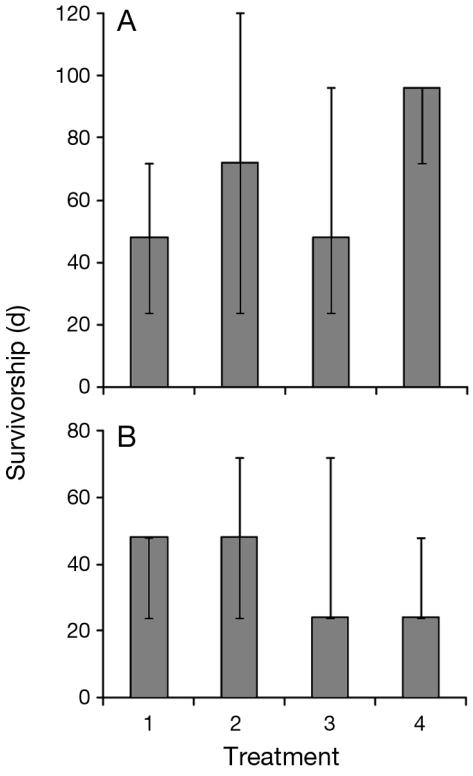

Fig. 2. Survivorship (median age in days of larvae as estimated by Kaplan-Meier analysis) in 2 assays (A: *A. tenuis;* B: *A. millepora* Nov) under 4 acidity treatments (1 = pH 8.2; 2 = 8.1; 3 = 8.0; 4 = 7.9). Error bars are the 95% confidence intervals (CI) around the median. In some cases, Kaplan-Meier analysis does not produce an upper or lower CI

Effect of pH on larval survivorship

Median survivorship did not vary significantly among pH treatments in either of the 2 species tested (Fig 2). In *Acropora tenuis*, median survivorship was highest in the lowest pH treatment; however, the 95% confidence intervals indicate that this was not significantly different to Treatment 1 (the control) (Fig 2A). In *A. millepora* Nov, median survivorship was lower in the 2 lowest pH treatments; however, there was no significant difference between these values and the control (Fig 2B).

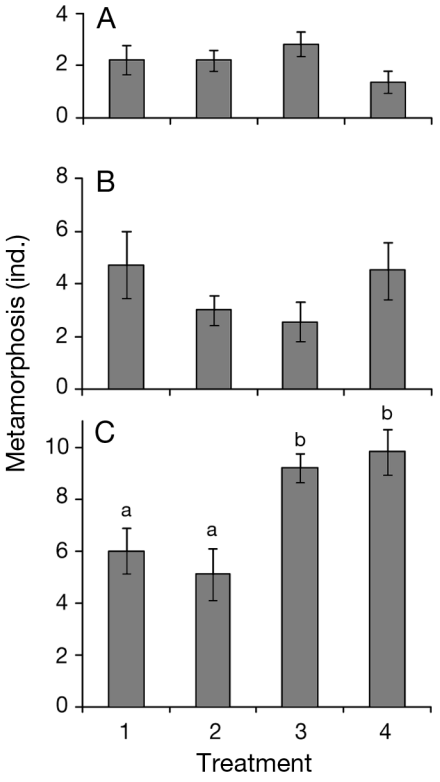

Fig. 3. Metamorphosis (mean % ±SE) in 3 separate assays (A: *Acropora hyacinthus*; B: *A. millepora* Nov; C: *A. millepora* Dec) under 4 acidity treatments (1 = pH 8.2; 2 = 8.1; 3 = 8.0; 4 = 7.9). Tukey's groups indicated by lower case letters

Effect of pH on metamorphosis

The mean number of larvae completing metamorphosis did not vary consistently among species as a function of pH (Fig. 3). The number of larvae completing metamorphosis did not differ among the pH treatments in *Acropora hyacinthus* (Fig. 3A) ($F_{(3,2)}$ = 1.54; p < 0.211) or *A. millepora* Nov (Fig. 3B) ($F_{(3,2)}$ = 0.71; p = 0.551). In contrast, the mean number of *A. millepora* Dec that completed metamorphosis was significantly higher in the 2 lowest pH treatments (Fig. 3C) ($F_{(3,2)}$ = 7.77; p < 0.001).

DISCUSSION

Simulated levels of pH projected to occur at various stages later this century did not have consistent effects on the early life history stages of *Acropora hyacinthus*, *A. millepora* or *A. tenuis*. In 4 out of 9 assays, no significant differences were apparent between the 3 pH treatments and controls (Table 3). In the 4 assays where an effect was detected, this was generally opposite to the result expected if CO_2 was toxic. For example, metamorphosis of *A. millepora* was higher in the 2 lowest pH levels and rates of development were faster in the lowest levels of pH in *A. tenuis* and *A. millepora* Dec (Table 3). In fact, only 1 of the 9 assays responded in a way that was consistent with a toxic effect of low pH (Table 3). These results indicate that projected levels of pH in the oceans will not directly threaten early life-history stages of these corals species in the near future.

Development rates of coral embryos were not consistently affected by pH. In one assay the prediction of a slower rate of development at reduced pH did occur (Table 3); however, the effect was very small, with an increase in the mean time to complete gastrulation of 2 to 4 h (approximately 15%). This difference is much less than typical differences among individual larvae within a cohort in the time taken to reach other important dispersal related stages, such as the time to become competent (Connolly & Baird 2010). These results are in contrast to the effects of pH on development rates in other organisms. For example, *Littoria obtusata* embryos at a pH of 7.6 took 1.5 d longer to hatch when compared with controls (Ellis et al. 2009). Similarly, larval development in sea urchins (Kurihara & Shirayama 2004) and oysters (Kurihara et al. 2007) is slower at reduced pH. However, both these species have a larval skeleton, so it is perhaps the absence of calcareous skeleton that makes coral larval development less likely to be affected by reduced pH.

Table 3. Summary of experimental results. 'ns' means no significant difference when compared with the control. Percentage values are the increase (+) or decrease (–) in the response variable when compared with controls

Response variable	pH		
	8.1	8.0	7.9
Time to gastrulation			
Acropora tenuis	ns	ns	+16
Acropora hyacinthus	ns	–8	–8
Acropora millepora Nov	ns	ns	ns
Acropora millepora Dec	ns	ns	+5
Larval survivorship			
Acropora tenuis	ns	ns	ns
Acropora millepora Nov	ns	ns	ns
Metamorphosis			
Acropora hyacinthus	ns	ns	ns
Acropora millepora Nov	ns	ns	ns
Acropora millepora Dec	ns	+50	+50

Rates of larval survivorship were not affected by reduced pH (Table 3). Similarly, larval survivorship did not differ between controls and reduced pH treatments for *Acropora digitifera* or *A. tenuis* larvae (Suwa et al. 2010). In contrast, in *Pocillopora damicornis*, larval survivorship was 25% lower in a high pCO_2 treatment (Cumbo et al. 2013), possibly because larvae of this species contain *Symbiodinium*, which may make larvae more susceptible to stress (Baird et al. 2009). Similarly, larval survivorship in sea urchins (Kurihara 2008) and brittle stars (Dupont et al. 2010) was lower at reduced pH. However, once again, both these species have a larval skeleton, which may predispose them to being affected by low pH.

Metamorphosis was not consistently affected by pH. Indeed, metamorphosis in *Acropora millepora* Dec was 50% higher in the 2 lowest pH treatments (Fig. 3C, Table 3). Results from the literature are similarly inconsistent. Albright et al. (2008) found no effect of pH on metamorphosis in *Porites asteroides* larvae. Similarly, rates of metamorphosis in *P. panamensis* were not affected by a 0.20 to 0.25 unit decrease in pH (Anlauf et al. 2011). In contrast, Nakamura et al. (2011) did find an effect, but only in *A. digitifera* larvae exposed for 7 d to pH levels not expected until well into the next century. While Albright et al. (2010) did record reduced metamorphosis under reduced pH treatments, they suggested the effect was indirect, i.e. through changes in the nature of the settlement substratum rather than a direct effect on the larvae, a hypothesis supported to some extent by more recent work (Albright & Langdon 2011, Doropoulos et al. 2012).

The gametes and larvae of many marine invertebrates are exposed to large daily fluctuations in environmental variables, including pH. For example, the pH in many shallow coastal areas, including coral reefs, varies markedly over very short periods. For example, in subsurface waters directly above the reef crest, pH varied by 0.2 units in 4 h (Gagliano et al. 2010). Similarly, diurnal oscillations in pH above coral colonies varied by 0.5 units (Ohde & van Woesik 1999). Indeed, naturally oscillating pH actually stimulates the growth of coral recruits (Dufault et al. 2012). The gametes of many species are equipped with constitutive defenses against low pH to deal with these environmental fluctuations (Hamdoun & Epel 2007, Byrne et al. 2009). Given these fluctuations in pH in the reef environment, it is perhaps no surprise that effects of pH are generally inconsistent and often only evident at very low levels (Tables 1 & 3).

In conclusion, it seems unlikely that projected near-future OA levels will have major direct effects on the non-calcifying early life-history stages of corals. Our results (Table 3), and previous research (Table 1), suggest that direct effects are only evident at very low pH levels (Nakamura et al. 2011), or when gametes (Albright et al. 2010) or larvae (Nakamura et al. 2011) have lost vitality. One possible source of the inconsistency in these results is the small number of adults generally used to produce the larvae for experiments: typically between 4 and 6 individuals. Sampling effects from the use of low numbers of brood stock may result in high variability in the genetic composition among different larval cultures. Parental effects on coral larval traits, such as metamorphosis and metabolism, can be large (Meyer et al. 2009). Consequently, future work should aim to incorporate parental effects into experimental designs. An alternative explanation for the inconsistency is that organisms may be able to acclimatize relatively quickly to changes in pH, particularly as large diurnal fluctuations seem to be common in the environment.

The lack of major effects on the early life-history stages of corals does not imply that OA is not a threat to stages later in life. There are strong theoretical reasons for expecting an effect on physiology (Pörtner et al. 2004); indeed, patterns of gene expression vary dramatically in coral juveniles as pH levels decrease (Moya et al. 2012). The consequences of energy expenditure on cellular acid-base regulation and lowered metabolism are unlikely to affect larval ecology in the short term. In particular, growth, reproduction and competitive ability are all likely to be affected by increases in ocean acidity over a longer time frame (Anthony et al. 2008, Fabricius et al. 2011). Finally, increased concentrations of atmospheric CO_2 are also resulting in the warming of the oceans (Hendriks et al. 2010). Consequently, marine organisms must deal with both low pH and high temperatures, and future work should explore the possible synergistic effects of these stressors on coral larval ecology.

Acknowledgements. We thank P. Munday for the original design of the CO_2 manipulation system and JCU Marine and Freshwater Aquarium research assistants for technical assistance. We thank E. Woolsey, L. Huisman, P. Cross and G. Torda for field assistance and L. Harrington for CCA identification. This project is funded by an ARC Linkage grant to W.L., an ARC Future Fellowship to A.H.B. and a Ministry of Higher Education of Malaysia PhD scholarship to C.M.C. Author contributions: A.H.B., C.M.C., B.L. and A.M. designed the study; C.M.C. and A.M. collected the data; A.H.B. and C.M.C. wrote the paper; and W.L. and A.M. edited the manuscript.

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Editorial responsibility: Peter Edmunds, Northridge, California, USA

Submitted: November 9, 2012; Accepted: February 25, 2013
Proofs received from author(s): June 18, 2013