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A corrosive concoction: The combined effects of ocean warming and acidification on the early growth of a stony coral are multiplicative

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ABSTRACT

Survival of coral planulae, and the successful settlement and healthy growth of primary polyps are critical for the dispersal of scleractinian corals and hence the recovery of degraded coral reefs. It is therefore important to explore how the warmer and more acidic oceanic conditions predicted for the future could affect these processes. This study used controlled culture to investigate the effects of a 1 °C increase in temperature and a 0.2–0.25 unit decrease in pH on the settlement and survival of planulae and the growth of primary polyps in the Tropical Eastern Pacific coral *Porites panamensis*. We found that primary polyp growth was reduced only marginally by more acidic seawater but the combined effect of high temperature and lowered pH caused a significant reduction in growth of primary polyps by almost a third. Elevated temperature was found to significantly reduce the amount of zooxanthellae in primary polyps, and when combined with lowered pH resulted in a significant reduction in biomass of primary polyps. However, survival and settlement of planula larvae were unaffected by increased temperature, lowered acidity or the combination of both. These results indicate that in future scenarios of increased temperature and oceanic acidity coral planulae will be able to disperse and settle successfully but primary polyp growth may be hampered. The recovery of reefs may therefore be impeded by global change even if local stressors are curbed and sufficient sources of planulae are available.

1. Introduction

Predictions suggest that up to 70% of the world's coral reefs may be lost within the next four decades if the current trend in the intensity and frequency of impacts caused by climate change and coastal human populations persists (Wilkinson, 1993). If stony coral species and the reefs they form do survive these mounting regional and global threats, their future success will be dependent upon sufficiently high levels of recruitment (Fan et al., 2002; Arthur et al., 2005). Even under contemporary conditions, the unsuccessful recovery of degraded reefs is principally attributable to failed recruitment (Hughes and Tanner, 2000), yet little is known about how recruitment in stony corals will be affected by the combination of increased temperatures and oceanic acidity that are predicted for the future.

Elevated sea surface temperatures (SSTs) have already caused extensive coral bleaching during El-Niño-Southern Oscillation (ENSO) events resulting in the widespread degradation of coral reef ecosystems worldwide (Glynn, 1993; Hoegh-Guldberg, 1999; Glynn et al., 2001). The strongest ENSO-event so far reported in 1997–98 caused a loss of around 16% of coral reefs on a global scale (Wilkinson, 2004) and virtually destroyed some reefs (McClanahan, 2000). The eastern Pacific region was particularly affected by the 1982–83 ENSO-event, that resulted in up to 85% mortality across the Gulf of Panama (Glynn et al., 1988), and reefs were hit again by warming during the 1998 ENSO-event (Glynn and Ault, 2000). Given the predicted rise in SSTs in the equatorial Pacific of 1.2–1.8 °C by the year 2100 (Timmermann et al., 1999), and the fact that tropical corals already live close to their upper thermal tolerance, bleaching events and coral reef degradation are likely to become more frequent in the tropics (Buddemeier et al., 2004).

Increasing concentrations of the greenhouse gas carbon dioxide (CO_2) in the atmosphere not only contribute to global warming but simultaneously cause ocean acidification and shifts in the seawater carbonate system because 25% of CO_2 is absorbed by the surface ocean forming carbonic acid (Canadell et al., 2007). Concentrations of atmospheric CO_2 naturally fluctuate between below 200 up to around 280 ppm from glacial to interglacial cycles (Fischer et al. 1999), but have risen dramatically in the last 200 years from the 280 ppm post-glacial and pre-industrial levels to modern concentrations of approximately 380 ppm (Feely et al., 2004). Ocean surface water pH has already fallen by 0.1 unit, compared to pre-industrial times, which equals a 30% increase of the H^+-concentration (Caldeira and Wickett, 2003). Models

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forecast that with increasing atmospheric CO_2, seawater pH may decrease by 0.3–0.4 units by 2100 (Haugan and Drange, 1996; Brewer, 1997; Caldeira and Wickett, 2005). Under such a scenario, experimental data suggest an alarming 11–40% decline in the calcification of reef building organisms (Gattuso et al., 1998, Langdon et al., 2000; Marubini et al., 2001; Leclercq et al., 2002; Reynaud et al., 2003).

Although both warming and acidification represent serious threats to reefs, it is their combined effect that is of greatest concern (Buddemeier et al. 2004). In adult corals, elevated temperatures can actually increase calcification rates (Clausen and Roth, 1975), probably due to the higher metabolic rates, but when combined with more acidic conditions, calcification decreases significantly (Reynaud et al., 2003). There is evidence that corals are already responding to the changing conditions: *In vivo* cores from adult *Porites* colonies reveal that calcification has reduced since 1990 by 14.2% (De'ath et al., 2009).

Although several advances have been made in understanding the individual effects of increased seawater temperature or ocean acidification on coral physiology (e.g. Dove and Hoegh-Guldberg, 2006; Schneider and Erez, 2006), the potential cumulative effects of both remain unexplored, especially on the early life-stages of coral reef builders.

Coral planulae, like adult corals, are presumed to thrive close to their upper temperature limit (Glynn, 1993; Edmunds et al., 2001), and are therefore potentially vulnerable to high SST anomalies, such as those associated with ENSO-events (Hoegh-Guldberg, 1999). Settlement and recruitment of coral planulae are known to be affected by several other abiotic factors, including the amount of visible spectra solar irradiance (Maida et al., 1994; Babcock and Mundy, 1996), UV radiation (Kuffner, 2001, Gleason et al., 2005), elevated temperatures (Coles, 1985; Edmunds et al., 2001; Putnam et al., 2008) and temperature in combination with increased levels of ammonia (Bassim and Sammarco, 2003), and high rates of sedimentation (Babcock and Davies, 1991).

Declining growth of early life stages in Caribbean corals has already been shown to correspond with increasing temperatures and reduced aragonite saturation states (Edmunds, 2007) and experimental data suggests that skeletal extension of primary polyps (the first polyp developing from metamorphosed coral larvae) may decrease by up to 78% under CO_2 concentrations that have been projected for 2100 (Albright et al., 2008).

The aim of the present study is to investigate the effects of elevated temperature and seawater acidity at levels predicted for the second half of the 21st century (Caldeira and Wickett, 2005) on the settlement of planulae and primary polyp growth of the eastern Pacific endemic brooding stony coral *Porites panamensis*.

2. Methods

2.1. Sampling of corals

Porites panamensis (Verrill, 1866) is a common coral of patch reefs occurring along the Pacific coasts of Panama, Mexico south of 9°N and the Gulf of California (Glynn and Ault, 2000), where it often builds mono-specific coral communities (Halfar et al., 2005). *P. panamensis* is a gonochoric brooder. In Eastern Pacific populations of *P. panamensis* adult colonies showed a sex-ratio of approximately 1:1, whereas mother colonies release planulae in close lunar periodicity over a period of around 11 months (Glynn et al., 1994).

In September 2004, 40 colonies of *P. panamensis* between 5 and 15 cm in diameter were collected using hammer and chisel at Taboga Island, located 16 km south of Panama City, from 3 to 6 m below mean water level during low to incoming tide. The area of collection was restricted to 50 × 50 m. Colonies were transported to the Naos Marine Laboratory of the Smithsonian Tropical Research Institute within 2 h of collection in insulated coolers half-filled with seawater and continuous aeration. Upon arrival, colonies were cleaned of burrowing and encrusting organisms and shaded from direct sunlight in two seawater flow-through 200 L aquaria. Seawater was pumped from the Naos Island pier, Bay of Panama, passed through a sand-filter and re-filtered in Stainrite polyester felt filter bags (pore size ~10 μm) before being supplied to the experimental setups and holding aquaria.

2.2. Collection of planulae

Previous work revealed that most planulae of *P. panamensis* were released between 06:00 and 08:00 h. Planulae were therefore collected each day at 09:00 h from the overflowing seawater of the holding aquaria using windowed 500 ml plastic collection-beakers (window 7 cm × 7 cm, made of 50 μm plankton mesh). Planulae were collected with a plastic pipette, counted, pooled and haphazardly assigned to the replicates of the experimental treatments. The daily rate of planulae release was insufficient to allow experimental replicates to commence concurrently. *A posteriori* analysis, using start time as a covariate, showed that staggering the replicates in this way had no significant effect on any of the experimental variables.

2.3. General experimental setup

The experimental design (Fig. 1) consisted of four treatments: (a) ambient temperature + ambient pH (Control), (b) ambient temperature + low pH (low pH), (c) high temperature + ambient pH (high T), and (d) high temperature + low pH (high T + low pH). Five beakers per treatment contained a settlement chamber and another five beakers held Petri-dishes with primary polyps, hereafter referred to as two experiments: (a) Planula settlement experiment, and (b) primary polyps experiment.

In a flow-through seawater system, filtered seawater was supplied to four reservoir-aquaria of 160 L, where seawater was heated with thermostats (VISI Therm, model VTH 300, 300 W) to 1–1.2 °C above ambient and/or pH was lowered by 0.2–0.24 units by bubbling CO_2 gas. Such a moderate increase in temperature and decrease in pH corresponds to values predicted by atmosphere–ocean scenarios for the low latitudes in the late 21st Century (Caldeira and Wickett, 2005; Orr et al., 2005; Timmermann et al., 1999).

PVC-pipes and polyethylene tubing supplied ten 0.5 L replicate-beakers per treatment (see Fig. 1). Sufficient mixing was provided by water-inflow, CO_2 and air bubbling into the reservoirs. Average water-exchange rate in replicate-beakers was 119 ml min^{-1} ($n = 60$). Water flow and CO_2 bubbling was manually controlled on a regular basis, both day and night, and these conditions were maintained throughout the experiment. The setup was shaded from direct sun by the translucent roof of the aquarium pavilion. Furthermore, the translucent plastic replicate beakers allowed light to diffuse. The irradiance levels during the experiments were not monitored, however, daily average light intensities were measured earlier from September to November 2001, being at 134.94 ± 78.95 (S.D.) micro Einstein square $meter^{-1}$ s^{-1}. The position of the replicates was rearranged randomly each week to reduce the effects of spatial heterogeneity of light.

2.4. Planula settlement experiment

Blocks of smooth surfaced limestone (4 cm × 1 cm × 1 cm) cut from a coral reef core sample were used as substratum for coral planulae to settle. The substratum was pre-conditioned in flow-through aquaria with ambient seawater for one week. Limestone substrata were visually inspected to confirm the presence crustose coralline alga (CCA) — a possible planula settlement trigger, before one block of limestone was placed in each settlement chamber. The settlement chamber was constructed from a translucent plastic tube (5 cm

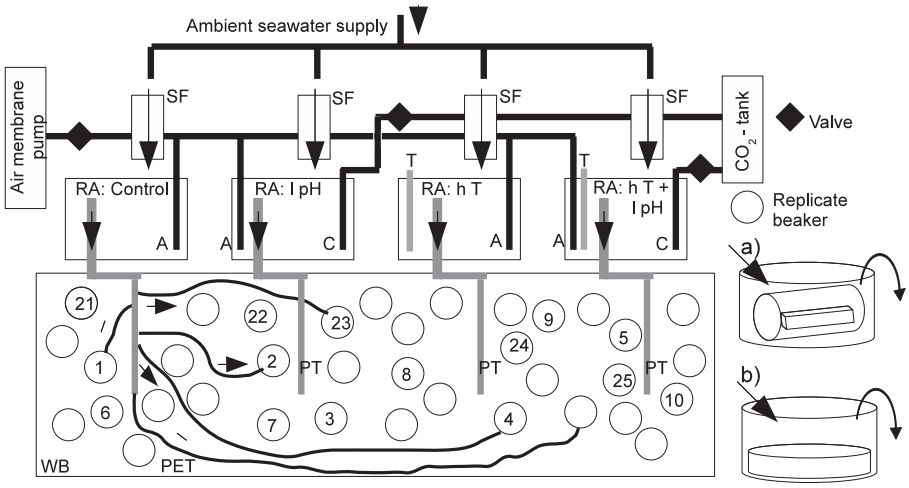

Fig. 1. Experimental setup. RA: reservoir aquarium of Control, low pH, high T, high T + low pH. SF: Strainrite Polyester filter bags, C: bubbling siphon for CO_2 or A: Air, T: thermostats, PT: PVC tubing (2.5 m with 2 cm diameter) from RA to level of WB: wet-bench on which replicate beakers for settlement and primary polyp experiments were aligned. PET: black foil wrapped polyethylene tubing (limits algae growth, 2.5 m with 2 mm inner diameter). Numbers 1 to 5 indicate replicates of the control in settlement experiment and numbers 21 to 25 indicate replicates in primary polyp experiment. Replicate beakers of all experimental treatments were similarly arranged. Waterflow into RA (160 L) was adjusted to supply 10 beakers per treatment at all times. a) Settlement chamber with block of limestone in replicate beaker and b) Petri-dish with primary polyps in replicate beaker. Arrows indicate water flow.

diameter, 7 cm long) with both ends covered by a 50 μm plankton-net mesh.

Thirty motile planulae, from the daily collection, were transferred to plastic tubes and randomly assigned to a treatment. Subsets were allowed 30 min to adjust to the treatments' temperature before application. All planulae subsets were carefully injected with a plastic pipette through a porthole in the chamber within 5 to 10 min. The porthole was then immediately sealed with plastic tape. Planulae were allowed 10 days to settle.

After the incubation period, planulae were sorted according to the following categories: (i) settled planulae (settled planulae that had developed living primary polyps) on available substrata, (ii) swimming planulae, (iii) settled and metamorphosed planulae, secreting a small corallite structure, but not alive (hereafter referred to as post settlement mortality; or p.s.m.) and, (iv) dead (i.e., planulae not found plus observed dead planulae).

2.5. Primary polyps experiment

Under laboratory conditions, 40 newly-released planulae were randomly transferred to Petri-dishes pre-conditioned in an aquarium with continuously flowing filtered seawater for one week. Planulae were given 4 days to settle after which remaining swimming planulae were removed. Planulae settled individually and in aggregations of numerous fused primary polyps (hereafter referred to as 'spat'). Each Petri-Dish containing between 6 and 32 developed primary polyps was placed at the bottom of a 500 ml replicate-beaker under continuous flow of experimental treatment water and incubated for 42 days. Every 14 days, Petri-dishes were inspected for dead or bleached polyps under a dissection microscope. After 42 days, the survival of primary polyps was counted and a digital photograph of each polyp captured.

The different numbers of primary polyps and spats developing on Petri Dishes meant that the number of samples varied amongst replicates. However, half of the primary polyps per Petri-Dish were allocated to quantify (i) biomass (the burned fractions of lipids and non-lipids and ash-free dry weight), dry weight, skeletal mass (skeleton + ash weight) and (ii) the number of zooxanthellae per polyp. Prior to these determinations, primary polyps were rinsed with a few drops of fresh water to remove the salt-water. The primary polyps were then picked from the Petri-Dish and positioned on pre-heated 0.5 cm high-quality aluminum troughs. Drying was conducted at 110 °C for 12 h when constant weight was achieved and muffled at 500 °C for 2 h to determine the skeletal mass, following methodology of Holme and McIntyre (1984). After drying and muffling, each primary polyp was weighed to an accuracy ± 1 μg and biomass determined. Ideally the skeletal mass was the desired variable to measure calcium carbonate accumulation, but due to a malfunction in a muffling furnace a number of samples were lost and dry weight received higher consideration.

For the zooxanthella counts, primary polyps and spats were picked from the Petri-Dish and homogenized with a glass tissue grinder in 1 ml deionized water. This homogenate was transferred into an Eppendorf-tube (1.5 ml) and centrifuged at 2500 rpm for 10 min. The zooxanthella pellet was re-suspended in 50 μl deionized water and three aliquots per sample were counted in a Neubauer Chamber (haemocytometer). Zooxanthellae on the entire chamber surface (9 mm^2) were counted.

2.6. Monitoring

Water temperature, salinity (YSI Model 85) and pH (Thermo Orion 410A pH) were measured in five randomly chosen replicate-beakers per treatment (from both the settlement and primary polyp experiment) three times per day (09:00, 13:00, and 17:00) to ensure stable treatment conditions. The pH meter was 2-point calibrated with standard NBS-buffer in advance of each monitoring session.

Water samples were taken every third day from each reservoir to determine phosphate, silicate, and total alkalinity. Phosphate and silicate concentrations were quantified by photometric standard methodology and total alkalinity was analyzed by titration (Grasshoff and Kremling, 1998). The parameters of the carbonate system were calculated with the program CO2SYS (Lewis and Wallace, 1998), using the Peng choice (Mehrbach et al., 1973; Peng et al., 1987; Dickson, 1990; Lewis and Wallace, 1998).

2.7. Statistical analyses

Results of planula settlement were presented in percent and arcsine-transformed prior to analysis (Sokal and Rohlf, 1995). Unbalanced one-way and 2-way multivariate ANCOVA designs, with the covariate start time, were applied to test for the effect of

temperature, pH, and their interaction on settlement and post settlement mortality of planulae. Data not meeting MANCOVA model specifications were tested with Kruskal-Wallis ANOVA for effects of treatments.

Data sets from the primary polyp experiment were normalized per polyp and transformed using log or square root functions to achieve normal probability. Responses of primary polyps to the main effects of temperature, pH, and their interaction were tested on the assessed variables using unbalanced 2-way ANCOVA, and if not significant, one-way ANCOVA general linear models, with the covariate start time. The Tukey–Honest Significance Difference test (HSD) was conducted post-hoc to significant one-way ANCOVAs in order to resolve differences between treatments. The suitability of the ANCOVA model specification was verified by testing homogeneity of slopes, normal probability graphically and with Shapiro–Wilk W test in the data and the residuals. Because of different sample sizes across replicates, homogeneity of variance was confirmed after Brown and Forsythe (1974) for all data. Descriptive statistics in the text are reported as means and standard error (±SE). The significance level was $p<0.05$.

3. Results

3.1. Experimental condition

Average treatment conditions and calculated carbonate system parameters are presented in Table 1. Seawater temperature in the control and in the elevated temperature treatments were influenced by natural and diurnal fluctuations in the water pumped from the Bay of Panama, namely rainfall, runoff, and cloud cover. The 1 °C difference between control and high T-treatments remained stable throughout the experiment except in 15 October 2004 when ambient seawater temperature rose 1–2°C above normal to 30.6 °C for approximately 12 h. During this ambient seawater temperature peak, the high T-treatments showed only a difference of 0.4 °C in comparison to the control.

3.2. Settlement of planulae

Settlement and survival of planulae were unaffected by elevated temperatures nor the reduced pH conditions (two-way ANCOVA; $p>0.05$, Table 2). More details of the settlement results are presented in Fig. 2.

3.3. Development of primary polyps

A total of 340 primary polyps of *Porites panamensis* were successfully reared on Petri-Dishes from planulae for all treatments. Polyp survival was high, reaching 100% in the control and low pH-treatment. In the high temperature + low pH and high temperature-treatment survival of primary polyps was 96% (±3) and 90% (±2), respectively. Polyp budding was observed in four colonies in the control treatment and in one colony in the high temperature-treatment.

Table 2
Two- and one-way multivariate Analysis of Covariance (MANCOVA) of settlement data, using "start" as a covariate. ns = non significant.

MANCOVA (settled planulae, post settlement mortality)				
	df	Wilk's	F-value	*p*-value
Source – 2-way				
Start	2,13	0.925	0.530	0.601 ns
l pH	2,13	0.897	0.746	0.494 ns
h °T	2,13	0.980	0.134	0.875 ns
l pH*h °T	2,13	0.885	0.846	0.452 ns
Source – One-way				
Start	2,13	0.908	0.698	0.516 ns
Treatment	2,13	0.729	0.743	0.620 ns
Kruskal–Wallis ANOVA (treatment)				
	df		H	*p*-value
Dead planulae	3		2.50	0.475 ns
Swimming planulae	3		0.44	0.931 ns

Elevated temperature significantly reduced the number of zooxanthellae in primary polyps (two-way-ANCOVA; $p<0.05$; Table 3). Primary polyps showed only half of the zooxanthellae numbers in the elevated temperature compared to the ambient control (Fig. 3A).

Biomass was significantly affected by the treatments (one-way ANCOVA of biomass polyp^{-1}; $p<0.05$). Compared to the control, biomass was significantly reduced in the high temperature + low pH treatment (Tukey HSD; $p<0.01$; Fig. 3B, Table 3).

Calcification in primary polyps was significantly reduced by low pH and the combination of high temperature and low pH (two-way ANCOVA of dry weight polyp^{-1}; $p<0.01$ and $p<0.01$, respectively; Table 3). This response is corroborated by skeletal mass data (Fig. 3C, Table 3). Skeletal mass and dry-weights dropped by 28% in the high temperature + low pH treatment and by roughly 3% in the low pH treatment. In contrast, polyps exposed to just the high temperatures gained a 9% increase in average skeletal mass and a 20% increase in mean dry weight relative to those in the control group (Fig. 3C).

4. Discussion

4.1. Settlement success

Neither planulae mortality nor settlement success were affected by the increased temperatures or decreased acidities of the experimental conditions despite evidence that higher temperatures can shorten the time of planula metamorphosis (Coles 1985; Edmunds 2004) and increase planula mortality (Edmunds et al., 2001). Likewise, Albright et al. (2008) and Jokiel et al. (2008) observed no significant effect on planula settlement success in reduced aragonite saturation conditions. Given the limited experimental data of the

Table 1
Experimental conditions during the *Porites panamensis* planula settlement and primary polyp growth experiments. *** = $p<0.001$, significant multiple Kruskal–Wallis–ANOVA comparison of treatments against control, ns = non-significant.

	Planula settlement experiment (10 days, Oct.–Nov.'04, $n=23$)				Primary polyp experiment (42 days, Sept.–Nov.'04, $n=119$)			
	Control	l pH	h T	l pH + h T	Control	l pH	h T	l pH + h T
T [°C]	28.4	28.4 ns	29.6***	29.5***	28.9	28.9 ns	29.9***	29.9***
Range T [°C]	27.3–29.2	27.3–29.2	28.5–30.2	28.2–30.2	27.3–30.6	27.3–30.6	28.5–31.1	28.5–31.1
pH_{NBS}	8.08	7.85***	8.07 ns	7.83***	8.03	7.83***	8.04 ns	7.81***
Range pH_{NBS}	8.03–8.19	7.77–7.92	8.02–8.17	7.77–7.91	7.87–8.19	7.68–7.93	7.87–8.17	7.64–7.91
pCO_2	487 ± 42	861 ± 93	493 ± 47	950 ± 94	546 ± 83	926 ± 120	540 ± 85	1006 ± 140
Ω_{arag}	2.17 ± 0.28	1.36 ± 0.14	2.14 ± 0.17	1.35 ± 0.11	2.±0.25	1.35 ± 0.18	2.06 ± 0.24	1.34 ± 0.15
Total alkalinity [μmol*kg SW^{-1}]	1798 ± 76	1764 ± 57	1762 ± 52	1801 ± 78	1792 ± 76	1791 ± 73	1774 ± 80	1827 ± 65

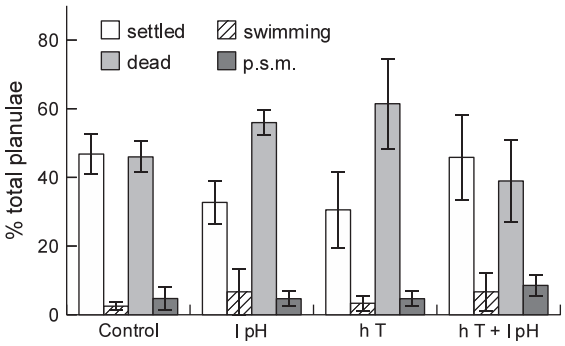

Fig. 2. Results of *P. panamensis* planula settlement experiment after 10 days at ambient conditions (control), low pH (l pH), elevated temperature (h T), and the combination of both (l pH + h T), showing percent planulae settled, swimming, dead and those found dead after settlement — post settlement mortality (p.s.m.). Means ± SE shown; replicates of settlement chambers per treatment was 5, except in the high T + low pH-treatment with only 4 replicates.

effects of climate change on the survival of coral planulae and indications that planulae can attach to substrata even in highly acidified seawater (Edmondson, 1946), brooded planulae may therefore be resilient to the acidic oceans predicted for the future. However, how ocean acidification and sea warming might affect survival, settlement and the inoculation with zooxanthellae of planulae from broadcast spawning coral remains an important field of future research.

4.2. Development of primary polyps

Juvenile corals may be more susceptible to elevated temperatures than adults (Edmunds, 2004), and although higher temperatures did not significantly increase mortality in *P. panamensis*, a loss of zooxanthellae in the primary polyps was common when exposed to just a one degree rise in temperature. Seasonal fluctuations in temperature are also known to reduce the number of zooxanthellae in the coral tissue (Fitt et al., 2000). Moreover, corals like *P. panamensis* that live in upwelling environments such as the Bay of Panama could be more sensitive to elevated temperatures because the mean annual temperature they experience is lower than those from non-upwelling environments and the host and zooxanthellae may have limited genetic diversity (Hueerkamp et al., 2001; D'Croz and Maté, 2004). Accordingly, the thermal bleaching threshold for primary polyps might be below that reported (30–31 °C) for most adult coral species in the eastern Pacific (Glynn and D'Croz, 1990; Glynn and Colgan, 1992; Podestá and Glynn, 1997; D'Croz et al., 2001; Hueerkamp et al., 2001).

Low pH by itself was not found to act as a bleaching agent corroborating data by Anthony et al. (2008). In fact, high temperature + low pH resulted in greater zooxanthellae numbers compared to the high temperature only treatment. Likewise, Reynaud et al. (2003) found that zooxanthellae densities in adult *Stylophora pistillata* increased with exposure to elevated pCO_2 under low irradiance levels, a response that could be related to the reported higher availability of nutrients to zooxanthellae when pH is lowered (Fitt et al., 1995).

Table 3
Statistical results (two- and one-way ANCOVA) of *Porites panamensis* primary polyp growth variables "start" as covariate. ANCOVA assumption of homogeneity of slopes among groups is given next to each variable. ([a]square root and [b]log-transformed data). * = $p<0.05$, ** = $p<0.01$, ns = non significant effect.

Variable	Source two-way	df	MS	F	*p*-value
Zoox. polyp^{-1}[a]	Start	1, 54	124.7	0.37	0.548 ns
($F_{1,56}=0.67$, $p=0.416$)	l pH	1, 54	281.7	0.83	0.367 ns
	h T	1, 54	1559.7	4.58	0.037*
	l pH × h T	1, 54	735.2	2.16	0.146 ns
Biomass polyp^{-1}[a]	Start	1, 54	0.166	0.17	0.681 ns
($F_{1,57}=0.01$, $p=0.921$)	l pH	1, 54	2.878	2.96	0.091 ns
	h T	1, 54	3.469	3.56	0.064 ns
	l pH × h T	1, 54	0.045	0.05	0.831 ns
	Source one-way				
	Start	1, 54	0.166	0.17	0.681 ns
	Treatment	3, 54	3.791	3.89	0.014*
	Source two-way				
Skeletal mass[b]	Start	1, 53	0.014	0.37	0.545 ns
($F_{1,56}=1.88$, $p=0.176$)	l pH	1, 53	0.218	5.59	0.022*
	h T	1, 53	0.023	0.59	0.447 ns
	l pH × h T	1, 53	0.159	4.09	0.048*
	Source two-way				
Dryweight	Start	1, 97	31	0.02	0.881 ns
($F_{1,101}=0.10$, $p=0.747$)	l pH	1, 97	14,487	10.58	0.002**
	h T	1, 97	193	0.14	0.708 ns
	l pH × h T	1, 97	10,616	7.76	0.006**

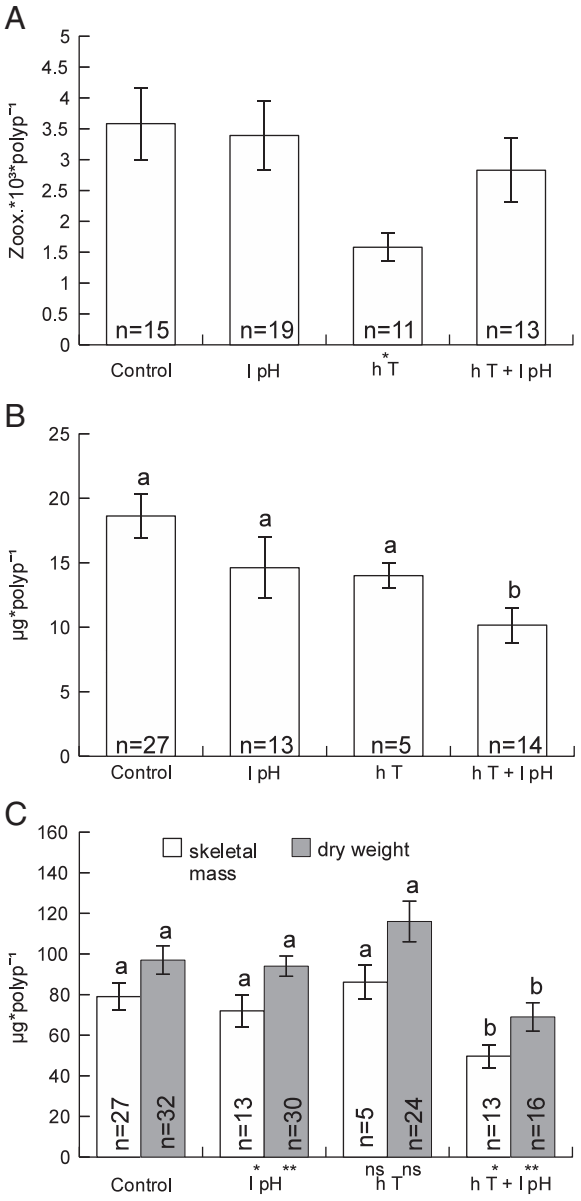

Fig. 3. Results of *Porites panamensis* primary polyp experiment after 42 days at ambient conditions (control), low pH, elevated temperature, and the interacting term; A) zooxanthellae per polyp; B) biomass; C) skeletal mass and dry weight; Error bars = ± SE shown; *$p<0.5$, **$p<0.01$ show significant effect of single treatment factors or the combination by 2-way ANCOVA; ns = non-significant; same letters show of non significant difference (Tukey HSD-test); *n* = number of samples per 5 replicates in each treatment.

Significantly reduced primary polyp biomass under combined higher temperature and reduced pH suggests that polyps insufficiently fix carbon under such conditions, even though zooxanthella numbers did not decline as much as in the higher temperature but normal pH-treatment. Polyp biomass in adult corals has been suggested to track seasonal fluctuations in temperature, falling under higher temperatures due to the associated increase in metabolic rate (Fitt et al., 2000). However, net productivity was observed to decrease in adult corals under higher temperatures and elevated pCO_2 by both Crawley et al. (2010) and Anthony et al. (2008). The cumulative increase in metabolism of primary polyps in the high temperature and low pH could be associated with the additional energy required to drive proton pumps to maintain sufficient pH-levels in the calcifying space (Cohen et al., 2009) or alternatively, an inefficiency of photosynthesis (Buxton et al., 2009) and more severe photorespiration compared to low pH and subsaturated light conditions (Crawley et al., 2010). A speculative conclusion is that combined high temperatures and low pHs reduce biomass because of the reduction of phosphoglycolate phosphatase and resulting increase in the inhibition of carbon fixation via phosphoglycolate in the Calvin cycle (*c.f.* Crawley et al., 2010). Further work is clearly required to elucidate the underlying mechanisms, but reduced biomass in primary polyps could possibly reflect the alteration of the assimilation of carbon and higher energy demands when both temperature and CO_2 are elevated.

4.3. Calcification in primary polyps

The water of the Bay of Panama is naturally of a lower pH compared to the open ocean because seasonal upwelling brings CO_2 enriched deep water to the surface (Manzello et al., 2008; D'Croz and O'Dea, 2007). Thus, the only 3% reduction in calcification observed in the low pH-treatment (Fig. 3C) could indicate that the primary polyps of *P. panamensis* from the Bay of Panama posses an inherent tolerance to reduced pH. In order to clarify this hypothesis, calcification in genetically-distinct corals from non-upwelling environments could be assessed, as was done with respect to differential responses to temperature (D'Croz and Maté, 2004).

Naturally reduced pH conditions in the Bay of Panama are never coupled with an increase in seawater temperature because the CO_2 enriched water originates from below the thermocline. This may help explain the striking ~30% decline in calcification when low pH was combined with elevated temperature (Fig. 3C). Nonetheless, these results mirror data obtained from adult corals. Under elevated pCO_2 *Stylophora pistillata* showed normal growth rates (Gattuso et al., 1998), but under a combination of increased pCO_2 and elevated temperatures it showed a reduction in calcification of 50% (Reynaud et al., 2003). Similarly, adult *Acropora intermedia* revealed a reduction in calcification when exposed to both increased seawater acidification (pH 7.6–7.7) and elevated temperature (Anthony et al. 2008).

On the other hand, the growth-rate of juvenile *P. astreoides* decreased between 45 and 56% when pH was lowered by just 0.07 units without invoking increasing temperatures (Albright et al., 2008). Likewise, Cohen et al. (2009) reported reduced skeletal growth of the cross-sectional area in newly-reared primary polyps of *Favia fragum* under lowered aragonite saturation and calculated a nearly 80% decrease in the precipitated aragonite. These strong reductions of calcification without invoking increasing temperature, in contrast to our findings, can be explained by the exposure of planulae to lowered seawater aragonite saturation states during settlement and secretion of the primary corallite (Cohen et al. 2009). This suggests that the planulae may be highly susceptible to the effects of seawater acidification during the period of early calcification in metamorphosis. We suggest that the decline in calcification rates found by Cohen et al. 2009 and Albright et al. 2008 were greater compared to our experiment because our treatment exposures did not cover the initial calcification period.

Calcification in corals is known to be enhanced with increasing temperatures (Clausen and Roth, 1975; Reynaud-Vaganay et al., 1999; Lough and Barnes, 2000; Bessat and Buigues, 2001) up to an optimum temperature of ~27 °C (Clausen and Roth, 1975; Marshall and Clode, 2004; Cooper et al., 2008). Over 27 °C calcification rates tend to decrease (Cooper et al., 2008; Tanzil et al., 2009), but dry-weight data that reveal increased calcification at higher temperatures in the primary polyps of *P. panamensis* (Fig. 3C) suggest that this may not be the case in all corals.

4.4. Implications for the future of reefs

Reflecting on the results of our experimental data may help make predictions about how *P. panamensis* will respond to the warmer and more acidic conditions that are predicted for the future of tropical oceans for the latter half of this century. Our data suggest that the survival and successful settlement of planulae will not be appreciably reduced, and primary polyps will be able to develop and survive remarkably well under the low pH-values that are predicted. However, growth rate and biomass of polyps will be severely adversely affected, especially when acidification is combined with increased mean water temperatures. Inhibited growth in early life stages will have important consequences for the ability of corals to survive, compete and reproduce.

Repeating this study on a wide range of common and rare taxa is required to make reliable predictions about the future of entire coral communities and reefs in general. However, if the profoundly impeded development of early colony growth observed here is widespread amongst reef building taxa, it is likely to have very serious implications for the restoration of reefs if other stressors are not curbed. For example, reduced fitness in corals like *P. panamensis* could make the benthic community structure of reefs more susceptible to competition from macroalgae whose growth is, somewhat paradoxically, predicted to accelerate in a high CO_2 world (Pittcock, 1999).

More optimistically, the resilience of planulae to predicted climatic conditions suggests that healthy coral reefs should be able to regenerate naturally after catastrophic events (such as ENSO induced coral bleaching), if source populations can provide planulae in sufficient quantity and local stressors such as over-fishing, pollution and habitat destruction are controlled. This should be the case even in reefs that are exceptionally discontinuous, such as those across the Tropical Eastern Pacific.

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