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REPORT

Coral growth with thermal stress and ocean acidification: lessons from the eastern tropical Pacific

D. P. Manzello

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Abstract The rapid growth of scleractinian corals is responsible for the persistence of coral reefs through time. Coral growth rates have declined over the past 30 years in the western Pacific, Indian, and North Atlantic Oceans. The spatial scale of this decline has led researchers to suggest that a global phenomenon like ocean acidification may be responsible. A multi-species inventory of coral growth from Pacific Panamá confirms that declines have occurred in some, but not all species. Linear extension declined significantly in the most important reef builder of the eastern tropical Pacific, *Pocillopora damicornis*, by nearly one-third from 1974 to 2006. The rate of decline in skeletal extension for *P. damicornis* from Pacific Panamá (0.9% year^{-1}) was nearly identical to massive *Porites* in the Indo-Pacific over the past 20–30 years (0.89–1.23% year^{-1}). The branching pocilloporid corals have shown an increased tolerance to recurrent thermal stress events in Panamá, but appear to be susceptible to acidification. In contrast, the massive pavonid corals have shown less tolerance to thermal stress, but may be less sensitive to acidification. These differing sensitivities will be a fundamental determinant of eastern tropical Pacific coral reef community structure with accelerating climate change that has implications for the future of reef communities worldwide.

Keywords Calcification · Ocean acidification · Climate change · Eastern tropical Pacific · Panamá

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D. P. Manzello (✉)
UM/CIMAS, NOAA/AOML/OCD, 4301 Rickenbacker Cswy.,
Miami, FL 33149, USA
e-mail: Derek.Manzello@noaa.gov

Introduction

Processes of construction and destruction are often closely balanced on coral reefs (Glynn 1997). Any disturbance that impairs coral growth can potentially push coral reefs into a state of degradation. Coral mortality events illustrate an endpoint of the dynamics between reef construction and destruction, as they are usually followed by a decline in topographic complexity and can even result in the loss of framework structures (Alvarez-Filip et al. 2009; Manzello 2009).

Ocean acidification is the progressive decline in seawater pH due to the oceanic uptake of anthropogenic CO_2 (Kleypas et al. 1999). Acidification results in a decrease in the concentration of the carbonate ion in seawater $[CO_3^{2-}]$ and, consequently, a decrease in the saturation state (Ω) of carbonate minerals ($\Omega = [CO_3^{2-}][Ca^{2+}]/K'_{sp}$, where K'_{sp} is the solubility product for a carbonate mineral). Rising seawater acidity is expected to elicit reductions in coral calcification, thus threatening the foundation of coral reef ecosystems (Kleypas et al. 1999).

Coral growth rates (skeletal extension, density, and calcification) were measured in six species over 2 years (2003–2004, 2005–2006) from the Uva Reef in the Gulf of Chiriquí of Pacific Panamá. This site is far removed from human impacts that could influence coral growth (Glynn and Maté 1997) and historical, multi-species records of growth rates and zooxanthellae diversity from these coral populations provide a robust context for not only detecting, but more importantly, understanding any recent change (Glynn et al. 2001).

Materials and methods

Linear extension was measured using the Alizarin staining technique (Lamberts 1978). The species measured in the growth inventory were chosen based on their abundance and ecological importance (Glynn and Maté 1997), and included *Pocillopora damicornis*, *Pocillopora elegans*, *Pavona clavus*, *Pavona gigantea*, *Pavona varians*, and *Gardineroseris planulata*. Corals were secured by affixing colonies with cable ties to rebar hammered into the reef at a depth of 2–3 m below mean low tide to match previous investigations. Sea temperature was measured every 30 min for the duration of the coral deployments with HOBO temperature loggers (Onset Corp.) affixed to the reef.

After 1 year (March 8, 2003 to March 6, 2004, March 14, 2005 to March 14, 2006), stained corals were collected and all tissue, epibionts, and infaunal organisms were removed via bleaching in non-aerated buckets. Massive corals were sliced perpendicular to the growth axis using a diamond blade rotary saw, and extension was measured with a hand-held ruler to the nearest millimeter. For *P. damicornis* and *P. elegans*, each individual branch tip was sliced adjacent to the top of the stain line and extension was measured for each branch with calipers.

Bulk skeletal density was determined using Archimedes principle and was compiled from Bucher et al. (1998) and Smith et al. (2007). For coral species with a massive morphology, samples were cut from below the alizarin stain line (Smith et al. 2007) and any areas of infaunal bioerosion were avoided (e.g., *Lithophaga* spp. boreholes). For *Pocillopora* spp., samples were excised proximal, but above the stain line to represent new growth since staining. The motivation was to assess the amount of new calcium carbonate produced on a branch-by-branch basis for each pocilloporid colony. This was a conservative estimate of growth as it did not take into account the thickening and widening of the colony below the stain line.

All subsamples for density measurements were soaked in a solution of sodium hypochlorite for 24 h or until all organic material was removed. Samples were then baked for 24 h at 60°C, cooled, and then a dry weight was taken (DW_{clean}). Corals were then dipped in molten paraffin wax maintained at ~110 to 115°C (Smith et al. 2007). Once the samples cooled, a dry weight with wax was obtained (DW_{wax}), immediately followed by the measurement of a buoyant weight (BW_{wax}). Buoyant weight refers to the weight of an object suspended in H_2O at 20°C. Bulk density was determined by the following equations: Bulk Density $= DW_{clean}/V_{enclosed}$, where $V_{enclosed} = [DW_{wax} - BW_{wax}] \times [1.00\ \mathrm{g\ cm^{-3}}]$. Calcification, the product of linear extension and skeletal density (Lough and Barnes 2000), was determined on a branch-by-branch basis for the pocilloporidae. One value of linear extension was obtained for each massive and encrusting colony (Electronic Supplemental Material, ESM Table S1), which was then multiplied by each individual density subsample from the same colony to obtain an estimate of calcification per colony and subsample (ESM Table S2).

The annual growth rates determined herein (2003–2004, 2005–2006) were compared to published values from the same reef to determine if any changes had occurred over the past 30 years. The percent change in growth (Table 1) were calculated by comparing recent mean values (ESM Tables S1 and S2) with those reported in the primary literature prior to 2003 (Tables 2 and 3).

Results

Linear extension declined significantly in the most important reef builder of the eastern tropical Pacific, *Pocillopora damicornis* (Cortés 1997; Glynn and Maté 1997), by nearly

Table 1 Species-specific long-term trends in coral growth from Panamá

Species	% Change in density	% Change in extension	% Change in calcification
Pocillopora damicornis	?	−14.0% (−0.87% year^{-1}): 1974–1990	
		−26.9% (−0.90% year^{-1}): 1974–2004	Likely
		−28.8% (−0.90% year^{-1}): 1974–2006	
Pocillopora elegans	?	Likely equal to *Poc. damicornis*	Likely equal to *Poc. damicornis*
Pavona clavus	−10.3%: 1979–2004	+30.1%: 1979–2004	+16.2%: 1979–2004
	−9.1%: 1979–2006	−15.1%: 1979–2006	−23.7%: 1979–2006
	Avg. = −9.1% since 1979	Avg. = + 5.4% since 1979	Avg. = −5.2% since 1979
Pavona gigantea	?	+24.4%: 1979–2004	
		−16.7%: 1979–2006	
		Avg. = + 2.2% since 1979	?
Gardineroseris planulata	?	−53.8%: 1983–2006	?
Pavona varians	?	?	?

Table 2 Comparison of linear extension measured in *Pocillopora* across the eastern tropical Pacific

Species	Location	*N*	*n*	Date range of skeletal deposition	Depth (m)	Extension (cm year^{-1}) Mean of all branches per colony	References
Pocillopora damicornis	Secas Is. (non-upwelling), Panamá	16	160	1972–1974	3.3–4.6	3.86 (3.39–4.33)	Glynn (1977)
	Caño Is. (non-upwelling), Costa Rica	11	?	1985–1987	2–3	3.46 (2.13–4.37)	Guzman and Cortés (1989)
	Uva Reef (non-upwelling), Panamá	?	122	1989–1990	2–3	3.32 (3.17–3.47)	Eakin (1996)
	Uva Reef (non-upwelling), Panamá	18	228	2003–2006	2–3	2.78 (2.40–3.30)	This study
	Saboga Reef (upwelling), Panamá	26	260	1971–1974	3.2	3.08 (2.55–3.61)	Glynn (1977)
	Onslow Is. (upwelling), Galápagos	12	?	1975	1–4	2.24	Glynn et al. (1979)
	Golfo de Papagayo (upwelling), Costa Rica	?	60	1991–1992, 1996–1997	3–5	4.78 (2.8–7.56)	Jiménez and Cortés (2003)
Pocillopora elegans	Caño Is. (non-upwelling), Costa Rica	10	?	1985–1987	2–3	3.48 (2.45–3.86)	Guzman and Cortés (1989)
	Uva Reef (non-upwelling), Panamá	15	168	2003–2006	2–3	2.74 (2.44–3.11)	This study
	Onslow Is. (upwelling), Galápagos	12	?	1975	1–4	2.24	Glynn et al. (1979)
	Golfo de Papagayo (upwelling), Costa Rica	?	91	1991–1992, 1996–1997	3–5	4.45 (2.9–6.72)	Jiménez and Cortés (2003)

N is the number of colonies, whereas *n* is the number of individual branch tips measured. For data from Panamá, 95% confidence limits are in parentheses, whereas for data from Costa Rica, the range of values is in parentheses

one-third from 1974 to 2006 ($R^2 = 0.999$, $P < 0.001$), which corresponds to an average decline of 0.35 mm year^{-1}, or 0.9% year^{-1} (Fig. 1a, Table 1). When data for *P. damicornis* obtained in 1987 from a similar environment and depth in Costa Rica are included (Guzman and Cortés 1989), the regression line of extension with time does not change (ANCOVA: $F_{1,5} = 0.007$, $P > 0.7$), predicting zero extension around the year 2085 ($R^2 = 0.998$, $P < 0.001$, Fig. 1b). This suggests that a large-scale factor is depressing the extension rates of this species in the eastern tropical Pacific. The extension rates of *P. elegans* were roughly equal to *P. damicornis* in studies from Panamá and Costa Rica (Table 2), making it probable that this congener has experienced a similar decline in growth rate regionally.

The extension rates of the massive pavonid species showed little or no change over 27 years (Table 1). Density and calcification of *Pavona clavus* averaged over both years were 9 and 5% lower, respectively, than 1979 (Wellington and Glynn 1983), but it is unknown if any changes occurred in *P. gigantea* (Table 1). Extension in *G. planulata* was 54% lower than 1983, but this was not significant because of the small sample size of the earlier study (Table 3). Extension was lower in this study for *P. varians* than previously reported (Table 3), but it is unknown if any changes occurred in Panamá.

Despite these opposing trends, extension and calcification of the two *Pocillopora* species were still more than twice that of the four other species. *P. damicornis* had a higher calcification rate than *P. elegans* despite similar extension rates because it secreted a significantly denser skeleton (Mann–Whitney *U*-tests, $P < 0.0001$). Bulk skeletal density, linear extension, and calcification varied significantly between species of coral for both years (Kruskal–Wallis tests, $P < 0.0001$ for density, extension, and calcification) (Fig. 2).

Values of density, extension, and calcification for *P. clavus* and *P. gigantea* were less than the two *Pocillopora* species. (Fig. 2, ESM Tables S1 and S2). The encrusting coral, *Pavona varians*, had a density comparable to the pocilloporids, but extension and calcification were the lowest of all species. Calcification and extension rates for *G. planulata* were only slightly greater than *P. varians,* while density was similar to *P. clavus*.

Mean density was inversely related to mean extension in all species except *P. varians*, but this relationship was only significant for *P. damicornis* in the latter time period ($R^2 = 0.61$, $P < 0.01$, $n = 13$) or when both years were pooled ($R^2 = 0.42$, $P < 0.01$, $n = 18$). The density of individual branch tips of *P. damicornis* was negatively related to their extension, albeit not strongly, for both time

Table 3 Mean skeletal density, annual extension, and calcification rate for *Pavona clavus, Pavona gigantea, Pavona varians*, and *Gardineroseris planulata* across the eastern tropical Pacific

Species	Location	*N*	Date range of skeletal deposition	Depth (m)	Density (g cm^{-3})	Extension (cm $year^{-1}$)	Calcification (g cm^{-2} $year^{-1}$)	References
Pavona clavus	*Non-upwelling*							
	Panamá (Uva Reef)	13	2003–2006	2–3	1.69 (1.44–1.85)	0.98 (0.2–1.7)	1.64 (0.34–2.69)	This study
	Panamá (Uva Reef)	7	1975–1979	5–7	1.86	0.93	1.73	Wellington and Glynn (1983)
	Costa Rica	12	1985–1987	2–3	?	0.96 (0.54–1.34)	?	Guzman and Cortés (1989)
	Upwelling							
	Panamá (Contadora Reef)	5	2003–2004	1	?	1.25	?	Matthews et al. (2008)
	Panamá (Contadora Reef)	5	2003–2004	7	?	1.47	?	Matthews et al. (2008)
	Panamá (Saboga Reef)	7	1975–1979	5–7	1.44	1.32	1.90	Wellington and Glynn (1983)
	Costa Rica	58	1986–1997	3–5	?	1.82 (0.9–2.8)	?	Jiménez and Cortés (2003)
	Galápagos	52	1938–1976	1–5	?	1.22 (0.6–1.9)	?	Glynn and Wellington (1983)
Pavona gigantea	*Non-upwelling*							
	Panamá (Uva Reef)	11	2003–2006	2–3	1.48 (1.31–1.87)	0.92 (0.3–1.3)	1.35 (0.42–2.06)	This study
	Panamá (Secas Reef)	1 (15)[a]	1870–1980	?	?	0.90 (0.8–1.1)[a]	?	Glynn (1985)
	Costa Rica	11	1985–1987	2–3	?	0.83 (0.62–1.28)	?	Guzman and Cortés (1989)
	Upwelling							
	Panamá (Contadora Reef)	5	2003–2004	1	?	1.45	?	Matthews et al. (2008)
	Panamá (Contadora Reef)	5	2003–2004	7	?	0.90	?	Matthews et al. (2008)
	Panamá (Saboga Reef)	7	1975–1979	5–7	1.75	0.85	1.49	Wellington and Glynn (1983)
	Galápagos	32	1938–1976	1–5	?	0.86 (0.3–1.5)	?	Glynn and Wellington (1983)
Pavona varians	*Non-upwelling*							
	Panamá (Uva Reef)	9	2003–2006	2–3	1.96 (1.84–2.18)	0.32 (0.2–0.5)	0.63 (0.38–0.94)	This study
	Costa Rica	7	1985–1987	2–3	?	0.35 (0.19–0.44)	?	Guzman and Cortés (1989)
Gardineroseris planulata	*Non-upwelling*							
	Panamá (Uva Reef)	9	2005–2006	2–3	1.63 (1.46–1.80)	0.61 (0.4–1.25)	0.98 (0.55–1.83)	This study
	Panamá (Uva Reef)	1	1791–1983	2–3	?	1.32 (1.2–1.4)	?	Glynn (1985)
	Costa Rica	15	1985–1987	2–3	?	1.04 (0.63–1.26)	?	Guzman and Cortés (1989)

Minimum and maximum values are in parenthesis if available

[a] Values in parenthesis are range in median colony growth of 15 colonies (Glynn et al. 1983)

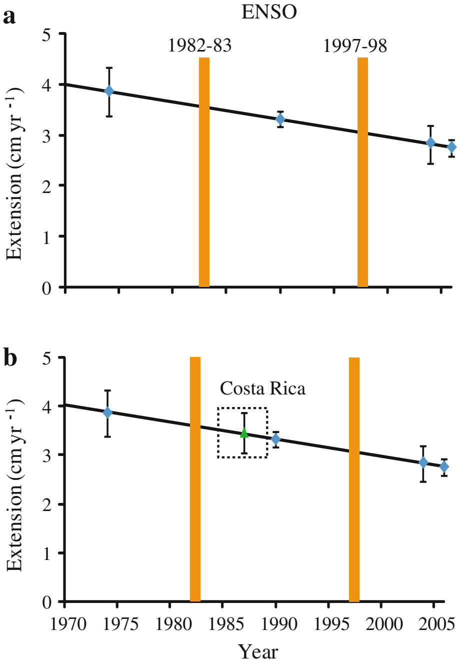

Fig. 1 Mean linear extension rates (±95% confidence limits) measured for *Pocillopora damicornis* from 1974 to 2006 from **a** Uva Reef, Gulf of Chiriquí, Panamá, by itself (*blue diamonds*) and **b** with inclusion of data point from Caño Is., Costa Rica (*green triangle*). The *orange vertical bars* indicate timing of severe El Niño-Southern Oscillation (ENSO) warming events in 1982–1983 and 1997–1998. Note that *error bars* for Caño Is. data represent standard error (±SE). Regression equations are: **a** Extension = 72.476 − 0.0348 × year and **b** Extension = 73.182 − 0.0351 × year. *Line* **a** predicts a zero extension rate in the year 2085 (±8.4 months), whereas *line* **b** has an *x*-intercept of 2084 (±1 year and 10.3 months). Earlier data presented in Table 2

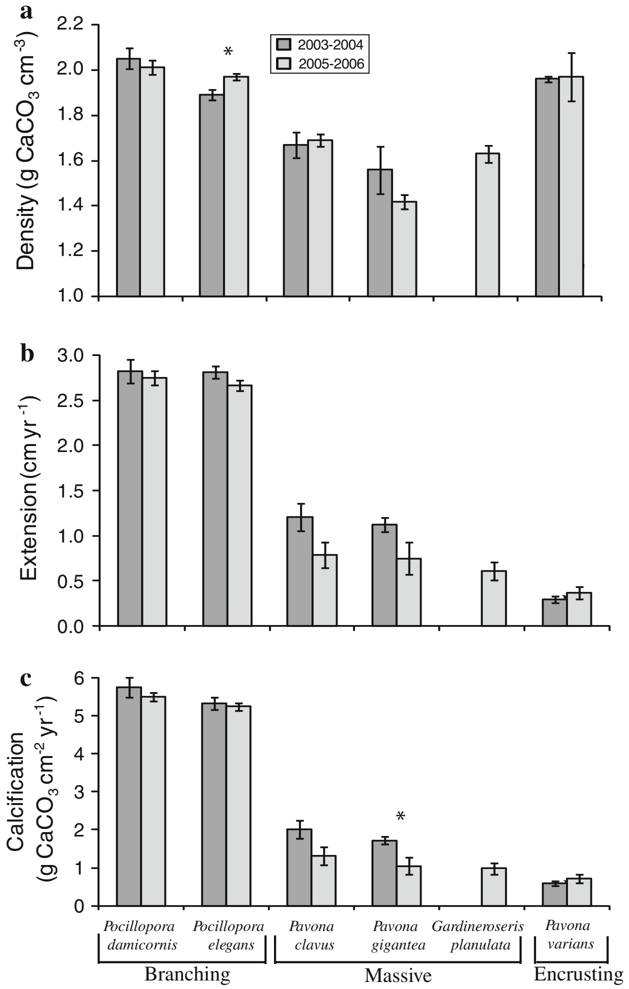

Fig. 2 **a** Bulk skeletal density, **b** linear extension, and **c** calcification for six species of reef-building coral from Uva Reef, Gulf of Chiriquí, Panamá. Sample sizes listed in Table S1. Values plotted are means of all colonies (±SE)

periods (2003–2004: $R^2 = 0.13$, $P < 0.01$, $n = 76$; 2005–2006: $R^2 = 0.05$, $P < 0.01$, $n = 152$) and when pooled together ($R^2 = 0.06$, $P < 0.001$, $n = 228$). This trend was only weakly apparent for *P. elegans* branch tips when both time periods were pooled ($R^2 = 0.04$, $P < 0.05$, $n = 168$).

There was a decline in extension and calcification from the earlier (2003–2004) to the later (2005–2006) time period for all species except *Pavona varians* (Fig. 2), but this was only significant in calcification for *P. gigantea* ($P < 0.05$). Given that it was only 0.11°C warmer during the earlier annual interval (mean ± SE = 28.67°C ± 0.005 and 28.56°C ± 0.007 for the 2003–2004 and 2005–2006 intervals, respectively), these differences may reflect normal inter-annual variability due to some other factors like cloudiness, irradiance, or turbidity.

Discussion

Rapid growth of pocilloporid corals provides a competitive advantage for space on ecological timescales, while high skeletal density imparts a greater preservation potential on geologic timescales (Fig. 2). These traits help explain why these two species are dominant reef builders throughout the eastern tropical Pacific (Cortés 1997; Glynn and Maté 1997). The rate of decline in skeletal extension for *Pocillopora damicornis* from Pacific Panamá (0.9% year^{-1}) is nearly identical to that reported for massive *Porites* in the Indo-Pacific over the past 20–30 years (0.89–1.23% year^{-1}: Cooper et al. 2008; De'ath et al. 2009; Tanzil et al. 2009). Rates of decline in the Pacific have been faster than the Atlantic where a decline in the extension of 0.23–0.35% year^{-1} was observed in *Acropora palmata* over the past 31 years (Bak et al. 2009). The Pacific Ocean has an overall lower Ω than the Atlantic (Kleypas et al. 1999) and it is expected that acidification affects will be more severe where Ω is lower (Orr et al. 2005). If declines in extension rates in both regions are due to acidification, the lower Ω in the Pacific could explain the faster regional declines there. However, Edmunds (2007) found that juvenile corals in St. John grew at one-tenth to one-third the rate shown in historical investigations (≥25 years prior) over a recent 9-year period (1996–2005). This large discrepancy between historical and recent growth rates for juvenile corals is puzzling, but may indicate that the younger life stages of corals are particularly vulnerable to climate change stressors (Edmunds 2007).

It is unlikely that the decline in extension for *P. damicornis* can be explained by an increase in density (i.e., no change in calcification). Corals with a massive morphology can respond to a harsher physical environment (e.g., increase in suspended sediment and decrease in light availability) by extending their skeleton at the same or greater rates at the expense of skeletal density (Carricart-Ganivet and Merino 2001; Carricart-Ganivet 2004). However, this phenomenon of ‘stretch-modulation’ operates over a limited range of extension and density. For the extension rate measured in 1974 by Glynn (1977) (Table 2) to correspond to the range of calcification reported in this study, mean colony density would need to have been substantially lower (1.27–1.72 g cm^{-3}) in the past than the range of 228 branches measured here (ESM Tables S1 and S2).

Pocilloporid corals at the Uva Reef had a lower prevalence of bleaching (loss of symbiotic algae due to high temperature) and mortality associated with the 1997–1998 El Niño-Southern Oscillation (ENSO) relative to the 1982–1983 event, despite a comparable amount of thermal stress (Glynn et al. 2001). The ability of *Pocillopora* to host the thermally tolerant D clade of zooxanthellae was hypothesized to contribute to its increased tolerance (Glynn et al. 2001). However, thermo-tolerant zooxanthellae likely represent a trade-off to the coral host, as they are known to cause reduced rates of growth (Little et al. 2004; Cantin et al. 2009). Genetic analysis of the zooxanthellae associated with the corals measured in this study found high abundances of clade D during the period of study (2003–2006) (Correa 2009). This implies that selection for thermo-tolerant zooxanthellae by recent ENSO events could have caused and/or contributed to the growth decline of the pocilloporid corals shown here.

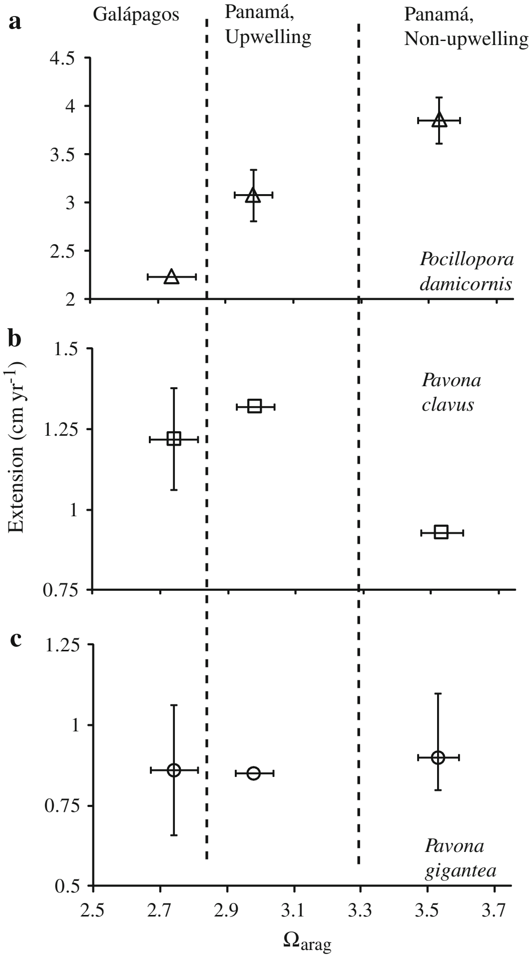

Fig. 3 Mean extension rates for **a** *Pocillopora damicornis*, **b** *Pavona clavus*, and **c** *Pavona gigantea* from the Galápagos Islands and upwelling and non-upwelling locations in Panamá plotted against mean aragonite saturation, Ω_{arag} (±SE) (Manzello 2010). Aragonite is the type of $CaCO_3$ deposited by scleractinian corals. Growth rates presented are those prior to 1980 and are presented in Tables 2 and 3. *Error bars* for extension represent Std. deviation (*SD*) except for *P. gigantea* from the non-upwelling environment in Panamá, which represents range in median growth (Table 3)

The precipitation of inorganic carbonate cement tracks the geographic variability of Ω in the eastern tropical Pacific (Manzello et al. 2008), but the regional trends in biological calcification are far more complex. Ω is significantly lower in the upwelling areas of the Galápagos Islands and Panamá relative to the non-upwelling Gulf of Chiriquí (Manzello 2010), yet *Pavona clavus* and *P. gigantea* grew as fast or faster prior to 1980 in these upwelling zones (Fig. 3). Conversely, *Pocillopora damicornis* grew fastest where Ω is highest, in the warmer Gulf of Chiriquí (Fig. 3) (Glynn 1977; Manzello 2010). Ω approximates what is expected with a doubling and tripling of atmospheric CO_2 in the upwelling areas of Panamá and Galápagos, respectively (Manzello 2009). It has been recently argued that corals may be utilizing bicarbonate (HCO_3^-) from seawater and not CO_3^{2-} as their carbon source for calcification (Jury et al. 2010). The equal and even faster growth rates where Ω is lower, but HCO_3^- higher, as well as the equivocal trends with time at the Uva Reef could potentially indicate that the two *Pavona* species use HCO_3^-. The growth rates of *Pocillopora* with time and across the regional gradient in Ω follow the expected trend assuming corals use CO_3^{2-} for calcification. If some coral species utilize HCO_3^-, whereas others use CO_3^{2-}, then the response to acidification will be species specific rather than universal. It is equally possible that the massive pavonids are simply exhibiting stretch modulation where Ω is lower, as density measurements were not obtained from the different locations (Carricart-Ganivet and Merino 2001; Carricart-Ganivet 2004). In other words, although extension of the pavonids is equal or greater where Ω is lower, their calcification rates may still be lower if their skeletons have a lower density, which was not assessed. Additionally, an increased reliance on heterotrophy may allow the massive pavonids to compensate for physical changes (temperature, Ω) in their environment as originally suggested by Wellington and Glynn (1983). The pavonids do indeed have higher feeding rates when compared to the pocilloporids (Palardy et al. 2005) and it has recently been shown that compensatory heterotrophy can counteract the effect of declining Ω in some coral species (Cohen and Holcomb 2009). The studies of Cohen and Holcomb (2009) considered alongside the very high extension rates reported from the upwelling Gulf of Papagayo in Costa Rica for all species, including *Pocillopora* (Jiménez and Cortés 2003), suggest that increased heterotrophy in upwelling zones may explain these trends, rather than utilization of bicarbonate. Stimulation of skeletal growth via higher feeding rates in upwelling zones may explain why rates of growth for *P. damicornis* in the eastern tropical Pacific are higher than reported anywhere else in the world (Glynn 1977). As pointed out by Kleypas (2007), the effect of changes in seawater chemistry will likely vary with species and growth strategy, as well as interact with tolerance to thermal stress (Lough and Barnes 2000; Carricart-Ganivet 2004, 2007).

This leads to four conceptual models of coral growth as a function of acidification, thermal stress, or as a combination of the two (Fig. 4). These models are qualitative and only intended to illustrate what is expected to occur to coral growth over time with warming and acidification. Andersson et al. (2005) provides quantitative model simulations of calcification with respect to temperature and Ω projections. The conceptual models here assume that the dependence of calcification on Ω is either curvilinear or linear, whereas the response to temperature is negative parabolic (Andersson et al. 2005). In the acidification model, declines in growth (i.e., extension and calcification) reflect the chronic effect of declining Ω, irrespective of bleaching (Fig. 4a). There are at least four lines of field evidence that are suggestive of an acidification effect: (1) the nearly identical rate of decline in different species of coral throughout the Pacific over the past 20–30 years (*Pocillopora* in Table 1 and massive *Porites* in Australia and Thailand: Cooper et al. 2008; De'ath et al. 2009; Tanzil et al. 2009); (2) the greater rate of decline for adult corals in the Pacific where Ω is lower (Kleypas et al. 1999); (3) a greater decline during the winter in Curaçao (Bak et al. 2009), which is when Ω is seasonally lowest (Gledhill

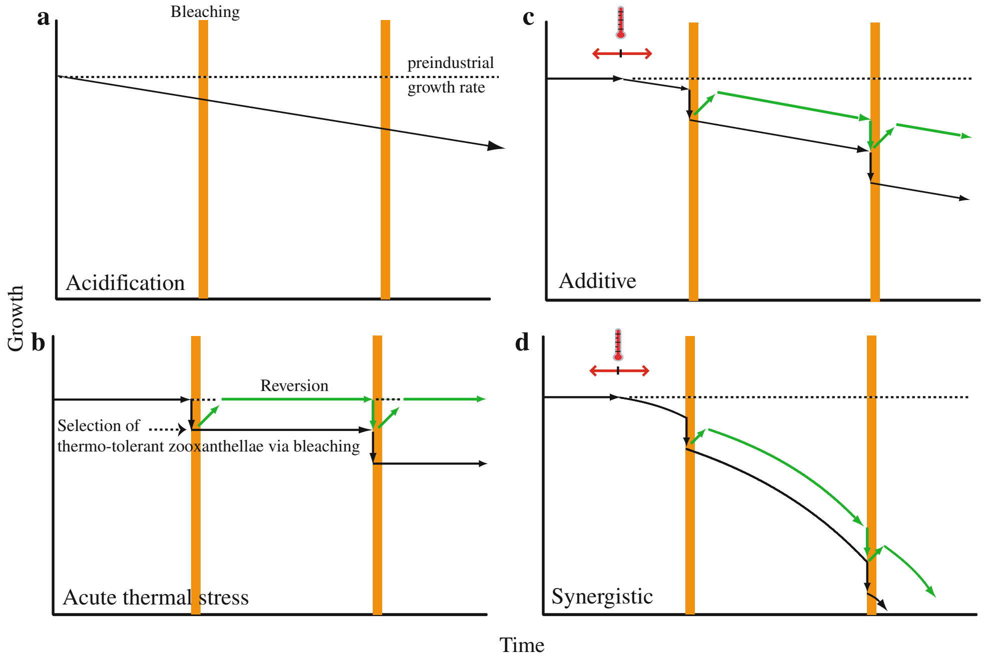

Fig. 4 Model of declining coral growth with time based on **a** cumulative ocean acidification, **b** acute thermal stress, the combined effects of acidification and thermal stress as **c** additive or **d** synergistic stressors. The *dashed line* represents preindustrial rates of coral growth and the *orange bars* indicate coral bleaching events. The *red bounding arrows* in models **c** and **d** assume a threshold temperature must be met or exceeded for the effects of acidification to manifest (Reynaud et al. 2003). The *green lines* in **b**–**d** illustrate a return to preferential zooxanthellae post-bleaching

et al. 2008); and (4) the growth data for *P. damicornis* from Costa Rica falling exactly on the negative regression line with time for nearby Panamá (Fig. 1b). However, acidification by itself seems unlikely to explain the drastic declines in massive *Porites* growth on the Great Barrier Reef (GBR) within the last 20 years (De'ath et al. 2009). The coincidence of severe bleaching over this time period (Berkelmans and Oliver 1999; Berkelmans et al. 2004) implies a bleaching or thermally associated response. Acute thermal stress and coral bleaching are known to cause declines in extension and calcification (Goreau and Macfarlane 1990; Leder et al. 1991). However, pre-stress growth rates are usually regained within 2 years (Suzuki et al. 2003). In the thermal stress model, declines are either step-wise due to the trade-offs in colony growth rates that result from the selection of thermo-tolerant zooxanthellae or short-term depressions that rebound with the reversion to preferential, 'high-performance' zooxanthellae during recovery from bleaching (Fig. 4b) (Thornhill et al. 2006). Interestingly, reversion appears to occur over a much longer time period in *Pocillopora* from Panamá than has been documented for corals elsewhere (Correa 2009). Alternatively, growth declines may be because temperatures have exceeded the optimal range for coral calcification, irrespective of bleaching or acidification (Tanzil et al. 2009). In this case, declines in coral growth rate could mimic those expected from acidification if thermal stress has indeed become chronic. The additive model assumes that both bleaching and acidification affect coral growth, and that the combination of both is equal to the sum of their individual effects (Fig. 4c). The synergistic model assumes that the rate of decline is non-linear, increasing disproportionately with rising temperature and CO_2 (Fig. 4d) (see Dunne 2010 for thorough discussion of additive versus interactive effects). High-CO_2 and temperature may interact such that the effects of high-CO_2 do not manifest at low temperatures (Reynaud et al. 2003). Declines would not begin until a threshold temperature is met or exceeded (illustrated by red arrows in Fig. 4c, d). Furthermore, heterotrophy may counteract the effect of declining Ω over some unknown, but limited range (Cohen and Holcomb 2009).

The recent decline in *Porites* growth on the GBR (De'ath et al. 2009) is most like the synergistic model (Fig. 4d), even though rising temperatures over the twentieth century appear to have had an antagonistic effect on any declines in Ω from ocean acidification, as calcification actually increased over this time (Lough and Barnes 2000). For *Pocillopora* in Panamá, the linear decline could be explained by acidification, selection for thermo-tolerant zooxanthellae without reversion, or the additive model (Fig. 4a–c). Based on the observed increase in atmospheric CO_2, it is estimated that calcification has declined about 6–14% since pre-industrial times (Kleypas et al. 1999). The low ambient Ω in Panamá (Manzello 2010) could be contributing to the greater decline than would be anticipated from acidification alone, or selection for thermo-tolerant zooxanthellae could be directly causing and/or contributing to the decline.

In contrast, pavonid corals have maintained extension rates with acidification so far, but have shown less tolerance than the pocilloporidae to repeated bleaching, presumably because of less flexibility in their algal symbioses (Glynn et al. 2001). However, bleaching and consequent mortality in the pavonids is often limited to the tops of colonies, with tissues surviving on the sides and edges that can then regenerate when thermal stress subsides (Glynn et al. 2001). The extension rates of pavonid corals were historically unaffected by the regional Ω gradient in the eastern tropical Pacific, thus these species may be able to maintain optimal growth rates with acidification via compensatory heterotrophy, which conceptually mimics the trend illustrated by the thermal stress model with reversion (Fig. 4b). Even though the response is complex, it seems that the massive pavonid corals may be more tolerant to the combination of thermal stress and acidification. Although extension is usually positively correlated to calcification, this correlation may not always be high, particularly in species with a massive morphology (Dodge and Brass 1984). Dodge and Brass (1984) showed that extension, density, nor calcification by itself is a perfect predictor of the other and that at least two of these parameters should be measured (and the third calculated) for a complete description of coral growth. Future work is necessary to determine if the calcification rates of the massive pavonids in the eastern tropical Pacific are indeed insensitive to the regional Ω gradient, or if these species are simply 'stretching' their skeletons at the expense of density in the lower Ω locations.

These models illustrate thermal stress events as acute disturbances that occur with approximate ENSO frequency. If the frequency of thermal stress events increases or if temperatures surpass the optimal range for coral growth, warming would then act like a chronic disturbance and any associated growth declines would increase accordingly. It is important to realize that these simplistic models only represent those individual corals that are able to survive the lethal effects of acute thermal stress. The growth and calcification of coral populations and reefs will decline from bleaching mortality, regardless of acidification.

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