

## RESEARCH LETTER

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## Key Points:

- Galapagos coral reefs lost after 1982–1983 ENSO where  $\text{pH} < 8$  and have not recovered
- Coral reef resilience to warming depressed by ocean acidification
- High nutrients increase coral growth at low pH but depress skeletal density

## Supporting Information:

- Texts S1–S3, Figures S1–S3, and Table S4
- Table S1
- Table S2
- Table S3
- Table S5
- Table S6

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## Galapagos coral reef persistence after ENSO warming across an acidification gradient

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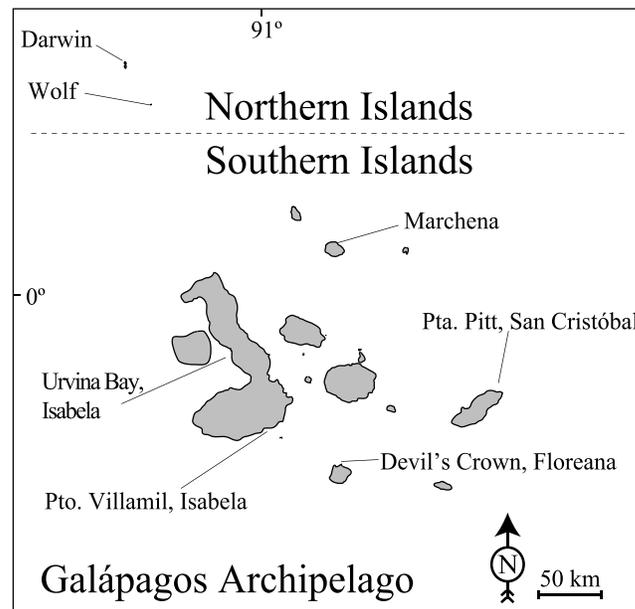
**Abstract** Anthropogenic  $\text{CO}_2$  is causing warming and ocean acidification. Coral reefs are being severely impacted, yet confusion lingers regarding how reefs will respond to these stressors over this century. Since the 1982–1983 El Niño–Southern Oscillation warming event, the persistence of reefs around the Galapagos Islands has differed across an acidification gradient. Reefs disappeared where  $\text{pH} < 8.0$  and aragonite saturation state ( $\Omega_{\text{arag}}$ )  $\leq 3$  and have not recovered, whereas one reef has persisted where  $\text{pH} > 8.0$  and  $\Omega_{\text{arag}} > 3$ . Where upwelling is greatest, calcification by massive *Porites* is higher than predicted by a published relationship with temperature despite high  $\text{CO}_2$ , possibly due to elevated nutrients. However, skeletal P/Ca, a proxy for phosphate exposure, negatively correlates with density ( $R = -0.822$ ,  $p < 0.0001$ ). We propose that elevated nutrients have the potential to exacerbate acidification by depressing coral skeletal densities and further increasing bioerosion already accelerated by low pH.

## 1. Introduction

The burning of fossil fuels by humans is leading to changes in climate and ocean chemistry, both of which are negatively impacting coral reefs [Hoegh-Guldberg *et al.*, 2007]. Reef-building corals thrive within a narrow thermal range and deviations of a few degrees Celsius above and below monthly climatological highs and lows, respectively, for a month or more cause bleaching and mortality [Hoegh-Guldberg *et al.*, 2007; Lirman *et al.*, 2011]. The oceanic uptake of anthropogenic  $\text{CO}_2$  is lowering seawater pH and the saturation state of aragonite ( $\Omega_{\text{arag}}$ ), depressing coral calcification [Langdon and Atkinson, 2005]. Despite these concerns, we still have a relatively undeveloped understanding of how the combination of continued climate change and ocean acidification will impact coral reefs.

The coincidence of naturally high  $\text{CO}_2$  conditions, periodic warming events caused by the El Niño–Southern Oscillation (ENSO), and long-term (~40 years) monitoring make Galapagos coral reefs ideal for understanding the effects of warming and acidification. This long-term understanding provides an unparalleled context to predict the response of reefs to warming in a high  $\text{CO}_2$  world that is not possible at other high  $\text{CO}_2$  sites. The high nutrients in upwelled waters around the Galapagos Islands, rather than being a confounding factor, actually provide insight into how coastal eutrophication, a major concern for coral reefs [Pandolfi *et al.*, 2005], might interact with high  $\text{CO}_2$  and warming.

Before the 1982–1983 ENSO, coral reefs existed throughout the Galapagos archipelago [Glynn and Wellington, 1983]. Galapagos reefs were generally thin accumulations of  $\text{CaCO}_3$  relative to those in the Indo-Pacific and Caribbean, small, and patchily distributed [Glynn and Wellington, 1983; Colgan, 1990]. These were true reefs in that they were wave-resistant, 3-D structures created by the calcification of reef-building corals and other calcareous organisms that contributed to the accretion of the framework on which they grew. A coral reef contrasts with a coral community, which refers to scattered corals that do not contribute to the accretion of framework, but grow on top of antecedent topography, such as basalt. The Galapagos is marginal for reef growth and generally unfavorable for the deposition and preservation of  $\text{CaCO}_3$  [Manzello *et al.*, 2008]. Bioerosion is a major limiting factor to reef growth in the Galapagos Islands and the dominant bioeroder is the echinoid *Eucladaris galapagensis* [Glynn *et al.*, 1979; Reaka-Kudla *et al.*, 1996].



**Figure 1.** Study sites in Galápagos Islands.

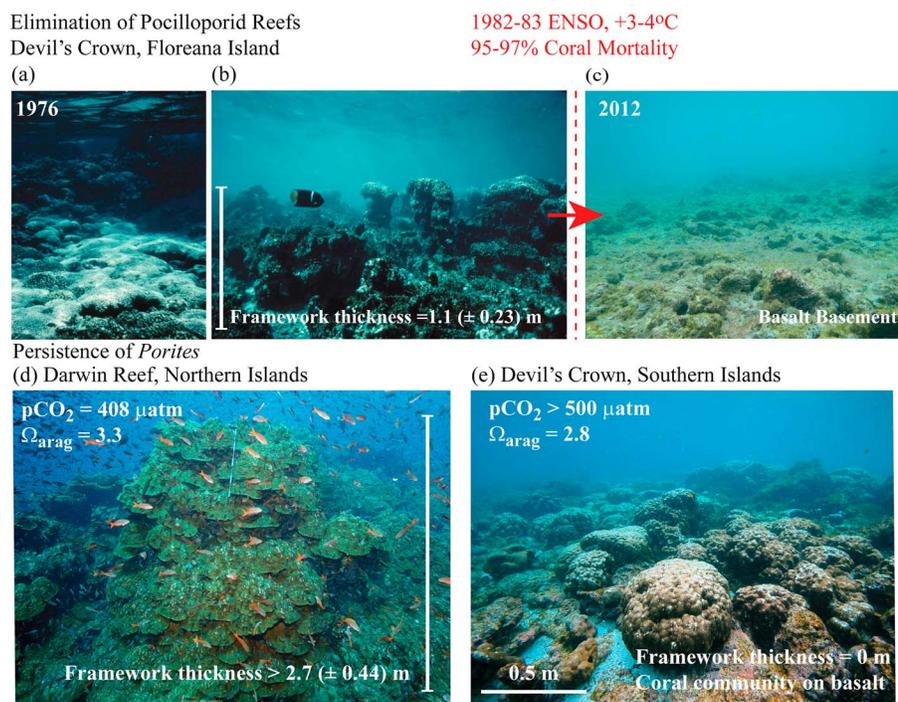
Galápagos reef communities experienced extreme high-temperature anomalies due to the 1982–1983 and 1997–1998 ENSO (+3–4°C for >2 months) [Podestá and Glynn, 2001], and also experience very low  $\Omega_{\text{arag}}$ , currently encompassing what is estimated to occur for reefs globally with a doubling and tripling of atmospheric  $\text{CO}_2$  [Manzello et al., 2008; Manzello, 2010]. Only one coral reef persists today within the Galápagos archipelago and this is located in the remote northern island of Darwin [Glynn et al., 2009] (Figure 1 and Table S1 in the supporting information). This reef is a monospecific buildup of the massive coral *Porites lobata*, one of the most widely distributed and common corals in the world [Veron, 2000]. There is considerable coral cover at nearby Wolf Island, with large colonies of *P. lobata*,

*Pavona clavus*, and *Pavona gigantea* [Banks et al., 2009], but this community does not construct a true reef due to a very steep slope that is poorly suited for carbonate accumulation. The northern islands of Darwin and Wolf are ~150 km northwest of the largest southern island of Isabela. Many studies have broken the Galápagos Islands into regions, but for simplicity we separate them into the northern and southern islands (Figure 1).

There has been little recovery since the bleaching mortality associated with the 1982–1983 ENSO in the southern Galápagos Islands and reef framework structures > 1000 years old were completely bioeroded in <10 years (Figures 2a–2c) [Glynn, 1994]. Although many studies have cited the loss of reefs, the Galápagos example is unique in that it represents the only known case where complete elimination of the reef framework occurred following coral mortality, rather than just the loss of live coral. The high  $\text{CO}_2$  conditions in the southern Galápagos Islands limit carbonate cementation, providing a key piece to the puzzle of why these reefs disappeared so quickly [Manzello et al., 2008]. In the southern Galápagos, a small *Porites* population has survived repeated ENSO events but does not construct any appreciable framework. Reefs constructed by the branching coral, *Pocillopora damicornis*, were lost from both the northern and southern Galápagos after the 1982–1983 ENSO [Glynn et al., 2009].

The oceanographic conditions of the Galápagos Islands are dynamic and complex, influenced by the interaction of several major currents. The North Equatorial Counter Current extends south from the Panama Bight, bringing surface waters to the far northern islands that are consistently 1–2°C warmer than those in the southern islands [Palacios, 2004; Schaeffer et al., 2008]. The southern islands are influenced by the northern extension of the Peru current, which brings cool, nutrient-rich waters to this area. The easterly flowing Equatorial Undercurrent (EUC) collides with the archipelago, causing strong upwelling along the western shores of Isabela and Fernandina, creating cold-water habitats unique to the tropics. The EUC also meanders around Isabela and results in enhanced, but less persistent upwelling in the islands to the east [Schaeffer et al., 2008]. During El Niño years, waters warm throughout the archipelago and upwelling is dampened. During La Niña, the regional differences and upwelling intensify. In summary, the intensity of upwelling increases from north to south, and is greatest on the western shores of Isabela.

We hypothesized that the upwelling gradient across the Galápagos would result in different carbonate chemistry conditions. In this study, we determined if differences in  $\text{CO}_2$  across the Galápagos correlated with calcification of massive *Porites* and reef persistence after ENSO warming. Our results provide field evidence that the ability of coral reefs to persist with warming declines with acidification and this



**Figure 2.** Photographs of the former Pocilloporid reef at Devil's Crown, Floreana Island in (a, b) 1976 and (c) 2012 illustrating the rapid destruction and poor resilience following the 1982–1983 ENSO. Framework thickness is average maximum thickness of all Pocilloporid reef sites prior to the 1982–1983 ENSO [Glynn and Wellington, 1983]. Value is mean (± std. error of the mean) of 12 reefs from 25 individual measurements. Contrasting *Porites* reef structure with carbonate chemistry at (d) Darwin Reef, northern Galápagos Islands. Reef thickness measurements represent minimum values because basalt basement was not reached with a hand-held metal probe used to penetrate the seafloor. Reef framework stacks >3 m were measured. Stick on upper center of coral colony is 1 m. (e) Population of *Porites lobata* adjacent to where the pocilloporid reef existed prior to ENSO. This community has persisted but does not accumulate framework. Photographs of Figures 2a and 2b are by P. Glynn, Figure 2c is by D. Manzello, and Figures 2d and 2e are by J. Feingold.

depressed resilience is likely reduced further by high nutrients [Pandolfi et al., 2005; Hoegh-Guldberg et al., 2007; Pandolfi et al., 2011].

## 2. Materials and Methods

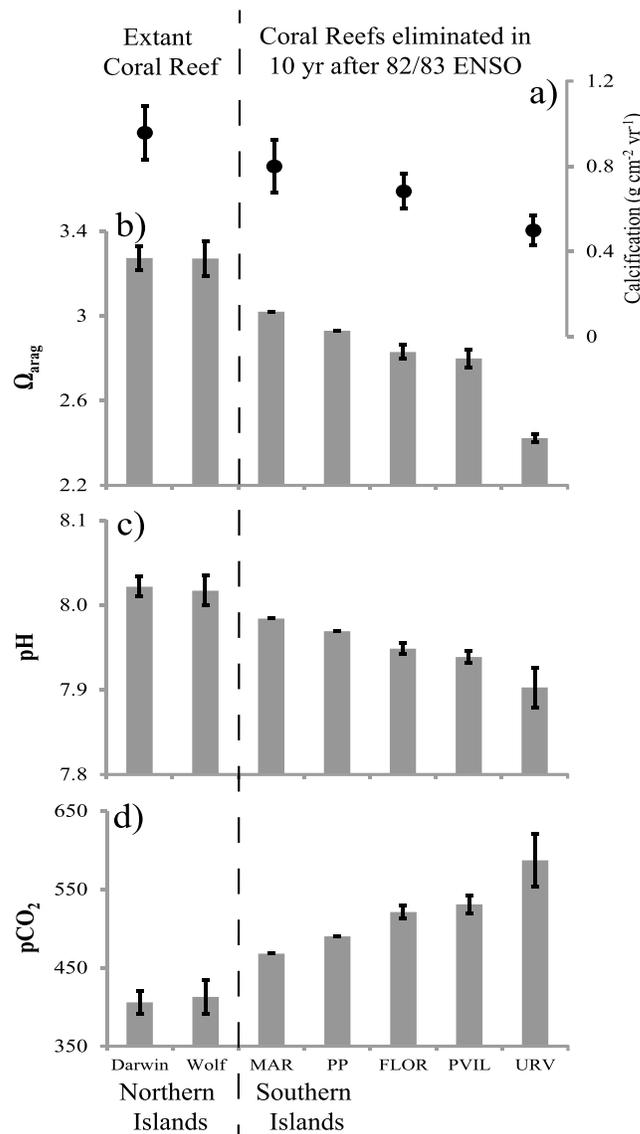
Seawater carbonate chemistry was measured using bottle samples, as well as in situ instrumentation (see supporting information). Coral extension, density, calcification, and skeletal P/Ca, a proxy for phosphate exposure [LaVigne et al., 2008], were determined from coral cores of *P. lobata* collected at Darwin, Marchena, Devil's Crown, and Urvina Bay in June 2012 ( $n = 7\text{--}8$  cores per site). Table S1 provides information on the different sites sampled. Coral growth was measured utilizing a micro-CT. For detailed methods please see supporting information.

Relationships between environmental variables (e.g., sea surface temperature (SST) and carbonate chemistry) and coral growth were ascertained with correlation analysis using SigmaPlot. To help isolate the role of temperature versus CO<sub>2</sub> and nutrients on coral growth, we compared our data to Lough's [2008] model of temperature-dependent calcification for massive *Porites* derived from 49 Indo-Pacific reefs. Correlations were determined between measured growth, as well as the deviation in growth from Lough's [2008] predicted values ( $\Delta$  Growth metric = Measured – Predicted value)

## 3. Results

### 3.1. Seawater Carbonate Chemistry

The northern Galápagos Islands had lower partial pressure of CO<sub>2</sub> (pCO<sub>2</sub>), and higher values of pH<sub>T</sub> and Ω<sub>arag</sub> relative to the southern islands (Figure 3) ( $p < 0.05$ , One-way analysis of variance (ANOVA),



**Figure 3.** Mean seawater carbonate chemistry values by Galápagos site. (a) Calcification rate of *Porites lobata*, (b) Aragonite saturation state ( $\Omega_{arag}$ ), (c) pH (total scale), and (d)  $pCO_2$  ( $\mu atm$ ). Site abbreviations: MAR, Marchena; PP, Punta Pitt; FLOR, Devil's Crown, Floreana Island; PVIL, Puerto Villamil, Isabela Island; and URV, Urvina Bay, Isabela Island. Error bars are standard error of the mean.

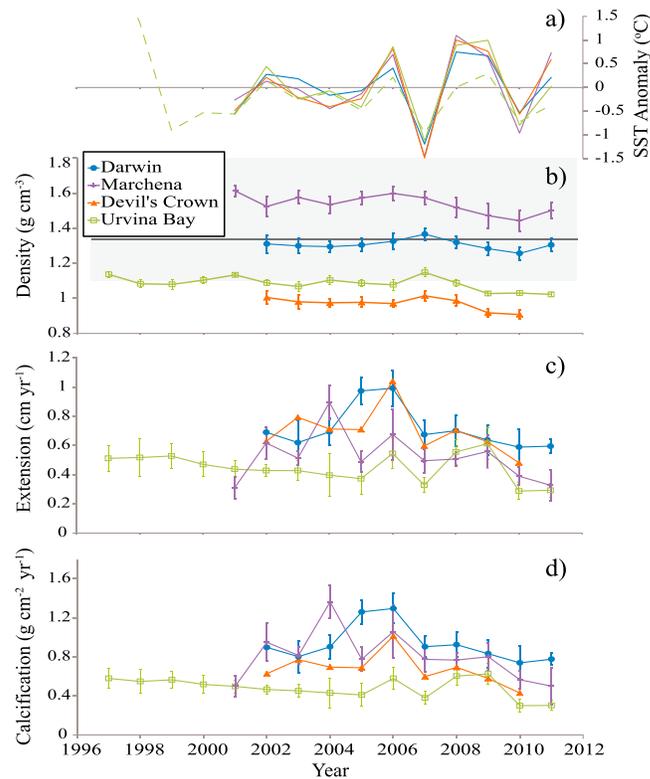
greatest at Darwin but similar at Devil's Crown. Skeletal density was very low at the southern island sites of Devil's Crown and Urvina Bay (Figure 4). Calcification and density varied significantly between sites ( $p < 0.001$ , One-Way ANOVAs, Holm-Sidak tests).

The coral growth patterns at all sites were indicative of some stressor. Density was within 10% of the value predicted by Lough's [2008] regression where  $\Omega_{arag} \geq 3$  (Darwin and Marchena), but extension was ~25% lower than expected (Table S4). Likewise, calcification was below the predicted value by 16.8% and 25.8% at Marchena and Darwin, respectively. The sites most influenced by upwelling, Devil's Crown and Urvina Bay, had extension rates far greater than expected (Table S4), whereas density was >30% lower. Calcification was close to predicted for Devil's Crown, and nearly 50% greater than expected at Urvina Bay. All growth parameters at all sites declined over the past decade, but only the density trends where  $\Omega_{arag} \leq 3$  were significant. See supporting information results for further information on trends in coral growth with time.

Holm-Sidak post hoc tests). The mean values of  $\Omega_{arag}$  and  $pH_7$  were 3.3 and 8.02, respectively, in the northern islands, whereas mean values in the southern islands ranged from 2.4 to 3.0 and 7.90 to 7.98 (Figure 3). These trends were verified by independent measurements taken with an infrared  $CO_2$  analyzer and a SeaFET pH sensor (Figure S1). These data are in agreement with previous sampling in Galápagos that coincided with climatological low and high SST conditions in 2003 and 2009, respectively [Manzello, 2010]. Although this is the first time  $CO_2$  data were collected from the northern islands, we expect that the diurnal and seasonal variability there is similar, or even less than the rest of the archipelago due to the smaller range in SST relative to the southern islands (Figure S2). Our data suggest that large-scale oceanographic variability drives the carbonate chemistry conditions throughout the archipelago, with biologically driven diurnal variability being less important. The evidence supporting this hypothesis is provided in the results section of the supporting information.

### 3.2. Coral Skeletal Extension, Density, Calcification, and P/Ca: Correlations and Trends

Mean calcification rate correlated with mean SST,  $\Omega_{arag}$ ,  $pCO_2$ , and  $pH_7$  (Table S2), with the highest measured rates at Darwin, followed by Marchena, Devil's Crown, and the lowest at Urvina Bay (Figure 4 and Table S3). Extension was not correlated with  $pCO_2$ , as rates were



**Figure 4.** Sea surface temperature anomaly and coral growth. (a) Annual sea surface temperature (SST) anomaly, (b) *Porites* mean skeletal density, (c) linear extension, and (d) calcification rate per site with time. SST data from 2001 to 2011 are advanced very high resolution radiometer, whereas dashed line is HadISST. Error bars are standard error of the mean. Gray area in Figure 4b is range of data, and black line is mean of massive *Porites* skeletal density from 55 Indo-Pacific reefs including Western Australia [Lough, 2008; Cooper et al., 2012].

phosphate [Dunn et al., 2012], given that there was no impairment of *Porites* density at the CO<sub>2</sub> seeps in Papua New Guinea [Fabricius et al., 2011]. The P/Ca values in the coral cores support this hypothesis. In fact, the skeletal density at Devil's Crown was lower than the entire range of Lough's [2008] large data set that spans 55 reefs when recent data from Western Australia were considered [Cooper et al., 2012] (gray shaded area in Figure 4b illustrates typical range).

Experiments have shown that high nutrients or enhanced heterotrophy can ameliorate the depression in coral calcification from high CO<sub>2</sub> [Langdon and Atkinson, 2005; Cohen and Holcomb, 2009]. However, the impact of high nutrients on reefs in general is negative, despite stimulating coral extension and calcification [Edinger et al., 2000]. One of the hypotheses for why elevated nutrients negatively impact reefs is that they depress coral skeletal density [Dunn et al., 2012], impairing the construction of rigid skeletons necessary for framework development and maintenance. We suggest that elevated nutrients in upwelled waters and/or increased heterotrophy from elevated water-column productivity stimulate extension and calcification of massive *Porites* in the southern Galápagos Islands, but impair skeletal density. The population of *P. lobata* at Devil's Crown has a limited potential to construct a framework due to the very low density skeletons, lack of cementation, and very high rates of bioerosion [Reaka-Kudla et al., 1996; Manzello et al., 2008], despite the fact that extension rates were nearly identical to Darwin (Figure 4c). Conversely, skeletal densities at Darwin were within the normal range measured for massive *Porites* from 55 reefs across the Indo-Pacific (Figure 4b), CaCO<sub>3</sub> cement abundances were among the highest found in the eastern Pacific (mean (± std. error) % of pores with cement = 17.0 [0.02], Range = 0.6–47.5), and the reef framework exceeds heights of 3 m [Glynn et al., 2009] (Figure 2d).

P/Ca in the coral cores were negatively related to skeletal density and calcification (Figure S3, Table S2). When growth was expressed as the deviation from the value predicted by Lough's [2008] regression, P/Ca was positively correlated to extension and calcification, while density remained negatively correlated (Table S2). The correlation between  $\Delta$  calcification and the other environmental parameters reversed signs. This reversal is because calcification was higher than expected where pH,  $\Omega_{\text{arag}}$ , and SST were lowest and pCO<sub>2</sub> highest (Urvina, Devil's Crown), but lower than expected where pH,  $\Omega_{\text{arag}}$ , and SST were highest (Darwin, Marchena). Thus, as SST decreased,  $\Delta$  extension and calcification increased from negative to positive, whereas  $\Delta$  density became increasingly negative.

## 4. Discussion

### 4.1. Interaction of Temperature, Nutrients, and CO<sub>2</sub> on Coral Calcification

The ability of *Porites* to achieve the expected calcification rates based on SST came at the cost of very low density skeletons. The fragile nature of corals in the southern Galápagos is likely due in part to high nutrients, particularly

*Eucidaris galapagensis* population densities are lower in the northern islands versus the southern islands, which is likely an important factor explaining the persistence of Darwin Reef [Glynn *et al.*, 2015]. The higher echinoid abundances in the southern islands are likely due to elevated productivity of benthic algae, their primary food source, which is associated with increased upwelling [Glynn, 1994]. The low pH and high nutrients likely stimulate the biologically mediated chemical dissolution by endolithic algae and sponges [e.g., Tribollet *et al.*, 2009; Wisshak *et al.*, 2012; Reyes-Nivia *et al.*, 2013], which may contribute to the very high bioerosion rates of this area. All of these factors interact to create an unfavorable environment for the preservation of CaCO<sub>3</sub>.

#### 4.2. Are There Acidification Thresholds for Coral Reefs?

Comparison of our results with the CO<sub>2</sub> seeps in Papua New Guinea (PNG), which provide a high CO<sub>2</sub> future reef analog without elevated nutrients [Fabricius *et al.*, 2011], allows insight into how acidification with and without high nutrients might impact reefs in the future. There are striking parallels and differences. First, *P. damicornis* and *P. lobata* are primary reef-builders throughout the eastern Pacific and are also the two most abundant species found in the depauperate community near the CO<sub>2</sub> seeps in PNG [Cortés, 1997; Fabricius *et al.*, 2011]. This indicates that both species possess a capacity to withstand high CO<sub>2</sub>. *P. lobata*, however, is better suited to survive the combination of acidification and warming given its higher survivorship after ENSO events in Galápagos; *P. damicornis* build-ups were eliminated from both the northern and southern islands after the 1982–1983 ENSO [Glynn *et al.*, 2001, 2009]. At the CO<sub>2</sub> seeps in PNG, reef framework disappears at pH<sub>T</sub> = 7.7 [Fabricius *et al.*, 2011], whereas in Galápagos this occurs at higher values (pH<sub>T</sub> = 8.0) (Figure 3). We propose five hypotheses to explain why reef framework occurs at lower pH values in PNG versus Galápagos: (1) coral communities in PNG have not experienced the thermal stress and coral mortality that Galápagos has; coral bleaching and mortality directly reduce CaCO<sub>3</sub> production, affecting framework production and persistence [Glynn, 1988], (2) bioerosion rates are stimulated by high nutrients and high CO<sub>2</sub> in the Galápagos, leading to the very high rates [Reaka-Kudla *et al.*, 1996], (3) the normal skeletal densities in PNG result in more rigid framework construction, (4) warmer temperatures in PNG (27–29°C) allow more rapid calcification even with high CO<sub>2</sub>, and (5) corals recruit to vent areas at higher rates than Galápagos because they come from nearby, nonacidified areas.

The recent discovery of naturally acidified coral communities in Palau provide an intriguing contrast that, at first, seems to contradict the findings presented here, as well as those from PNG. Within Palau's Rock Island Bays, Shamberger *et al.* [2014] measured average  $\Omega_{\text{arag}}$  values of 2.7 or lower and reported high coral diversity and cover. Similarly to PNG, calcification in *P. lobata* was not impacted by low  $\Omega_{\text{arag}}$ . Four of the five hypotheses that we presented above to explain the disparity between the pH values where reefs presently exist in Galápagos and PNG also apply to Palau (Hypotheses 1 and 2 and 4 and 5). We cannot address hypothesis three because densities were not reported for *P. lobata* from Palau. It is unclear if rigid framework accretion occurs in the low  $\Omega_{\text{arag}}$  Palau environments that could resist high wave exposure. Widespread coral bleaching occurred in Palau in 1997–1998 and 2010 [van Woessik *et al.*, 2012], but a maximum thermal anomaly of only +1.25°C for 1–2 months occurred during the most severe event [Bruno *et al.*, 2001], far less than what Galápagos has experienced (+3–4°C for >2 months during the 1982–1983 and 1997–1998 ENSO) [Podestá and Glynn, 2001].

The Palau Rock Island Bays are completely protected from waves and flow rates are low [Bruno *et al.*, 2001; Penland *et al.*, 2004], resulting in the high residence times that are, in part, responsible for the low  $\Omega_{\text{arag}}$  [Shamberger *et al.*, 2014]. Although coral diversity was higher at the low pH sites than offshore, Shamberger *et al.* [2014] did not report which species or genera were present, or metrics of community structure like relative abundance. The coral communities of these sites are dominated by species in the families Faviidae, Poritidae, and Mussidae, with the fleshy corals in the genera *Symphylia* and *Lobophyllia* being particularly conspicuous [Golbuu, 2011]. "Fleshy" corals are those with thick tissues with a swollen appearance that cover skeletal structures that are weaker than those corals important to reef accretion like the acroporids. This is illustrated by the photograph presented by Shamberger *et al.* [2014] that shows a characteristic low pH site [Shamberger *et al.*, 2014, Figure S4]. The conspicuous and abundant genera in Palau, *Symphylia* and *Lobophyllia*, are usually most abundant in backreef/lagoonal environments, protected from strong waves and surge, likely because they secrete fragile skeletons [Veron, 2000]. The Palau sites could thus represent a shift in community structure to species without robust skeletons, suggesting that fleshy corals might be better able

to compete for and occupy space in a high CO<sub>2</sub> world. At another volcanic CO<sub>2</sub> seep in Japan, a shift from hard to soft corals occurred with increasing CO<sub>2</sub>, although at the highest CO<sub>2</sub> levels both were eliminated [Inoue *et al.*, 2013]. If a community shift to more fleshy or soft corals occurs as pH declines, it is unclear if this would be possible in unsheltered locations, or if this would lead to 3-D framework accretion.

### 4.3. Conclusions

Coral calcification and reef structural persistence correlate with the regional trend in seawater pH in the Galápagos Islands. Interestingly, values of  $\Omega_{\text{arag}}$  where the sole remaining reef persists today in Galápagos were identical to the critical  $\Omega_{\text{arag}}$  value experienced by all reefs prior to the industrial revolution [Hoegh-Guldberg *et al.*, 2007]. The “CO<sub>2</sub> tipping point,” whereby coral reefs cease to exist in PNG is pH<sub>T</sub> = 7.7 [Fabricius *et al.*, 2011], whereas in Galápagos it is pH<sub>T</sub> = 8.0. In the absence of CO<sub>2</sub> emission reductions, the warming and acidification that eliminated coral reefs from the Galápagos Islands will occur for nearly all reefs by midcentury [van Hooidonk *et al.*, 2014].

Increased nutrients may stimulate coral growth with high CO<sub>2</sub>, but the response of the low pH Galápagos reefs to warming suggests that elevated nutrients ultimately increases reef sensitivity to acidification by reducing skeletal density and further stimulating bioerosion already accelerated by low pH. Excess nutrients can also exacerbate coral sensitivity to warming [Fabricius *et al.*, 2013]. The recent history of Galápagos coral reefs provides field evidence that reefs exposed to elevated nutrients may be the most affected and least resilient to changes in climate and ocean chemistry.

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