Changes in coral reef communities across a natural gradient in seawater pH

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Ocean acidification threatens the survival of coral reef ecosystems worldwide. The negative effects of ocean acidification observed in many laboratory experiments have been seen in studies of naturally low-pH reefs, with little evidence to date for adaptation. Recently, we reported initial data suggesting that low-pH coral communities of the Palau Rock Islands appear healthy despite the extreme conditions in which they live. Here, we build on that observation with a comprehensive statistical analysis of benthic communities across Palau's natural acidification gradient. Our analysis revealed a shift in coral community composition but no impact of acidification on coral richness, coralline algae abundance, macroalgae cover, coral calcification, or skeletal density. However, coral bioerosion increased 11-fold as pH decreased from the barrier reefs to the Rock Island bays. Indeed, a comparison of the naturally low-pH coral reef systems studied so far revealed increased bioerosion to be the only consistent feature among them, as responses varied across other indices of ecosystem health. Our results imply that whereas community responses may vary, escalation of coral reef bioerosion and acceleration of a shift from net accreting to net eroding reef structures will likely be a global signature of ocean acidification.

INTRODUCTION

Shifts in ocean chemistry are likely occurring more rapidly now than in the past 300 million years (1). Excess CO2 released from fossil fuel emissions and deforestation is absorbed by the surface oceans, driving down seawater pH and calcium carbonate (CaCO3) saturation state (Ω), a process termed ocean acidification (OA) (2). Coral reefs are considered especially vulnerable to OA. Reefs are made of CaCO3 produced by calcifying organisms, including corals and coralline algae, and laboratory experiments have shown that biogenic calcification is slowed and its destruction is accelerated at levels of OA projected for the end of this century (2, 3). Some experiments have raised key questions regarding the potential for coral reef organisms to adapt to OA or for covarying environmental factors, such as light, water flow, and nutrient availability, to modulate the impacts of OA (4–8). However, most studies of naturally low-pH reefs, including CO2 vents in Papua New Guinea (PNG) and Japan, freshwater seeps in Mexico, and upwelling regions of the eastern tropical Pacific, have yielded no evidence to support either scenario (9, 10).

In our previous report (11), we presented our initial data showing that coral communities of the Palau Rock Islands, formed by a labyrinthine maze of uplifted karst, appear healthy despite the relatively extreme pH conditions in which they live. As water flows from the open ocean over the barrier reefs and into the Rock Island bays, its carbonate system chemistry is altered by a combination of biological and hydrographic processes that elevate pCO2 and drive down pH and Ω, a natural form of acidification (11). The long residence time of seawater within the Rock Islands exacerbates this process, and as a result, the benthic communities in Palau’s most acidified reefs live in conditions with pH and Ω levels equivalent to those predicted for the western tropical Pacific open ocean by 2100 (Fig. 1) (12). Recent continuous pH data collected in situ over multiple, consecutive diel cycles (Fig. 1, inset) reveal that whereas natural acidification decreases the mean pH within the Rock Islands, the diel range in pH is maintained across Palau’s natural OA gradient. The downward shift in pH and Ω without change in amplitude or frequency of variability contrasts the extreme and highly variable conditions at CO2 vent sites and freshwater seeps (13, 14), and is more consistent with the predicted nature of the progression of OA in the marine environment (12).

Here, we assess coral reef benthic community structure and key ecosystem processes across a natural gradient in seawater pH and Ω in Palau. We evaluate these response variables against a comprehensive characterization of carbon chemistry to investigate whether measurable changes in benthic community structure; coral community composition; declines in skeletal extension, density, and calcification; and/or increases in the prevalence and rates of bioerosion seen in laboratory experiments and analog sites can be detected and attributed to OA in Palau. Finally, we compare our data with those collected at other naturally low-pH reefs to identify response variables common across all sites, independent of the mechanism of acidification, biogeography, frequencies of variability, and presence of other environmental factors that may exacerbate or mask the OA impact.

RESULTS

Carbon system chemistry

Characterization of Palau’s carbonate chemistry environment was achieved by discrete water sampling at 11 study sites during multiple tidal cycles, seasons, and years from dawn (6:00 a.m.) to dusk (6:00 p.m.), combined with continuous, 4-day-long pH sensor deployment and water sampling to characterize diurnal variability at a subset of these sites (Fig. 1, fig. S1, and tables S1 and S2). Site average dawn-to-dusk pH and Ω of the CaCO3 mineral aragonite (Ωar) are typically within error of 24-hour mean values (15) and are thus considered representative.
of the full diel range in carbon system chemistry. Average pH/Ωar ranged from 8.05 (±0.04 SD)/3.7 (±0.3) at the highest-pH/Ωar barrier reef site to 7.84 (±0.03)/2.3 (±0.2) at the lowest-pH/Ωar, Rock Island site, falling as low as 7.61/1.86 in the early hours of the morning. Mean pH/Ωar levels were significantly different across study sites [ANOVA (analysis of variance), F_{10,14} = 21.4, P < 0.001], but were not correlated with concentrations of NO_3^-/NO_3^- (r = −0.42, P = 0.19), PO_4^{3-} (r = −0.36, P = 0.27), or NH_4^+ (r = −0.34, P = 0.31). A comparison of our mean 2011–2013 Ωar (3.68 ± 0.05 SE) measured at site 10 (Fig. 1) just offshore of Palau’s northwest barrier reef with Ωar at the same site in 1994 (3.87 ± 0.04) and 2000 (3.80 ± 0.02) (16, 17) shows a 0.19 decrease over 20 years (see the Supplementary Materials). This is similar to the direction and magnitude of change (−0.24) recorded at the open ocean station ALOHA over the same period (Ωar = 3.75 to Ωar = 3.51) (17), suggesting that the strong influence of local processes on Palau’s carbon system chemistry is superimposed on a steady decline in Ωar caused by air-sea exchange of anthropogenic CO_2.

**Benthic community cover**

Benthic communities were compared across eight sites spanning the full range of carbonate chemistry using cover and composition estimates derived from five 50-m transect lines per site collected at 3-m depth (Fig. S1 and tables S1 and S2). Despite the steep decline in pH and Ωar, our analysis revealed no significant change in the cover of live hard coral, macroalgae, and crustose coralline algae or in coral genera richness or diversity [Fig. 2 and table S3; generalized linear model (GLMs), P > 0.05]. Coral communities within the lowest-Ωar reef site (Ωar = 2.32) hosted the highest coral cover (>60%) and genus richness (12.6 genera transect^{−1}) and the lowest macroalgae cover (<1%).

**Coral community composition**

Whereas coral cover and richness were insensitive to differences in pH among sites, we detected a significant relationship between pH/Ωar and coral community composition as well as shifts in the presence and abundance of coral genera across sites (Fig. 3; redundancy analysis, pseudo-F_{7,32} = 8.80, P < 0.001). The coral compositions of the barrier sites (highest pH and Ωar) were similar to each other, defined by abundant Acropora, Montipora, and Pocillopora. Coral communities occupying the lagoonal sites (lowest pH and Ωar) were distinct from the barrier communities but were also distinct from each other: one site (Ωar = 3.24) was Porites-dominated, whereas another (Ωar = 2.67) was dominated by populations of Leptastrea, Platygrya, Favia, and Favia. Our lowest-Ωar site identified to date (Ωar = 2.32) uniquely hosted Pachyseris, Symphyllia, Mycedium, Lobophyllia, Plerogyra, and Merulina. In general, Porites abundance increased with decreasing pH (log-linear GLM, P < 0.05), whereas the abundances of Acropora, Montipora, and Pocillopora declined (negative binomial GLM, P < 0.01; table S4).

**Coral skeletal growth and macrobioerosion**

The skeletal extension, density, and calcification rates of two coral genera (Porites and Favia) did not exhibit statistically significant changes across the pH gradient (Fig. 4 and table S5; GLMs, P > 0.05). The presence of macrobioerosion in Porites corals increased significantly at low Ωar (logistic regression, P < 0.001), and the volume percent of skeleton removed by bioerosing organisms, predominantly the...
bivalve *Lithophaga*, increased 11-fold from the highest-Ω*ar* to the lowest-Ω*ar* sites (log-linear GLM, *P* = 0.03) in coral skeletons with nonzero bioerosion. We did not detect a significant relationship between skeletal density and the volume of coral skeleton eroded (log-linear GLM, *P* = 0.35), but the likelihood that *Porites* coral skeletons were bioeroded increased as skeletal density decreased (logistic regression, *P* < 0.001).

**DISCUSSION**

Despite the pH and Ω*ar* conditions already at predicted end-of-century open ocean levels and pCO₂ up to 720 µatm, the Rock Islands support high coral cover, richness, and diversity and very low macroalgal cover. This observation counters expectations based on some laboratory CO₂ manipulation experiments and studies of other naturally low-pH reefs in which severe declines in coral richness and coralline algal cover and increases in macroalga are signature impacts of OA (13, 14). In general, coral cover on Palau’s high-pH barrier reefs (28 to 37%) was lower than that of the low-pH bay reefs (32 to 63%), a trend likely exacerbated by a bleaching event in 1998 that caused declines in coral cover on the barrier reef but not the bays. Nevertheless, the relatively high cover and diversity in the low-pH reefs cannot be solely attributed to differential bleaching-induced mortality: the pre-1998 cover on the barrier (50% in 1992) was already lower than the current coral cover on Palau’s lowest-pH reefs (63%) (18). The skeletal extension, density, and calcification rates of *Porites* and *Favia* corals did not change significantly with declining pH and Ω*ar*, indicating that the rates of CaCO₃ production, a physiological process considered one of the most sensitive to OA, are maintained across Palau’s OA gradient. In contrast, many laboratory CO₂ manipulation experiments with *Porites* and *Favia* corals have shown significant declines in calcification of these genera with declining pH/Ω*ar* (7, 14, 19–21).

We observed significant changes in coral community structure that track changes in pH and Ω*ar*. However, the compositional heterogeneity among low-pH, low-Ω*ar* sites on Palau suggests that coral community structure under OA conditions is not deterministic, and there is no single community of acidification “winners” within Palau’s low-pH reefs. Indeed, other local environmental and/or ecological factors, including changes in wave energy, temperature, and/or light, all of which covary as pH decreases from the barrier reefs to the Rock Island bays, may play a larger role in shaping community composition.

Several observations support this interpretation. First, the shift from offshore *Acropora*-abundant to inshore *Porites*-abundant communities is consistent with worldwide reef zonation patterns (22). Second, the presence and abundance of other genera (including *Favia* and *Favites*)
did not change with decreasing pH. Finally, a number of branching and foliose genera (for example, Pachyseris, Anacropora, Mycedium, Merulina, and Lobophyllia) typically associated with lower wave energy and/or light levels, and not considered insensitive to pH (23), were more abundant on Palau’s lowest-pH reefs than on the high-pH barrier reefs.

We also found that coral macrobioerosion increases significantly as pH decreases in Palau. In contrast to the change in community composition, factors other than pH are unlikely to explain this trend. Across multiple studies of coral bioerosion, there is no consistent correlation between macrobioerosion rates and degrees of wave exposure or intensity of flow (24–28). Elevated nutrient concentrations have been shown to correlate with increased coral macrobioerosion (15, 29), but nutrient concentrations do not change with decreasing seawater pH or with increased bioerosion in Palau. Our hypothesis that low pH causes the observed increase in coral macrobioerosion is supported by multiple laboratory experiments that show elevated bioerosion at low pH (30–32). Furthermore, in a recent field study, pH/Ωar emerged as a consistent factor in Porites macrobioerosion on 11 Pacific reef systems (15) spanning a wide range of pH, wave energy, and flow conditions (33). There are several potential mechanisms by which OA can cause increased macrobioerosion of live corals. One hypothesis is that skeletons accreted under OA are less dense, making them easier for bioerosers to penetrate (34). Although low-pH conditions in Palau do not necessarily produce lower-density skeletons, colonies with less dense skeletons are, in general, more likely to show evidence of bioerosion. In addition, lower pH may facilitate bioerosion by increasing the efficiency of biochemical dissolution (30, 35), one of the methods Lithophaga employs to excavate coral skeletons (36).

We compared our results with those obtained from similar analyses of naturally low-pH coral reef ecosystems near volcanic CO2 vents in Milne Bay, PNG (13), submarine freshwater springs (ojos) in Puerto Morelos, Mexico (14, 37), and low-pH upwelling zones in the eastern tropical Pacific (38, 39) in an effort to identify common response variables solely attributable to changes in pH (Table 1). Despite the paucity of naturally more acidified reefs identified to date, across-site comparisons are necessary because none are perfect analogs for coral reefs under future OA. CO2 accumulation is not always the primary or only driver of low pH/Ωar, and pH variability can be extreme relative to projected future values, as well as spatially and temporally heterogeneous. Covariability among pH and other variables including nutrients, salinity, light, water flow, and/or temperature can make it difficult to attribute specific ecological changes solely to acidification. Furthermore, scales of larval connectivity and recruitment sources vary between sites and may influence the adaptive potential of coral communities.

Our across-site comparison reveals few commonalities among low-pH reefs studied to date (Table 1). Despite comparable natural gradients in pH/Ωar, trends in coral cover and richness and cover of macroalgae and coralline algae are inconsistent, with the Rock Islands unique in showing no sensitivity to pH in any of these response variables. Coral richness declined steeply with declining pH in Mexico, PNG, and the eastern tropical Pacific, but did not change in Palau. Macroalgae cover increased at low pH in PNG only. On a CO2 reef vent site in Japan (not included in Table 1), hard coral-dominated communities gave way to soft coral-dominated reef communities as pH declined from the fringing reef to the shallow back reef pools cut off from the ocean at low tide (40). This did not occur at the PNG CO2 vent site. Porites abundance increased with pH decline in Palau and PNG, but it was not affected by low pH in Mexico. Porites calcification in Palau and PNG was insensitive to decreasing pH, whereas in Mexico, the eastern tropical Pacific, and in laboratory OA experiments, Porites calcification declined with low pH (7, 19, 21, 41).

The inconsistencies in community responses to acidification across naturally low-pH reef systems, and between reefs and laboratory experiments, may be due to a number of different factors. Although ultimately producing similar average pH and Ωar conditions, distinct mechanisms of acidification at each site lead to differences in extremes and frequencies of variability. For example, whereas the maximum seawater pCO2 levels in the Palau Rock Islands (pCO2 ~720 μatm) are close to the 2100 AD projections for the open ocean, the maximum concentrations at the Yucatan (pCO2 ~5120 μatm) (14) and PNG (pCO2 ~5740 μatm) (13) sites are about seven to eight times higher. pH variability in Palau is dominated by the diurnal and tidal cycles as it will be on future reefs, whereas PNG and Mexico are characterized by high-frequency spikes associated with pulses of CO2 and groundwater discharge (13, 14, 42). Yet, the hydrographic and biological processes that lower pH/Ωar in Palau also result in low total alkalinity (TA) and dissolved inorganic carbon (DIC) conditions, which are not expected under future OA. Furthermore, in the eastern tropical Pacific, temperature and nutrient concentrations covary with pH, making it difficult to attribute patterns in reef communities solely to upwelling-driven acidification (39).

Across the handful of naturally low-pH sites studied to date, Palau appears unique in showing no obvious sensitivity to OA across a range

### Table 1. Diverse reef responses to natural acidification in the Palau Rock Islands, PNG CO2 vents, Mexico ojos, and eastern tropical Pacific (ETP) upwelling regions.

| Region     | Hard coral cover | Macroalgae cover | Coralline algae cover | Hard coral richness | Porites cover | Porites extension | Porites density | Porites calcification | Bioerosion |
|------------|------------------|------------------|-----------------------|--------------------|---------------|-------------------|-----------------|----------------------|------------|
| Palau      | 1.9 (+)          | 0.7 (+)          | 1.1 (+)               | 1.6 (+)            | 16.0 (+)      | 1.0 (+)           | 0.8 (+)         | 0.8 (+)              | 11.3 (+)   |
| PNG        | 1.1 (+)          | 2.1 (+)          | 0.2 (+)               | 0.6 (+)            | 2.3 (+)       | 1.1 (+)           | 0.8 (+)         | 1.1 (+)              | 1.9 (+)    |
| Mexico     | 0.5 (+)          | n.d.             | n.d.                  | 0.3 (+)            | 0.8 (+)       | 1.0 (+)           | 0.8 (+)         | 0.7 (+)              | 1.4 (+)    |
| ETP        | 0.0 (+)          | n.d.             | n.d.                  | 0.2 (+)            | 0.8 (+)       | n.d.              | 0.6 (+)         | 0.5 (+)              | 1.9 (+)    |

*For Palau, ratios are calculated for the two lowest and the two highest pCO2 reefs, and the indicated significance is for the trend across all sites (pCO2 = 3.7 to 2.3). †For PNG, ratios and trends are reported for pCO2 = 3.5 to 2.9 (13). ‡Community data for Mexico are reported for pCO2 > 2.5 to pCO2 < 2.5 (17), and skeletal growth parameters are reported for pCO2 > 2 to pCO2 < 2 (14). §For the ETP, hard coral cover, hard coral richness, and Porites extension, density, and calcification data are reported for four reef sites within the Galapagos (pCO2 = 3.3 to 2.6) (39). Porites macrobioerosion rates are compared across the Galapagos, the Gulf of Panama, and Gulf of Chiriqui (pCO2 = 3.5 to 2.5) (38). ‖Trends in bioerosion are estimated by the percent volume of macrobioerosion of Porites skeletal cores (Palau and Mexico), Porites bioracer density (PNG), or bioerosion rate (ETP).
of key ecological indices. Laboratory experiments suggest that co-varying environmental factors including light, flow, nutrients, and food availability can modulate the negative impact of OA on calcification. None of these factors can explain the apparent OA tolerance of Palau’s benthic communities. Most factors that alleviate the impacts of pH in laboratory experiments are absent from Palau’s Rock Island bays, where high temperature, high shade, low flow, and low nutrient concentrations accompany OA conditions (4, 5, 8, 18) (table S1). The low-pH communities in Palau differ from other naturally low-pH sites studied to date in their relative isolation within bays and inlets and in OA conditions that are chronic and of less extreme ranges. It is possible that selective pressure has driven local, community-wide adaptation to low pH over long time scales (that is, thousands of years). In contrast, in PNG and Mexico, low-pH communities are more exposed, scales of connectivity may be larger than in low-pH areas, and the possibility that larvae are recruited to low-pH reefs from populations under less acidification pressure may preclude adaptation (11).

Increases in macrobioerosion with declining pH are the only consistent coral reef community response to natural acidification across low-pH reefs. In Palau, bioerosion increased significantly at low pH and persisted coral reef community response to natural acidification across low-pH reefs. In Palau, bioerosion increased significantly at low pH and 11 consistent coral reef community response to natural acidification across low-pH reefs. In Palau, bioerosion increased significantly at low pH and (table S1). The low-pH communities in Palau differ from other naturally low-pH sites studied to date in their relative isolation within bays and inlets and in OA conditions that are chronic and of less extreme ranges. It is possible that selective pressure has driven local, community-wide adaptation to low pH over long time scales (that is, thousands of years). In contrast, in PNG and Mexico, low-pH communities are more exposed, scales of connectivity may be larger than in low-pH areas, and the possibility that larvae are recruited to low-pH reefs from populations under less acidification pressure may preclude adaptation (11).

Increases in macrobioerosion with declining pH are the only consistent coral reef community response to natural acidification across low-pH reefs. In Palau, bioerosion increased significantly at low pH. The same patterns have been reported at low-pH reef sites in PNG (93% increase in bioeroder density from high pH to low pH) and Mexico (78% increase in Porites coral skeleton eroded) (13, 14). In the eastern tropical Pacific, elevated rates of reef bioerosion (87% increase from \( \Omega_{\text{er}} = 3.5 \) to \( \Omega_{\text{er}} = 2.5 \)) and decreased reef cementation have also been observed in low-pH, nutrient-rich upwelling zones (38), a component of which is attributable to low pH (15). Enhanced bioerosion and lack of cementation threaten the structural integrity of corals and reef systems, increasing the impact of predation and the risk of physical destruction by storms (30, 43). Moreover, if macrobioerosion is indicative of larger-scale reef erosion and dissolution (15, 25, 44), increases in \( \text{CaCO}_3 \) erosion under OA will have significant implications for the persistence of reef structures. Structural fragility is incompatible with the ability of barrier and fringing reefs to absorb and dissipate the energy associated with the constant day-to-day pounding of waves, seasonal storms, and the less frequent but more catastrophic tsunamis. Indeed, that bioerosion rates are elevated in all naturally low-pH coral reef systems studied to date suggests that the signature of 21st century OA will emerge most strongly and most universally through its impact on reef structural integrity.

**MATERIALS AND METHODS**

**Water sample collection and analysis**

Surface water samples (0 to 3 m, \( n = 195 \)) for salinity, nutrients, TA, and DIC were collected at multiple time points between sunrise and sunset on 19 to 24 September 2011, 28 March to 7 April 2012, 7 to 9 December 2012, and 1 to 15 November 2013 [data for 2011–2012 previously published in (11)]. TA and DIC analyses were performed using a Versatile Instrument for the Determination of Total inorganic carbon and titration Alkalinity (VINDTA, Marianda Analytics and Data), which uses open cell potentiometric (TA) and coulometric (DIC) titrations, and standardized using certified reference materials obtained from Andrew Dickson [Scripps Institution of Oceanography (45)]. Analysis of replicate samples (\( n = 13 \)) showed a mean precision of \( \sim 2 \mu \text{mol kg}^{-1} \) for TA and \( \sim 1 \mu \text{mol kg}^{-1} \) for DIC. Full CO2 system parameters were calculated from temperature, salinity, TA, and DIC using CO2SYS (46) with the constants of Mehrbach et al. (47) refit by Dickson and Millero (48). In situ pH time series were collected using a SAMI-pH sensor (Sunburst Sensors) deployed at three sites (1, 2, and 10) for 4 days in November 2013 (sites 2 and 10) and August 2014 (site 1).

**Benthic community data collection**

At each of eight sites (fig. S1: sites 1, 2, 5, 6, 7, 9, 10, and 11), five 50-m transects were laid on the reef at 3-m depth and a photograph of a 0.5 m x 0.5 m quadrat taken every meter. Photographs were analyzed using Coral Point Count with Excel extensions (49). Benthic cover of each photograph was evaluated by randomly overlaying five crosses on each image and identifying the type of cover and taxa underneath each cross, with all corals identified to the genus level, for a total of 200 points evaluated per transect and 1000 points evaluated per site. Porites corals were identified as massive species, branching species, or other. All transects were conducted in 2010, except for those from site 2, which were conducted in 2012.

**Coral skeletal core collection and analysis**

Coral skeletal cores were collected on SCUBA from 86 massive Porites colonies (fig. S1: sites 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10) and 25 Favia colonies (sites 1, 2, 8, and 9) in April 2011, September 2011, March to April 2012, and November 2013. Cores were scanned using a Siemens Volume Zoom Helical Computerized Tomography (CT) scanner, and extension, density, and calcification rates were calculated using annual banding patterns visualized from three-dimensional CT images in MATLAB [detailed procedure for analyzing coral growth rates in (15)]. The 2006–2010 averages of these parameters for each coral were used to compare growth rates across reef sites. CT scan images were used to determine the proportion of the skeleton eroded (>1 mm boring diameter) by boring organisms (including bivalves, worms, and sponges), calculated as the total volume of \( \text{CaCO}_3 \) removed relative to the total volume of the coral core, for each Porites coral. Boring percentage data for sites 1, 2, 7, and 8 were previously published in (15).

**Statistical analysis**

Statistical analyses were conducted in R (version 3.0.1) (50). To assess the health of Palau’s benthic communities, percent cover (coral, macroalgae, and crustose coralline algae) and community ecological indices (genera richness, Shannon diversity, and Shannon evenness) were calculated for each of the five transects per reef site. GLMs were used to evaluate the relationship between \( \Omega_{\text{er}} \) and the site-mean benthic cover data and ecological indices. Linear, log-linear, and polynomial models were evaluated for all response variables, but no model fits showed significant relationships between any community index and \( \Omega_{\text{er}} (P < 0.05) \). DCA on coral genera abundance data was conducted using the vegan package (51) to evaluate spatial trends in community structure across reef sites. Differences in community structure across the \( \Omega_{\text{er}} \) gradient were formally tested using redundancy analysis with a Monte Carlo permutation test (10,000 permutations). Log-linear or negative binomial count models were constructed to assess the relationship between the presence/absence and abundance of the eight most abundant genera on Palauan reefs (total abundance > 50 individuals) and \( \Omega_{\text{er}} \). Linear models were used to evaluate the relationship between \( \Omega_{\text{er}} \) and Porites and Favia mean annual rates of extension, density, and calcification rates and Porites tissue thickness. Porites...
bioerosion data were fitted with two separate models to evaluate changes in the presence/absence of bioerosion and volume percent of boring with changes in $\Omega_{	ext{ar}}$ and skeletal density; binary presence/absence data were fit to a logistic regression model, and a log-linear model was fit to site means of all nonzero boring percent data.

**SUPPLEMENTARY MATERIALS**

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/5/e1500328/DC1

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Competing interests: The authors declare that they have no competing interests.

Data and materials availability: The data reported in this paper are tabulated in the Supplementary Materials and archived with Pangea and BCO-DMO (Biological and Chemical Oceanography Data Management Office) databases. Ecological survey data are archived with PICRC (www.picrc.org).

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