Coral macrobioerosion is accelerated by ocean acidification and nutrients

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ABSTRACT

Coral reefs exist in a delicate balance between calcium carbonate (CaCO₃) production and CaCO₃ loss. Ocean acidification (OA), the CO₂-driven decline in seawater pH and CaCO₃ saturation state (Ω), threatens to tip this balance by decreasing calcification, and increasing erosion and dissolution. While multiple CO₂ manipulation experiments show coral calcification declines under OA, the sensitivity of bioerosion to OA is less well understood. Previous work suggests that coral and coral reef bioerosion
increase with decreasing seawater Ω. However, in the surface ocean, Ω and nutrient concentrations often covary, making their relative influence difficult to resolve. Here, we exploit unique natural gradients in Ω and nutrients across the Pacific basin to quantify the impact of these factors, together and independently, on macrobioerosion rates of coral skeletons. Using an automated program to quantify macrobioerosion in 3-D computerized tomography (CT) scans of coral cores, we show that macrobioerosion rates of live *Porites* colonies in both low-nutrient (oligotrophic) and high-nutrient (>1 µM nitrate) waters increase significantly as Ω decreases. However, the sensitivity of macrobioerosion to Ω is ten times greater under high-nutrient conditions. Our results demonstrate that OA (decreased Ω) alone can increase coral macrobioerosion rates, but the interaction of OA with local stressors exacerbates its impact, accelerating a shift toward net CaCO₃ removal from coral reefs.

**INTRODUCTION**

Tropical coral reefs are oases of productivity that support some of the world’s most biologically diverse ecosystems and important fisheries. High productivity by sessile organisms on reefs requires formation of hard calcium carbonate (CaCO₃) substrate in the euphotic zone, where photosynthesis can occur. This is achieved through biogenic calcification by reef organisms such as corals, coralline algae, echinoids, foraminifera, and mollusks which, together with precipitation of abiogenic CaCO₃, build and cement the reef framework. Coral reef frameworks are degraded through bioerosion, the biologically mediated breakdown and dissolution of CaCO₃ skeletons, as well as natural dissolution and export of sand and rubble off the reef (Glynn, 1997). Today, net
CaCO₃ accretion typically exceeds, albeit barely, net erosion and dissolution, allowing reefs to remain near the sea surface (Stearn et al., 1977; Hubbard et al., 1990). Of mounting concern is that ocean acidification (OA), the decrease in ocean pH caused by absorption of anthropogenic CO₂, could shift this delicate balance toward a negative CaCO₃ budget where CaCO₃ loss exceeds CaCO₃ production. Addition of CO₂ to seawater decreases pH and lowers the CaCO₃ saturation state (Ω), creating a less favorable environment for CaCO₃ precipitation. Aragonite is the polymorph of CaCO₃ that corals use to build skeletons and the CaCO₃ saturation state with respect to aragonite (Ωₐrₐg) is therefore a useful quantity in identifying how OA impacts the reef CaCO₃ budget. CO₂ laboratory manipulation experiments show that as Ωₐrₐg decreases, rates of calcification by corals and coralline algae generally decline (Kroeker et al., 2010; Chan and Connolly, 2013). Additionally, laboratory CO₂ manipulation experiments show that rates of bioerosion of coral skeleton increase with decreasing pH (Tribollet et al., 2009; Wisshak et al., 2012; Reyes-Nivia et al., 2013). The combination of declining calcification and increasing bioerosion under low pH and Ωₐrₐg implies that OA alone could drive coral reefs toward a state of net CaCO₃ loss. However, the impact of OA on coral reef bioerosion has not been unequivocally demonstrated outside of the laboratory because in the tropical oceans, low Ωₐrₐg generally covaries with elevated nutrients, and high nutrient concentrations can drive high rates of coral bioerosion in the absence of acidification (Risk et al., 1995; Edinger et al., 2000; Holmes et al., 2000; Tribollet and Golubic, 2005).

We exploited natural gradients in Ωₐrₐg and nutrient concentrations across the Pacific basin to investigate the independent and interactive effects of ocean acidification
and nutrients on macrobioerosion rates of live colonies of the Indo-Pacific coral *Porites* spp. While macrobioerosion (>1 mm boring diameter including bivalves, worms, and sponges) of coral skeleton is a fraction of total CaCO₃ bioerosion on a reef (Glynn, 1997), independent studies show that macrobioerosion occurs in proportion to total bioerosion of coral rubble (Holmes et al., 2000) and experimental blocks of coral skeleton (Chazottes et al., 2002), and can thus be linked to total reef bioerosion. Macrobioerosion also affects the longevity of individual coral colonies, increasing their susceptibility to breakage and dislodgment by waves and storms (Scott and Risk, 1988; Chen et al., 2013).

**MATERIALS AND METHODS**

A total of 103 skeletal cores (3–7 cm diameter) were collected using underwater pneumatic/hydraulic drills from live *Porites* spp. coral colonies (~40–100 cm tall) that appeared visually healthy at 11 sampling locations within 7 reef systems across the Pacific basin (Fig. 1; Table 1). Cores were drilled downwards along the axis of maximum growth from approximately the center of the colonies, to an average depth of ~35 cm. Across the Pacific basin, strong natural gradients exist in $\Omega_{\text{Arag}}$ and nutrient concentrations (Fig. 1), and in general, this pattern is supported by in situ sampling of the carbonate chemistry and dissolved inorganic nutrients of reef seawater (Table 1). Two eastern Pacific reefs (Pearl Islands and Taboga) in the Gulf of Panama are exposed to local upwelling water of low $\Omega_{\text{Arag}}$ and high nutrient concentrations (D’Croz and O’Dea, 2007; Manzello et al., 2008). In the central Pacific, Jarvis Island, Palmyra Atoll, and Kingman Reef are located near the margin of the Pacific cold-tongue, where wind-driven upwelling along the Equator brings water to the surface that is relatively acidic and
nutrient-rich compared to surrounding water. Rose Atoll and Wake Atoll are not exposed to cold-tongue waters and are characterized by high $\Omega_{Arag}$, low nutrient conditions. On Palau, in the tropical western Pacific, a strong natural gradient in $\Omega_{Arag}$ exists across the archipelago, at persistently low nutrient concentrations (Table 1) (Shamberger et al., 2014). This reef system provides a unique opportunity to investigate the effect of low $\Omega_{Arag}$ on coral macrobioerosion in the absence of the confounding effect of elevated nutrients.

To characterize $\Omega_{Arag}$ and nutrient concentrations in reef seawater, samples were collected during multiple years, seasons, and times of day at the majority of our eleven reef locations (Table 1). Nevertheless, some degree of uncertainty remains because accurate estimates of the average $\Omega_{Arag}$ and nutritional environment over the lifetime of the coral requires sampling on all relevant timescales, including diurnal, seasonal, inter-annual and decadal. Comparison with other in situ datasets suggests that this uncertainty is small relative to the range captured by our study sites (details provided in the GSA Data Repository).

We developed an automated computer program to quantify calcification and macrobioerosion rates in coral skeleton cores scanned by computerized tomography (CT). The program quantifies coral extension rate following the methods of Cantin et al. (2010), with modification to automatically trace the 3-dimensional growth paths of individual corallites within the core. This enables growth information to be collected from the entire 3-D core. Bulk skeletal density was determined from CT scans by comparison to coral standards, cylinders of coral skeleton whose density is calculated from mass and volume. Annual coral calcification rate (g cm$^{-2}$ yr$^{-1}$) was calculated as the
product of skeletal density (g cm\(^{-3}\)) and extension rate (cm yr\(^{-1}\)). The automated program

is described in detail in the GSA Data Repository.

We define “bioerosion rate” as the average rate at which CaCO\(_3\) is removed from

the colony over the timespan represented by the core:

\[
\text{bioerosion rate (g CaCO}_3\text{ cm}^{-2}\text{ year}^{-1}) = \frac{(\text{volume bioeroded})(\text{skeletal density})}{(\text{coral surface area})(\text{core timespan})}
\]

Equation 1 is equivalent to the product of % volume bioeroded (Fig. 2) and coral
calcification rate. Converting % volume bioeroded to a mean bioerosion rate corrects
potential biases caused by differences in growth rates and density amongst corals.

The % volume bioeroded data were fit with \(\Omega_{\text{Ar}}\) as the predictor variable using a
generalized additive model for location, scale, and shape with a beta zero-inflated
distribution (GAMLSS-BID) (Rigby and Stasinopoulos, 2005). GAMLSS allows both the
mean % volume bioeroded and the skewness toward zero values (i.e. cores without
macrobioerosion) to depend on \(\Omega_{\text{Ar}}\) and nutrients. Sensitivity of macrobioerosion to
\(\Omega_{\text{Ar}}\) between low- (<1 \(\mu\)M nitrate) and high- (>1 \(\mu\)M nitrate) nutrient reefs was
evaluated by comparing slopes of ordinary least squares regressions fit to the reef mean
macrobioerosion rates. Heteroscedasticity of the data precluded significance tests using
linear regression, but did not invalidate the regression coefficients.

RESULTS AND DISCUSSION

Using only those cores collected from low-nutrient reefs spanning a natural
gradient in \(\Omega_{\text{Ar}}\) we first quantified the impact of ocean acidification on macrobioerosion
without the confounding influence of nutrients (Fig. 3). Our results show a significant (p
< 0.05) increase in macrobioerosion with decreasing seawater \(\Omega_{\text{Ar}}\). This result confirms
that ocean acidification alone increases rates of coral macrobioerosion, consistent with
laboratory experiments that show increased sponge (Wisshak et al., 2012) and micro-
(Tribollet et al., 2009; Reyes-Nivia et al., 2013) bioerosion of coral skeleton under
simulated OA/low-nutrient conditions. In our corals, macrobioerosion rates increase by
10 mg CaCO$_3$ cm$^{-2}$ yr$^{-1}$ per unit decrease of $\Omega_{Arag}$.

Other field studies have reported high rates of bioerosion where seawater $\Omega_{Arag}$ is
relatively low. For example, in the eastern tropical Pacific, high bioerosion rates (Reaka-
Kudla et al., 1996) were measured on coral reefs bathed with naturally low $\Omega_{Arag}$
upwelled water (Manzello et al., 2008). Similarly, the density of macrobioeroders
observed at the surface of live Porites colonies increased along a natural acidification
gradient caused by CO$_2$ venting onto reefs in Papua New Guinea (Fabricius et al., 2011).
Low pH seawater caused by submarine discharge was also linked to higher incidence of
bioerosion in Porites astreoides colonies in the Yucatan (Crook et al., 2013). In these
studies however, low pH and low $\Omega_{Arag}$ either covary with high nutrient concentrations
(Manzello et al., 2008; Crook et al., 2013), or nutrient data were not reported (Fabricius
et al., 2011), making it difficult to attribute increased bioerosion or bioeroder density
solely to OA.

Using a second set of cores, collected from high-nutrient reefs spanning a natural
gradient in $\Omega_{Arag}$, we investigated the combined impact of ocean acidification and
elevated nutrients on coral macrobioerosion rates (Fig. 3). Our results show that
sensitivity of macrobioerosion rate to $\Omega_{Arag}$ increases by an order of magnitude - from 10
to 110 mg CaCO$_3$ cm$^{-2}$ yr$^{-1}$ per unit decrease of $\Omega_{Arag}$ - from low-nutrient reefs to high-
nutrient reefs. The GAMLSS-BID analysis showed a significant effect of $\Omega_{Arag}$ on
macrobioerosion within high-nutrient reefs, and a significant effect of nutrients when all
reefs were included with $\Omega_{\text{Arag}}$ as a continuous predictor and nutrients as a categorical predictor. Our observation that nutrients accelerate coral bioerosion rates is consistent with that reported for live corals (Sammarco and Risk, 1990; Risk et al., 1995; Edinger et al., 2000; Holmes et al., 2000; Chen et al., 2013), coral rubble (Holmes et al., 2000), and experimental blocks of coral skeleton exposed on high-nutrient reefs (Chazottes et al., 2002; Tribollet and Golubic, 2005).

There are several potential mechanisms for coral macrobioerosion rates to increase with decreasing $\Omega_{\text{Arag}}$ and with increasing nutrients. First, relatively acidic seawater may increase the efficiency with which coral skeleton is dissolved by bioeroding organisms. For example, boring algae that infest live coral colonies, and increase their susceptibility to macrobioerosion, drive dissolution along the most soluble crystal surfaces (Kobluk and Risk, 1977). Second, nutrient enrichment may stimulate primary productivity, elevating particulate food availability and turbidity, making nutrient-rich reefs favorable environments for filter-feeding bioeroders. The role of coral skeletal density in determining sensitivity to macrobioerosion has been considered previously, with mixed results (Highsmith, 1981; Sammarco and Risk, 1990). We found no significant effect of skeletal density on macrobioerosion in the GAMLSS-BID analyses. Nor did we find a relationship to water depth or reef type (Table 1).

Bioerosion is a natural process on coral reefs that supplies carbonate sediments critical to the cementation of the reef (Glynn, 1997), and may contribute to propagation of certain coral species that reproduce by fragmentation (Tunnicliffe, 1981). However, calcification must exceed bioerosion in order for reefs to grow and persist in the euphotic zone. Ocean acidification will drive a decrease in rates of calcification by corals and
coralline algae, and ocean warming will exacerbate these impacts by inducing coral bleaching and mortality (Hoegh-Guldberg et al., 2007). If decreased calcification co-occurs with increased bioerosion, the CaCO3 balance will shift more rapidly toward a negative CaCO3 budget.

CONCLUSIONS

The results of this study show that the combination of OA (low $\Omega_{\text{Arag}}$) and nutrient loading is ten times more effective at driving coral macrobioerosion than OA alone. Over the next century, $\Omega_{\text{Arag}}$ of reef seawater will be governed by the ocean’s absorption of anthropogenic CO2, and local and regional variability in biogeochemical processes (e.g., net photosynthesis and net calcification). However, anthropogenic nutrient loading is already a major threat to coral reef ecosystems, with at least one quarter of coral reefs impacted by coastal development and watershed pollution (Burke et al., 2011). Curtailing global CO2 emissions, the primary driver of ocean acidification, cannot be tackled at a local level. However, effective local management strategies can limit anthropogenic nutrient fluxes to coral reefs, and are urgently needed to slow the shift to net CaCO3 removal for corals, and potentially coral reef ecosystems, worldwide.

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Figure 1. Study reef systems and climatological means of (A), aragonite saturation state ($\Omega_{Arag}$) and (B), nitrate concentration in surface waters of the tropical Pacific Ocean. $\Omega_{Arag}$ is calculated using the program CO2SYS (Lewis et al., 1998) with temperature, salinity, nitrate, phosphate, and silicate climatologies from the World Ocean Atlas (Levitus et al., 2010), dissolved inorganic carbon (DIC) climatology during the 1990s from the Global Ocean Data Analysis Project (Key et al., 2004), and total alkalinity (TA) calculated following Lee et al. (2006). Each reef system is colored by in situ seawater sample chemistry, except Wake Atoll. Palau is colored by values for Uchelbeluu.

Figure 2. Macrobioerosion (by *lithophagid* bivalves in this particular core) in a CT scan of a *Porites* skeleton core from Panama. (A-D), axial cross-sections showing measurement of % volume bioeroded. (A), Density variability (relatively light shading indicates high density) shows ~200 individual corallites (dark spots) and three borings (arrows). The image in (A) was filtered to reduce density variability of corallites in (B), converted to binary (coral / surrounding air) in (C), and fit with an ellipse to identify area
of borings (black regions within yellow circle) in (D). (E), Sagittal cross-section showing
annual density banding and borings. (F), Surface rendering showing outside of the core.
(G), translucent surface showing borings in the center of the core (blue) that are visible in
the cross-section in (E) but not in the outside surface of (F). Scale bar in upper left is 1
cm.

Figure 3. Relationship between macrobioerosion in the skeletons of living *Porites*
colonies and aragonite saturation state ($\Omega_{\text{Arag}}$) for low-nutrient (black) and high-nutrient
(red) reefs (solid lines are model fits; shading is standard error). Reef mean
macrobioerosion indicated with circles and linear fits with dashed lines. The inset shows
reef mean macrobioerosion rate.

\(^1\)GSA Data Repository item 2014xxx, supporting text for seasonal and diurnal $\Omega_{\text{Arag}}$
variability, and Figures DR1-2 (density calibration and coral calcification methods), is
available online at www.geosociety.org/pubs/ft2014.htm, or on request from
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