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1 Coral macrobioerosion is accelerated by ocean acidification  
2 and nutrients

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16 **ABSTRACT**

17 Coral reefs exist in a delicate balance between calcium carbonate (CaCO<sub>3</sub>)  
18 production and CaCO<sub>3</sub> loss. Ocean acidification (OA), the CO<sub>2</sub>-driven decline in  
19 seawater pH and CaCO<sub>3</sub> saturation state ( $\Omega$ ), threatens to tip this balance by decreasing  
20 calcification, and increasing erosion and dissolution. While multiple CO<sub>2</sub> manipulation  
21 experiments show coral calcification declines under OA, the sensitivity of bioerosion to  
22 OA is less well understood. Previous work suggests that coral and coral reef bioerosion

23 increase with decreasing seawater  $\Omega$ . However, in the surface ocean,  $\Omega$  and nutrient  
24 concentrations often covary, making their relative influence difficult to resolve. Here, we  
25 exploit unique natural gradients in  $\Omega$  and nutrients across the Pacific basin to quantify the  
26 impact of these factors, together and independently, on macrobioerosion rates of coral  
27 skeletons. Using an automated program to quantify macrobioerosion in 3-D computerized  
28 tomography (CT) scans of coral cores, we show that macrobioerosion rates of live *Porites*  
29 colonies in both low-nutrient (oligotrophic) and high-nutrient ( $>1 \mu\text{M}$  nitrate) waters  
30 increase significantly as  $\Omega$  decreases. However, the sensitivity of macrobioerosion to  $\Omega$  is  
31 ten times greater under high-nutrient conditions. Our results demonstrate that OA  
32 (decreased  $\Omega$ ) alone can increase coral macrobioerosion rates, but the interaction of OA  
33 with local stressors exacerbates its impact, accelerating a shift toward net  $\text{CaCO}_3$  removal  
34 from coral reefs.

## 35 **INTRODUCTION**

36 Tropical coral reefs are oases of productivity that support some of the world's  
37 most biologically diverse ecosystems and important fisheries. High productivity by  
38 sessile organisms on reefs requires formation of hard calcium carbonate ( $\text{CaCO}_3$ )  
39 substrate in the euphotic zone, where photosynthesis can occur. This is achieved through  
40 biogenic calcification by reef organisms such as corals, coralline algae, echinoids,  
41 foraminifera, and mollusks which, together with precipitation of abiogenic  $\text{CaCO}_3$ , build  
42 and cement the reef framework. Coral reef frameworks are degraded through bioerosion,  
43 the biologically mediated breakdown and dissolution of  $\text{CaCO}_3$  skeletons, as well as  
44 natural dissolution and export of sand and rubble off the reef (Glynn, 1997). Today, net

45 CaCO<sub>3</sub> accretion typically exceeds, albeit barely, net erosion and dissolution, allowing  
46 reefs to remain near the sea surface (Stearn et al., 1977; Hubbard et al., 1990).

47 Of mounting concern is that ocean acidification (OA), the decrease in ocean pH  
48 caused by absorption of anthropogenic CO<sub>2</sub>, could shift this delicate balance toward a  
49 negative CaCO<sub>3</sub> budget where CaCO<sub>3</sub> loss exceeds CaCO<sub>3</sub> production. Addition of CO<sub>2</sub>  
50 to seawater decreases pH and lowers the CaCO<sub>3</sub> saturation state ( $\Omega$ ), creating a less  
51 favorable environment for CaCO<sub>3</sub> precipitation. Aragonite is the polymorph of CaCO<sub>3</sub>  
52 that corals use to build skeletons and the CaCO<sub>3</sub> saturation state with respect to aragonite  
53 ( $\Omega_{\text{Arag}}$ ) is therefore a useful quantity in identifying how OA impacts the reef CaCO<sub>3</sub>  
54 budget. CO<sub>2</sub> laboratory manipulation experiments show that as  $\Omega_{\text{Arag}}$  decreases, rates of  
55 calcification by corals and coralline algae generally decline (Kroeker et al., 2010; Chan  
56 and Connolly, 2013). Additionally, laboratory CO<sub>2</sub> manipulation experiments show that  
57 rates of bioerosion of coral skeleton increase with decreasing pH (Tribollet et al., 2009;  
58 Wisshak et al., 2012; Reyes-Nivia et al., 2013). The combination of declining  
59 calcification and increasing bioerosion under low pH and  $\Omega_{\text{Arag}}$  implies that OA alone  
60 could drive coral reefs toward a state of net CaCO<sub>3</sub> loss. However, the impact of OA on  
61 coral reef bioerosion has not been unequivocally demonstrated outside of the laboratory  
62 because in the tropical oceans, low  $\Omega_{\text{Arag}}$  generally covaries with elevated nutrients, and  
63 high nutrient concentrations can drive high rates of coral bioerosion in the absence of  
64 acidification (Risk et al., 1995; Edinger et al., 2000; Holmes et al., 2000; Tribollet and  
65 Golubic, 2005).

66 We exploited natural gradients in  $\Omega_{\text{Arag}}$  and nutrient concentrations across the  
67 Pacific basin to investigate the independent and interactive effects of ocean acidification

68 and nutrients on macrobioerosion rates of live colonies of the Indo-Pacific coral *Porites*  
69 spp. While macrobioerosion (>1 mm boring diameter including bivalves, worms, and  
70 sponges) of coral skeleton is a fraction of total CaCO<sub>3</sub> bioerosion on a reef (Glynn,  
71 1997), independent studies show that macrobioerosion occurs in proportion to total  
72 bioerosion of coral rubble (Holmes et al., 2000) and experimental blocks of coral  
73 skeleton (Chazottes et al., 2002), and can thus be linked to total reef bioerosion.  
74 Macrobioerosion also affects the longevity of individual coral colonies, increasing their  
75 susceptibility to breakage and dislodgment by waves and storms (Scott and Risk, 1988;  
76 Chen et al., 2013).

## 77 **MATERIALS AND METHODS**

78 A total of 103 skeletal cores (3–7 cm diameter) were collected using underwater  
79 pneumatic/hydraulic drills from live *Porites* spp. coral colonies (~40–100 cm tall) that  
80 appeared visually healthy at 11 sampling locations within 7 reef systems across the  
81 Pacific basin (Fig. 1; Table 1). Cores were drilled downwards along the axis of maximum  
82 growth from approximately the center of the colonies, to an average depth of ~35 cm.  
83 Across the Pacific basin, strong natural gradients exist in  $\Omega_{\text{Arag}}$  and nutrient  
84 concentrations (Fig. 1), and in general, this pattern is supported by in situ sampling of the  
85 carbonate chemistry and dissolved inorganic nutrients of reef seawater (Table 1). Two  
86 eastern Pacific reefs (Pearl Islands and Taboga) in the Gulf of Panama are exposed to  
87 local upwelling water of low  $\Omega_{\text{Arag}}$  and high nutrient concentrations (D’Croz and O’Dea,  
88 2007; Manzello et al., 2008). In the central Pacific, Jarvis Island, Palmyra Atoll, and  
89 Kingman Reef are located near the margin of the Pacific cold-tongue, where wind-driven  
90 upwelling along the Equator brings water to the surface that is relatively acidic and

91 nutrient-rich compared to surrounding water. Rose Atoll and Wake Atoll are not exposed  
92 to cold-tongue waters and are characterized by high  $\Omega_{\text{Arag}}$ , low nutrient conditions. On  
93 Palau, in the tropical western Pacific, a strong natural gradient in  $\Omega_{\text{Arag}}$  exists across the  
94 archipelago, at persistently low nutrient concentrations (Table 1) (Shamberger et al.,  
95 2014). This reef system provides a unique opportunity to investigate the effect of low  
96  $\Omega_{\text{Arag}}$  on coral macrobioerosion in the absence of the confounding effect of elevated  
97 nutrients.

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

106 We developed an automated computer program to quantify calcification and  
107 macrobioerosion rates in coral skeleton cores scanned by computerized tomography  
108 (CT). The program quantifies coral extension rate following the methods of Cantin et al.  
109 (2010), with modification to automatically trace the 3-dimensional growth paths of  
110 individual corallites within the core. This enables growth information to be collected  
111 from the entire 3-D core. Bulk skeletal density was determined from CT scans by  
112 comparison to coral standards, cylinders of coral skeleton whose density is calculated  
113 from mass and volume. Annual coral calcification rate ( $\text{g cm}^{-2} \text{yr}^{-1}$ ) was calculated as the

114 product of skeletal density ( $\text{g cm}^{-3}$ ) and extension rate ( $\text{cm yr}^{-1}$ ). The automated program  
115 is described in detail in the GSA Data Repository.

116 We define “bioerosion rate” as the average rate at which  $\text{CaCO}_3$  is removed from  
117 the colony over the timespan represented by the core:

$$118 \text{ bioerosion rate } (\text{g CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}) = \frac{(\text{volume bioeroded})(\text{skeletal density})}{(\text{coral surface area})(\text{core timespan})} \quad (1)$$

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

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

## 131 **RESULTS AND DISCUSSION**

132 Using only those cores collected from low-nutrient reefs spanning a natural  
133 gradient in  $\Omega_{\text{Arag}}$  we first quantified the impact of ocean acidification on macrobioerosion  
134 without the confounding influence of nutrients (Fig. 3). Our results show a significant ( $p$   
135  $< 0.05$ ) increase in macrobioerosion with decreasing seawater  $\Omega_{\text{Arag}}$ . This result confirms  
136 that ocean acidification alone increases rates of coral macrobioerosion, consistent with

137 laboratory experiments that show increased sponge (Wisshak et al., 2012) and micro-  
138 (Tribollet et al., 2009; Reyes-Nivia et al., 2013) bioerosion of coral skeleton under  
139 simulated OA/low-nutrient conditions. In our corals, macrobioerosion rates increase by  
140  $10 \text{ mg CaCO}_3 \text{ cm}^{-2} \text{ yr}^{-1}$  per unit decrease of  $\Omega_{\text{Arag}}$ .

141 Other field studies have reported high rates of bioerosion where seawater  $\Omega_{\text{Arag}}$  is  
142 relatively low. For example, in the eastern tropical Pacific, high bioerosion rates (Reaka-  
143 Kudla et al., 1996) were measured on coral reefs bathed with naturally low  $\Omega_{\text{Arag}}$   
144 upwelled water (Manzello et al., 2008). Similarly, the density of macrobioeroders  
145 observed at the surface of live *Porites* colonies increased along a natural acidification  
146 gradient caused by CO<sub>2</sub> venting onto reefs in Papua New Guinea (Fabricius et al., 2011).  
147 Low pH seawater caused by submarine discharge was also linked to higher incidence of  
148 bioerosion in *Porites astreoides* colonies in the Yucatan (Crook et al., 2013). In these  
149 studies however, low pH and low  $\Omega_{\text{Arag}}$  either covary with high nutrient concentrations  
150 (Manzello et al., 2008; Crook et al., 2013), or nutrient data were not reported (Fabricius  
151 et al., 2011), making it difficult to attribute increased bioerosion or bioeroder density  
152 solely to OA.

153 Using a second set of cores, collected from high-nutrient reefs spanning a natural  
154 gradient in  $\Omega_{\text{Arag}}$ , we investigated the combined impact of ocean acidification and  
155 elevated nutrients on coral macrobioerosion rates (Fig. 3). Our results show that  
156 sensitivity of macrobioerosion rate to  $\Omega_{\text{Arag}}$  increases by an order of magnitude - from 10  
157 to  $110 \text{ mg CaCO}_3 \text{ cm}^{-2} \text{ yr}^{-1}$  per unit decrease of  $\Omega_{\text{Arag}}$  - from low-nutrient reefs to high-  
158 nutrient reefs. The GAMLSS-BID analysis showed a significant effect of  $\Omega_{\text{Arag}}$  on  
159 macrobioerosion within high-nutrient reefs, and a significant effect of nutrients when all

160 reefs were included with  $\Omega_{\text{Arag}}$  as a continuous predictor and nutrients as a categorical  
161 predictor. Our observation that nutrients accelerate coral bioerosion rates is consistent  
162 with that reported for live corals (Sammarco and Risk, 1990; Risk et al., 1995; Edinger et  
163 al., 2000; Holmes et al., 2000; Chen et al., 2013), coral rubble (Holmes et al., 2000), and  
164 experimental blocks of coral skeleton exposed on high-nutrient reefs (Chazottes et al.,  
165 2002; Tribollet and Golubic, 2005).

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

178         Bioerosion is a natural process on coral reefs that supplies carbonate sediments  
179 critical to the cementation of the reef (Glynn, 1997), and may contribute to propagation  
180 of certain coral species that reproduce by fragmentation (Tunncliffe, 1981). However,  
181 calcification must exceed bioerosion in order for reefs to grow and persist in the euphotic  
182 zone. Ocean acidification will drive a decrease in rates of calcification by corals and



183 coralline algae, and ocean warming will exacerbate these impacts by inducing coral  
184 bleaching and mortality (Hoegh-Guldberg et al., 2007). If decreased calcification co-  
185 occurs with increased bioerosion, the  $\text{CaCO}_3$  balance will shift more rapidly toward a  
186 negative  $\text{CaCO}_3$  budget.

## 187 **CONCLUSIONS**

188         The results of this study show that the combination of OA (low  $\Omega_{\text{Arag}}$ ) and  
189 nutrient loading is ten times more effective at driving coral macrobioerosion than OA  
190 alone. Over the next century,  $\Omega_{\text{Arag}}$  of reef seawater will be governed by the ocean's  
191 absorption of anthropogenic  $\text{CO}_2$ , and local and regional variability in biogeochemical  
192 processes (e.g., net photosynthesis and net calcification). However, anthropogenic  
193 nutrient loading is already a major threat to coral reef ecosystems, with at least one  
194 quarter of coral reefs impacted by coastal development and watershed pollution (Burke et  
195 al., 2011). Curtailing global  $\text{CO}_2$  emissions, the primary driver of ocean acidification,  
196 cannot be tackled at a local level. However, effective local management strategies can  
197 limit anthropogenic nutrient fluxes to coral reefs, and are urgently needed to slow the  
198 shift to net  $\text{CaCO}_3$  removal for corals, and potentially coral reef ecosystems, worldwide.

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

337 Figure 2. Macrobioerosion (by *lithophagid* bivalves in this particular core) in a CT scan  
338 of a *Porites* skeleton core from Panama. (A-D), axial cross-sections showing  
339 measurement of % volume bioeroded. (A), Density variability (relatively light shading  
340 indicates high density) shows ~200 individual corallites (dark spots) and three borings  
341 (arrows). The image in (A) was filtered to reduce density variability of corallites in (B),  
342 converted to binary (coral / surrounding air) in (C), and fit with an ellipse to identify area

343 of borings (black regions within yellow circle) in (D). (E), Sagittal cross-section showing  
344 annual density banding and borings. (F), Surface rendering showing outside of the core.  
345 (G), translucent surface showing borings in the center of the core (blue) that are visible in  
346 the cross-section in (E) but not in the outside surface of (F). Scale bar in upper left is 1  
347 cm.

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

353 <sup>1</sup>GSA Data Repository item 2014xxx, supporting text for seasonal and diurnal  $\Omega_{\text{Arag}}$   
354 variability, and Figures DR1-2 (density calibration and coral calcification methods), is  
355 available online at [www.geosociety.org/pubs/ft2014.htm](http://www.geosociety.org/pubs/ft2014.htm), or on request from  
356 [editing@geosociety.org](mailto:editing@geosociety.org) or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO  
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