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Keck Geology Consortium: Projects 2007-2008
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RATES AND STYLES OF BIOEROSION WITH VARYING SEDIMENTATION: HOLOCENE REEFS IN THE WESERN DOMINICAN REPUBLIC VERSUS MODERN REEFS OFF ST. CROIX, USVI

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INTRODUCTION

Bioerosion refers to the collective processes by biological agents that result in the destruction of hard substrate. A key component is macroboring, defined by Bromley (1994) as galleries larger than the millimeter scale. Modern assemblages of macroborers are commonly comprised of various species of sponges, bivalves, and worms (Hutchings, 1986). Many recognize bioerosional processes within coral reef systems for a gamut of consequences, such as fine-grained sediment production (Neumann, 1966; Futterer, 1974; Moore and Shedd, 1977), destruction of coral framework (Hutchings, 1986; Aronson and Precht, 1997; Perry, 2000) and the creation of key taphonomic indicators of paleoenvironment (Perry, 2000; Perry and Hepburn, 2007). This study examines possible indicators of paleoenvironment by comparing rates and styles of macroboring within modern reefs off St. Croix to those in fossil Holocene reefs in the western Dominican Republic. Coral samples were collected from each site and analyzed to quantitatively assess the different types of macroboring assemblages and their relative importance depending on sedimentation/nutrient regime and wave energy.

METHODS

Nineteen samples of dead Montastraea spp. were collected at 10-ft depth intervals (max = 80 ft) along three transects on the northern shore of St. Croix (see Fig. 1 in Hubbard et al., this volume). Two parallel transects were samples at Cane Bay on the northwest corner of the island (Fig. 1). Three additional samples were recovered from Tague Reef on northeastern St. Croix. The along-the-bottom distance between sample sites was used to reconstruct the profile along which samples were recovered (Fig. 1). Samples were washed in a bleach solution to remove organics and returned to the lab.

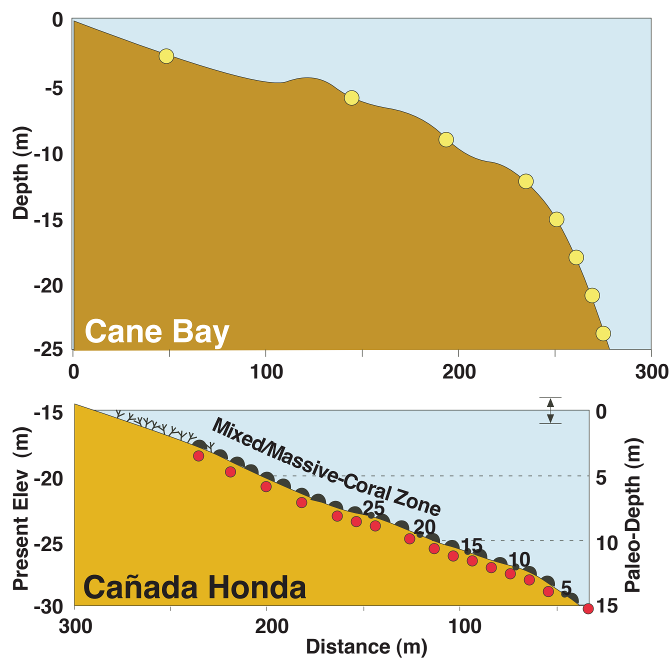


Figure 1. Sampling schemes for Cane Bay on NE St Croix (top) and Cañada Honda (bottom) in the Western Dominican Republic. Samples were collected using his scheme along two parallel transects. For further location information, see Figure 1 in Hubbard et al (this volume).

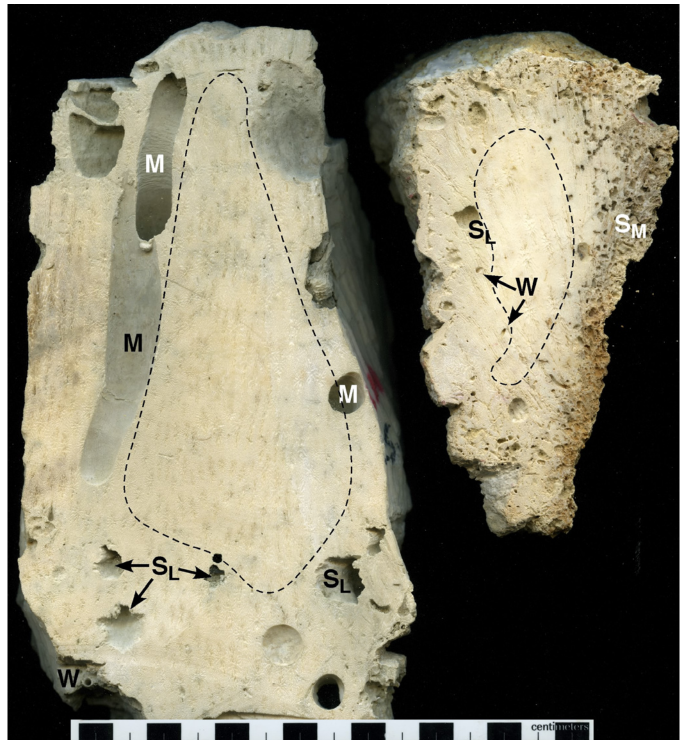
In the Dominican Republic, 19 samples of fossil S*iderastraea spp.* and 19 *Montastraea spp.* colonies were recovered from two exposed reef outcrops. At one outcrop (Cañada Honda), samples were collected at 10-m horizontal intervals along a time surface in the massive-coral facies (Fig. 1). The surface is defined by a storm-debris layer that is dominated by

Madracis auretenra transported downslope. Radiometric dates from the storm layer (ca. 8,000 Cal BP) and the record of Caribbean sea level were used to reconstruct paleo-water depth along the reef profile. Four additional samples were collected from the mixed-coral facies located up-outcrop. Four other samples were taken from a similar environment in another outcrop 15 km to the east (Las Clavellinas). The samples of *Montastraea spp.* were only lightly bored; high-resolution digital photographs were taken for lab analysis. All other samples were returned to the lab for analysis.

The 38 bioeroded samples were slabbed, and both faces were usually scanned at high resolution (Fig. 2). The bioerosion galleries of 73 total scans were traced and color-coded using Adobe Photoshop. Coding placed traces into three main categories: sponges, bivalves, and worms. Sponge galleries were sub-divided into: small sponge, large sponge, and meshwork sponge. Classifications of borers were based on descriptions and images from Perry (2000). Tracings were imported into NIH ImageJ, and the area of each type of gallery was tabulated within the bored coral rim or zone of bioerosion (ZoBE: Fig. 2). These were reported as a percent of substrate removed within the ZoBE (i.e., not for the entire colony) to eliminate biases related to colony size; the majority of macroboring generally occurs within the outer two centimeters of a colony (Neumann, 1966; Highsmith et al., 1973, Hutchings, 1986). Percent data were analyzed using Jmp 5.1 statistical analysis software. Sample localities (e.g., Cane Bay versus Cañada Honda) were then compared using a one-way analysis of variance (ANOVA) to determine significant differences between major borers.

RESULTS

Analyses revealed significant differences both regionally and locally. When grouped by island, the major bioeroders were different on St. Croix than those from the Dominican Republic ($p < .0001$). Figure 2 provides a visual comparison of samples from the two locations. The visually obvious domination of molluscs (mostly *Lithophaga spp*) and



Fugure 2. Digital scans of bioeroded corals from the Dominican Republic (left) and St. Croix (right). The approximate limit of bioerosion is shown by the dotted lines. The area outside this boundary is referred to in this paper as the "zone of bioerosion". Note the importance of molluscs in the DR sample, in contrast with the sponges on St. Croix.

large sponges in the DR reefs versus more complex mesh-works of boring sponges (probably *Cliona spp*.) appears to be the dominant difference driving the statistical separation discussed below. Table 1 summarizes bioerosion by individual contributors at all sites. Total bioerosion varied between 13 and 28%, with higher values generally occurring within the DR samples. Table 2 summarizes statistically significant differences among sites based on the ANOVA. Again, significant differences tended to exist between specific sites on different islands, rather than two sites on the same island. Visual examination of the Dominican samples from the mixed- and massive-coral facies at Cañada Honda revealed that three samples were bored much higher than any other samples from any site. To test the possibility that the high degree of significance was being driven by these three samples, they were removed and the analyses were re-run. The resulting comparisons were still significant. In another comparison, the samples from the mixed-coral (Chmas) and massive-coral facies were combined (Chcomb). Again, A)

Site	Cañada Honda Mixed	Cañada Honda Massive	Cañada Honda All	Las Clav	Cane Bay T1	Cane Bay T2	Tague Bay
n	2	10	12	5	8	8	3
Molluscs	12.70	12.70	12.25	11.89	0.00	0.00	0.85
Sponge	10.92	14.02	13.46	14.74	12.96	14.06	18.12
Worms	1.27	0.83	0.91	1.36	0.23	0.75	0.61
Total	24.89	27.01	26.26	27.98	13.19	14.81	19.58

B)

Site	% Mollusc	% Sponge	% Worm
St. Croix			
Cane Bay – T1	0.0	97.2	2.8
Cane Bay - T2	0.0	94.2	6.3
Tague Bay	3.5	92.7	3.8
Dominican Republic			
CH-Massive	51.7	45.1	3.2
CH-Mixed	44.4	52.7	2.9
CH-Combined	51.0	45.5	3.5
Las Clavellinas	34.8	60.2	5.0

Table 1. A) Mean percent of bioerosion (within the zone of bioerosion) for Dominican Republic and St. Croix sites. B) Percent of total bioerosion by major taxonomic groups. At all sites.

Transect	Chmix	Chmas	Chcomb	LC	CB T1	CB T2	TB
CHmix		N	N	N	Y (0.028)	N	N
CHmas	N		N	N	Y (0.003)	Y (0.007)	N
CHcomb	N	N		N	Y (0.001)	Y (0.005)	N
LC	N	N	N		Y (0.002)	Y (0.010)	N
CB T1	Y (0.028)	Y (0.003)	Y (0.001)	Y (0.002)		N	N
CB T2	N	Y (0.007)	Y (0.005)	Y (0.01)	N		N
TB	N	N	N	N	N	N	

Region	DR	STX
DR	N	Y (<.0001)
STX	Y (<.0001)	N

Table 2. The upper matrix summarizes statistically significant differences in grazer populations among reefs, transects and reef zones within them. The lower matrix compares all DR vs. all St. Croix samples combined. Gray boxes indicate self-comparisons.

the Cañada Honda samples separated significantly from any of the St. Croix sites (Table 2).

The most notable difference between assemblages, as illustrated by Figure 2, is the role of boring bivalves. In the DR reefs, bivalves exist as a prominent part of the macroboring assemblage (ca. 12%) and are roughly equal to the percentage of sponges (11-15%: Table 1). On the St. Croix reefs, bivalves are almost entirely absent from the suite, save a miniscule amount found in Tague Bay. Worms were nearly twice as important on DR reefs, but there were no reefs that reported worm galleries accounting for more than 1% of the total substrate removed. While sponges accounted for ~95% of the total macroboring in the St. Croix transects, there were no significant differences between boring rates of sponges in the DR and St. Croix.

DISCUSSION

The patterns described above are probably the result of many factors: sedimentation/nutrient loading, wave energy and residence time of exposed substrates on the reef surface, skeletal density, coral type and colony shape, varying grazing pressure, and the succession of bioeroders and encrusters. It appears, however, that the predominant factor is the combined role of sedimentation and nutrient loading. Rates of macroboring in the DR were nearly double those of Cruzan reefs where nutrient/sediment supplies are generally low. These results are similar to those of investigations that focused on the effects of known changes in nutrient input on the rates and styles of bioerosion (Highsmith et al., 1983; Perry, 1998; Perry, 2000; Perry, 2007). The importance of sponges on St. Croix (90%) mimics findings in other lower-nutrient reefs (Highsmith, 1980; Sammarco and Risk, 1990; Edinger and Risk, 1994; Chazottes et al. 2002). Using nutrient availability to explain the high incidence of mollusc bioerosion in the DR reefs is concordant with past studies that tied boring bivalves to well-documented high-nutrient environments (Highsmith, 1980; Sammarco and Risk, 1990; Perry and Hepburn, 2007).

Cañada Honda and Las Clavellinas are situated within a deeply embayed valley that was protected from open-Caribbean waves. Conversely, Cane Bay faces the open sea and is not provided the same shelter from wind and wave energy. Green and Pandolfi hypothesize that lower bioerosion in high energy areas is due to an increased chance that corals will be destroyed, broken, transported and/or buried before severe infestation can occur. This is also concordant with Hutchings et al. (2005), who noted that it took 4 years for a mature assemblage of macroborers to develop (sponge, bivalve, and worm representatives). Both hypotheses suggest a positive correlation between the degree of bioerosion and residence time of corals at the sediment water interface.

There have been numerous reports that macroborers prefer to bore into more dense substrates and that in many corals, skeletal density increases with depth (Highsmith et al., 1983; Greenstein and Pandolfi, 2003; Perry and Hepburn, 2007). *Siderastrea* samples from the DR do have higher densities than samples of *Montastraea spp*. collected from the same site. However, there also appears to be a shape-related preference for boring that covaries with species. Several studies have also shown macroborers to have a morphological preference (MacGeachy and Stearn, 1976; Mead et al., 2006; Perry and Hepburn, 2007). Endolithic bionts tend to prefer any morphology which favors the exposure of dead coral skeleton. Results from this study also are concurrent with this hypothesis as conical samples of *Siderastraea spp.* from the DR reefs are very clearly more heavily infested with endolithic bionts than the conical *Montastraea spp.* Similarly, samples of the columnar form of Montastraea spp. that stand above the reef on St. Croix are more heavily infested.

Grazing pressure has been cited as another factor which can alter the intensity of boring (Sammarco and Risk, 1990; Hutchings, 2005). Generally, there is an inverse relationship between grazing pressure and intensity of infauanl bioerosion. Taylor et al., (1985) posited bouts of extreme sedimentation that would nearly bury entire colonies and kill polyps around the edges. This might prevent the accumulation of algae and promote recruitment of infaunal bioeroders via reduced grazing pressure. Contrary to our findings of higher bioerosion associated with elevated sedimentation and nutrients, Hutchings (2005) cited lower rates of infaunal bioerosion with unusually high nutrients from agricultural runoff and high sedimentation that promoted algae and grazing pressure. All of this points out the complexity of the situation.

The typical succession of bioeroders suggested by Risk and MacGeachy (1978) involves an initial infestation of bacteria, followed by algae and fungi, then sponges and worms, and finally bivalves. In most Holocene reefs, the dominant community structure is one comprised primarily of sponges and followed by very minor contributions of worms and bivalves, if any contribution from the latter. In contrast, high nutrient levels may have allowed the DR reefs to bypass this progression in favor of molluscs with higher nutritional demands.

Coral reefs thrive in environments that are low in nutrients. It has also been shown that coral can be easily out competed by faster growing macroalgae. Studies seem to show that a mature community of macroborers will include higher quantities of sponges, worms, and, especially, bivalves. Studies also reflect that the majority of Holocene reefs do not contain mature communities of endolithic bionts, and are generally lacking significant numbers of bivalves. This suggests that there is a very specific set of circumstances that will allow for the growth of such communities. To be heavily bioeroded, reefs must exist within a low energy, high sedimentation/nutrient environment, but sedimentation and nutrification must not exceed some critical limit that would outpace coral growth or provide enough nutrients to promote algal dominance or increased grazing.

CONCLUSIONS

This study provides data which support several theories that might aid in explaining the environmental associations of varying macroboring communities. Based on this information, the following conclusions are offered:

1) Sediment and nutrient load are key factors in the development of macroboring communities. In particular, reefs experiencing high sediments and nutrients will exhibit heightened rates of bioerosion with a progressively higher influence of bivalves.

2) Assemblages are also affected by wave energy and exposure time of a recently killed surface.. High-energy environments can promote the removal of coral substrate from the taphonmically active zone, and inhibit macroborer recruitment.

3) Increased skeletal density and coral morphologies that expose large amounts of dead skeleton are both factors which can positively affect rates of infaunal bioerosion.

4) Absence of grazing pressure can also promote higher rates of bioerosion. Conversely, increased grazing can both inhibit infaunal boring and remove evidence of its existence.

5) Boring communities can provide insights to understanding taphonomic indicators that might be utilized to infer possible paleoecologic and paleoenvironmental settings within fossil reefs.

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