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Front Cover: Close-up view of a patch-reef coral head in Grahams Harbor, north of Dump Reef. As shown here, Caribbean shallow-water reefs have declined since the mid-1980s and are now largely overgrown by fleshy green macroalgae and a variety of encrusting organisms. See Curran et al., "Shallow-water reefs in transition," this volume, p. 13. Photograph by Ron Lewis.

Back Cover: Dr. A. Conrad Neumann, University of North Carolina, Chapel Hill, NC, Keynote Speaker for the 11th Symposium and author of "Cement loading: A carbonate retrospective," this volume, p. xii. Photograph by Mark Boardman.

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BIOEROSION IN THE CARIBBEAN: USING CORAL BLEACHING AS A NATURAL EXPERIMENT

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ABSTRACT

A regional coral bleaching episode in central Belize during August and September 1998, provides a natural experiment for studying rates of coral bioerosion. Samples of *Acropora cervicornis* and *Agaricia tenuifolia* collected two and three years after bleaching, and associated coral death, have bioerosion rates of around 8% of cross sectional area/year. This rate is linear over the three years and consistent between localities and species. While bioerosion rates will probably lessen in future years, the data suggest that branching and foliose coral rubble will be largely destroyed within the decade.

After 2 years, coral pieces were encrusted with an average thickness of 0.7 mm., primarily by coralline algae. Cover and thickness of encrustation is uncorrelated with internal bioerosion suggesting that encrustation does not impede (or enhance) the settlement of borers. The presence of algal accumulation and the lack of surficial erosion on coral pieces suggests that external bioerosion is less important than internal bioerosion in these settings. Comparing bioerosion patterns on patch reef crests with those from very shallow grassbeds and deeper (15 m) patch reef fronts suggest that in most Belize patch reef environments, bioerosion is dominated by internal (inside-out) bioerosion, rather than external (outside-in) bioerosion as previously suggested by experimental work in the Pacific.

INTRODUCTION

Since Conrad Neumann first examined rates of clionid sponge boring in Bermuda and

coined the term "bioerosion" (Neumann, 1966), numerous studies have sought to understand the processes and rates of skeletal breakdown from biological sources. Early experimental studies (e.g., Neumann, 1966; Rutzler, 1975) observed high rates of clionid sponge boring and stressed the importance of these borings to reef structure and sediment production. More recent studies, however, have begun to question the overwhelming importance of macroboring in the breakdown of reef substrates. For example, sponge boring may be quantitatively insignificant for the first one to two years of exposure (Bromley et al., 1990; Lescinsky et al., 2002), and experimental work in the Pacific Ocean (e.g., Pari et al., 1998) suggests that external bioerosion from the scraping of grazers is generally more than an order of magnitude greater than internal bioerosion. In addition, microborers (primarily algae) can excavate between 4 (Zubia and Peyrot-Clausade, 2001) to 13 times (Chazottes et al., 1995) as much material as macroboring. However, the abundance of coral and shell rubble that is riddled with clionid boring suggests that at least in some settings, boring must be a dominant process.

This study addresses which bioerosional processes are most important to patch reef corals along the coast of Belize. Is the best model for understanding bioerosion in these settings an "outside-in" model dominated by the external scraping of grazers or an "inside-out" model dominated by the internal bioerosion by macroborers?

Bioerosional rates have generally been examined by attaching experimental substrates such as calcite crystals (e.g., Neumann, 1966; Rutzler, 1975) and sawed coral blocks, usually *Porites* (e.g., Kiene and Hutchings, 1994; Chazottes et al.,

Site Name	Lat./Long.	Environment	Depth	Samples Collected
Wee Wee	16.62°N x 88.09°W	Reef	3-5m	3 yr. <i>Agaricia</i>
		Deeper Reef	15m-18m	Various species, <i>Agaricia</i> plates
		Grass Beds	1-2 m	<i>Porites</i> rubble
Peter Douglas	16.70°N x 88.17°W	Coral Reef	5 m	2 yr., 3 yr. <i>Agaricia</i>
Norvall	16.71°N x 88.17°W	Reef	3-5 m	2 yr., 3 yr. <i>Acropora</i>
Patch	16.75°N x 88.14°W	Reef	3-5 m	2 yr., 3 yr. <i>Acropora</i>
		Deeper Reef	15-18m	Various species, <i>Agaricia</i> plates
Bread and Butter	16.60°N x 88.16°W	Grass beds	1-2 m	<i>Porites</i> rubble

Table 1. Sample sites among back reef cays and patch reefs, south central Belize.

1995) to reef substrates and monitoring changes in volume or mass through time. These studies probably best capture rates of degradation of solid, exposed reef substrate, while other techniques may be better suited to capture bioerosion rates for branching and foliose corals. With the exception of Musso (1992) who found a 50% reduction in the planimetric area of killed branching *Acropora* after about 20 weeks, little experimental work has examined bioerosion rates of branching and foliose corals despite their traditionally high cover in many reef environments. Geographic patterns of internal bioerosion of branching corals have been investigated (e.g., Risk et al., 1995; Perry, 1998; Holmes et al., 2000), but because time of coral death was unknown, bioerosion rates are indeterminate.

Coral mass die-offs, such as those resulting from coral bleaching events, have the potential to serve as "natural experiments" for determining bioerosion rates. For example, Sheppard et al. (2002) examined bioerosion 3 years after widespread coral mortality on the Chagos Reefs, Indian Ocean. They found that most pieces of branching rubble were less than 33% bioeroded but that 5 to 15% of the pieces were heavily bored (>66% of skeleton removed). Unfortunately, average bioerosion rates cannot be determined because rubble pieces were scored visually into one of only three broad categories (<33%, 33-66%, >66%). In this study, I examine bioerosion intensity at 2 and 3 years following a regional bleaching event in central Belize (Aronson et al., 2000, 2002; Peckol et al., 2001) in order to calculate

natural bioerosion rates. The coral samples are also examined to estimate the effect of encrustation and grazing on the substrates.

METHODS

This study focused on the back-reef environments of the south-central portion of the Belize Barrier Reef (Table 1). The sites studied represented healthy coral assemblages prior to the 1998 bleaching (Paul Shave, pers. comm.). Stands of *Agaricia tenuifolia* and *Acropora cervicornis* killed during the fall of 1998 were sampled in December 2000 (2-year sample) and November 2001 (3-year sample). Rubble was collected directly from the sites of previous live colonies and, in general, did not appear to have been transported significantly: branches of *A. cervicornis* were long (many over 25 cm) and in large, conspecific assemblages, and *A. tenuifolia* pieces were adjacent to the in-place bases of dead colonies. A minimum of 30 pieces was collected from each site during each field season.

Samples of *Acropora* were broken in the field into approximately 10-cm pieces with no branches; *Agaricia* samples were a minimum of 5 cm in longest dimension. Samples were air dried and returned to the lab for examination. Pieces were dipped in a clear polyurethane coating to eliminate chipping of the edges, and then sectioned with a thin-bladed rock saw into 3-5 cm cross sections at 1-cm intervals. Cross sections were computer imaged using a Pixel digital cam-

era. The enlarged prints of coral cross sections were overlain by a grid of equally spaced points corresponding to an actual size of approximately 1 mm intervals. All points that were located over holes in the coral were tallied and the total percent of skeleton removed was calculated. Because corals, particularly acroporids, have high and variable porosity (Bucher et al., 1998), unbored cross-sections were examined using the same technique to determine the porosity of fresh skeleton at the scale of the overlay.

Encrustation on *Acropora* rubble was estimated from the printed cross sections by measuring the thickness of encrustation (mostly coralline algae) at 8 equally spaced points along the circumference of each piece. The average of the 8 measurements was taken as the average cross section thickness, and the average of all cross sections per sample (generally 5) was the average encrustation thickness of the sample.

In order to compare patterns observed from the reef crest with those from other nearby environments, coral rubble was also collected from shallow (1 m) sea-grass beds and deeper patch reef slopes (15-20 m). These zones were not affected by the 1998 coral-bleaching event, thus the samples were simply available dead coral, and the time of death is unknown.

RESULTS

Bioerosion Rates

A strong positive linear correlation exists between total bioerosion (percent skeleton removed) and the exposure time for *Agaricia* and *Acropora* coral at the two sites (Figure 1) as evidenced by the high r^2 values (.98, >.99, >.99). Two-year *Agaricia* samples were not available

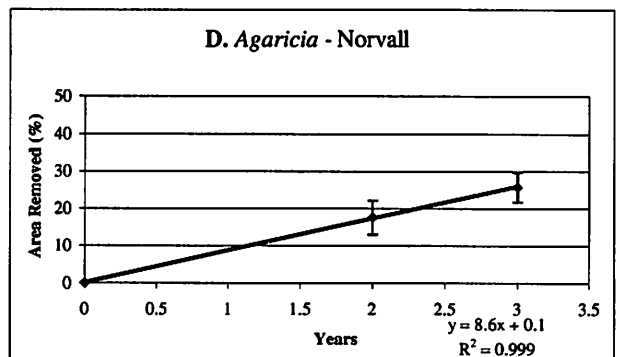
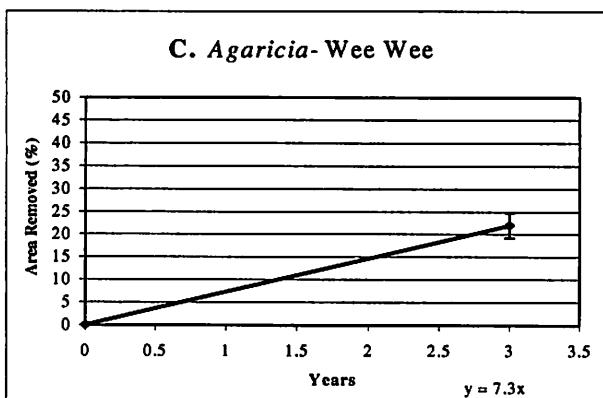
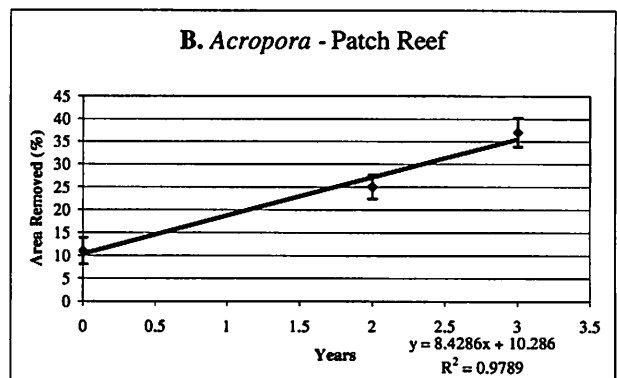
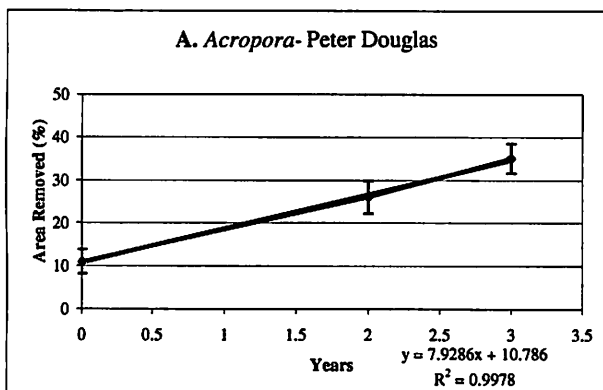


Figure 1. Bioerosion of *Acropora* (A, B) and *Agaricia* (C, D), at 2 and 3 years after bleaching episode. Note the strongly linear bioerosion rates closely comparable between the graphs. The y-intercept of the *Acropora* trend line reflects the original porosity as determined by data obtained from un-bored portions. Error bars are 95% confidence intervals.

Agaricia (C, D), at 2 and 3 years after bleaching (slopes of best fit lines) of about 8%/year that are intercept of the *Acropora* trend line reflects the original porosity as determined by data obtained from un-bored portions. Error bars are 95% confidence intervals.

from Wee Wee Cay and thus there is no correlation coefficient. After 3 years, *Acropora* skeletons were missing approximately 35% of their total volume, but analysis of controls suggests that about 11% of this volume (y-intercept on graphs) existed as original pore space in the living *Acropora*. By contrast, living *Agaricia* has no pore space (at the scale of the overlay used) and consequently had a lower overall excavated volume, but similar bioerosion rates. Bioerosion rates, as estimated from the slopes of the best-fit lines in Fig-

ure 1, are *Acropora*: 8.4%/yr (Patch) and 7.9%/yr (Peter Douglas), average 8.15%/yr; and *Agaricia*: 8.6%/yr (Norvall) and 7.3%/yr (Wee Wee), average 7.95%/yr.

Encrustation Patterns

All pieces of *Acropora* rubble were at least partially encrusted after two years. After three years, coralline algae formed crusts up to 4 mm thick in some areas but was absent from other

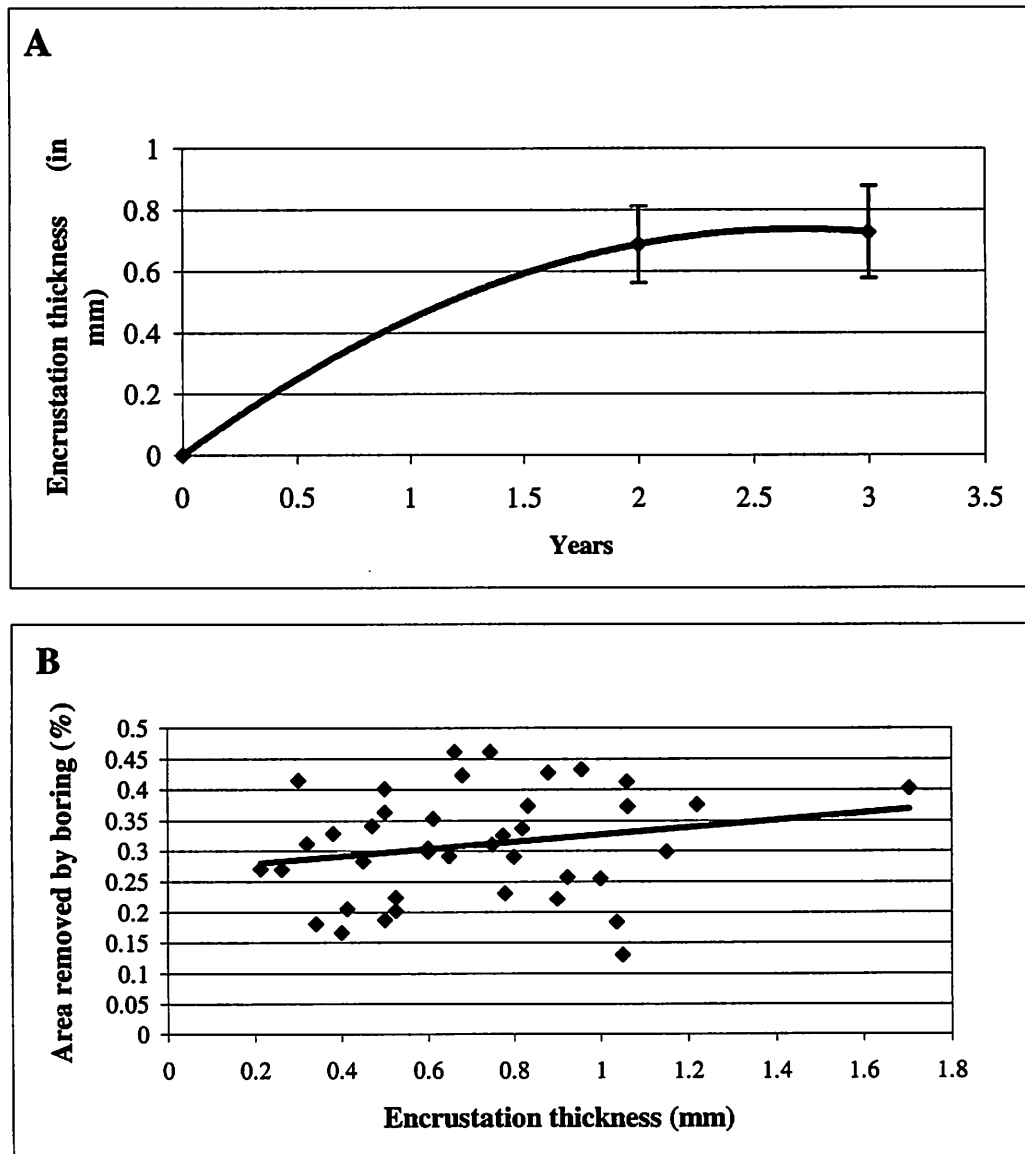


Figure 2. Encrustation thickness on *Acropora* from Patch Reef site. A. Encrustation as a function of exposure time. Note that encrustation has reached an average thickness of 0.7 mm by the second year, with no significant increase in the third year. Error bars are 95% confidence intervals. B. There is no correlation between encrustation thickness and boring intensity.

areas. The average encrustation thickness for *Acropora* samples was approximately 0.7 mm (Figure 2). This thickness was reached by the second year and did not change significantly during the third year of the study. There is no correlation (positive or negative) between encrustation thickness and internal bioerosion (Figure 3).

Corals from Grassbeds and Deeper Reef Slopes

Coral rubble (*Porites porites divaricata*) collected from shallow grass beds was apparently little grazed, as indicated by its well-preserved corallite texture, and was commonly heavily encrusted with coralline algae. Coral rubble from deeper environments was often dusted with sediment and had a higher proportion of animal encrusters. Surface detail of corals was well preserved even in pieces of rubble that were heavily bored.

DISCUSSION

Bioerosion Rates

Bioerosion rates observed in this study are remarkably consistent through time with little scatter and high r^2 values. A potential complicating factor for the study was the inadvertent inclusion of corals that had died prior to the 1998 bleaching episode. This was particularly problematic with *Acropora* rubble because even healthy *Acropora* colonies have nonliving sections (e.g., at the base of the thicket), and much of the *Acropora* in the area had died previously from White Band Disease a decade or so earlier (Aronson and Precht, 2001). The large increase in bioerosion from years two to three and the lack of scatter suggest that the inclusion of older skeletons was not a significant problem.

Linear trend lines for bioerosion document the apparent constancy of rates from initial exposure (bleaching) to three years post bleaching, although early boring rates are indeterminate because samples were first collected after two years of bioerosion. Uniform rates over the three years of the study were not predicted by earlier studies. Bioerosion may be initially high when an estab-

lished sponge is put in contact with a new substrate (Neumann, 1966; Rutzler, 1975), or rates may be initially low due to low recruitment and growth of boring organisms. Internal bioerosion rates may subsequently increase through time (e.g., Chazottes et al., 1995, Lescinsky et al., 2002) until they plateau or even decrease as clionids fully excavate a substrate. Continued sampling of the Belize localities over the next several years is needed to document how internal bioerosion rates change through time.

Observed bioerosion rates are much higher than most previously published rates (Table 2), with the exception of studies in which living sponges were attached to the experimental substrates (e.g., Neumann, 1966; Rutzler, 1975). Direct comparison with other studies is difficult, however, because internal bioerosion is generally reported as weight loss with respect to surface area, rather than weight loss with respect to volume. Loss per unit of surface area may be applicable for the flat surfaces of experimental blocks but its application to cylindrical coral rubble is problematical. For example, an 8%/yr erosion rate in coral of a density of approximately 1 g/cm^3 (Bucher et al., 1998) corresponds to a weight loss of approximately $80 \text{ kg m}^{-3} \text{ yr}^{-1}$. Since the ratio of surface area to volume varies with the size and shape of each coral piece, rates expressed as a function of area will also vary with the shape of the piece. For example, a 1-cm-long section of a cylindrical coral 2 cm in diameter with an 8%/yr skeleton loss will have a bioerosion rate of $0.4 \text{ kg m}^{-2} \text{ yr}^{-1}$; a similar coral 4 cm in diameter has a rate of $0.8 \text{ kg m}^{-2} \text{ yr}^{-1}$ because of reduced surface to volume ratio. In any case, both values are high compared to other studies. Even the Galapagos study (Reaka-Kudla et al., 1996), which reported unusually high rates relative to surface area (Table 2), found that the volume removed by internal eroders was 0.6-0.7%/yr, an order of magnitude less than the 8%/yr reported here.

Bioerosion at the rate observed in Belize will rapidly lead to the complete loss of rubble, probably within the decade. Continued monitoring of debris is necessary to establish if rates plateau at some point in the future and if there is a threshold value at which riddled skeletons lose strength

Location	Duration (months)	Rate of Internal Bioerosion (kg m ⁻² yr ⁻¹)	Internal:External Bioerosion	Reference
Bermuda	3	19.2	-	Neumann, 1966
Bermuda	10	7	-	Rutzler, 1975
French Polynesia	24	0.02-.14	1:17-49	Pari et al., 1998
Moorea, outer slope	24	0.09	1:25.9	Chazottes et al., 1995
Island, Indian Ocean	12	0.05-.47	1:30.2	Chazottes, 1996
Lizard Island	60-84	0.06-.24	1:5.8-10.3	Kiene and Hutchings, 1994
Galapagos	15	0.6-2.4, (0.6%/yr)	1:9.5	Reaka-Kudla et al., 1996
Belize	36	0.4-.8 (8%/yr)	1:<<1	This study

Table 2. Rates of macroborer bioerosion from various experimental studies. Note that the two Bermuda studies used experimentally attached sponges to initiate bioerosion. Numbers in parentheses are the percent of volume lost per year.

and collapse. Observed patterns should be applicable for most coral species on the reef. Although *Agaricia* and *Acropora* have similar bulk density, previous work (e.g., Reaka-Kudla et al., 1996) suggests that substrate density has little effect on internal boring, although it has substantial effect on grazing bioerosion.

Effects of Encrustation

It is possible for encrusting cover either to protect the substrate from boring, as noted on living gastropods (Smyth, 1989) and dead mollusk shells (Southward and Lescinsky, 1999), or to enhance boring by providing cover that disrupts grazing that would otherwise remove borer recruits (Kiene and Hutchings, 1992). Coral rubble sampled in this study was encrusted, primarily with coralline algae, across much of its surface, and yet was also heavily bored. The lack of correlation between encruster cover and bioerosion in individual samples supports a conclusion that borers gain access to coral skeletons independent of encrustation. High rates of boring bioerosion suggest that several factors may combine to facilitate rapid colonization of branching and foliose corals. The corals have high porosity in which boring larva can settle, and a large surface area including the undersides of coral rubble where coralline al-

gae cover is discontinuous and settling larva are protected from grazing.

Outside-in vs. Inside-out Models of Bioerosion

Recent experimental studies (Table 2) have found that rates of external bioerosion are often an order of magnitude greater than rates of internal bioerosion, suggesting an outside-in model of bioerosion for most reef substrates. In contrast, the results presented here suggest that internal bioerosion is of far greater importance to skeletal breakdown than grazing, at least in the patch reef settings typical of Belize.

The observed high rates of internal bioerosion in Belize are associated with estimated low rates of grazing bioerosion. Low grazing rates are suggested by the positive accretion rates of encrusting organisms, and the preservation of the surface features of the corals including the radial corallites in *Acropora* and epithelial growth lines in plate agariciids. Shallow sea grass beds, shallow coral reefs, and deeper reefs show similar patterns of internal boring and little evidence of external scraping.

Several explanations are possible for the differences observed between the Belize sites and those reported in the literature. Firstly, many differences probably result from the different experimental methods. Previous work has examined

bioerosion rates on rigid reef substrates as a function of exposed surface area. These substrates were in exposed settings that were fully available to grazing organisms. In contrast, the coral rubble studied here, was on the bottom and thus undersides were at least partially protected from grazing. In addition, bottom rubble may be sand scoured and a suboptimal environment for algal growth. High relative surface area in branching and foliose corals, including protected sides and crypts, may also lend itself to easy colonization and growth by boring organisms. Branching corals are also fast growing and have high porosity that may also facilitate borer settlement.

The extent to which bioerosion patterns on branching and foliose corals form a good model for the reef as a whole will vary within and between reef environments. Reef zones dominated by branching morphologies are common, and in these zones internal bioerosion may be important and should be investigated. Even reef environments dominated by exposed reef rock will have ample undersides and crypts where grazing is limited and internal bioerosion may predominate.

Belize patch reefs may also differ from the previously reported experimental sites in more fundamental ways. For example, the patch reefs are generally more turbid than open water sites and the reduced water clarity causes algal cover to drop off rapidly with depth. However, studies on the Great Barrier Reef (Kiene and Hutchings, 1992, 1994) found uniformly greater external than internal bioerosion over a suite of environments, including a restricted lagoon. In Belize patch reefs, grazing is common in the more shallow zones, such as where the majority of our samples were collected.

It is also possible that the differences reflect larger scale differences between the Pacific and the Caribbean. Observed lower rates of herbivory in the Caribbean as compared to the Pacific might lead to the reduced importance of grazing for Caribbean bioerosion. Additional work is needed to evaluate this possibility.

CONCLUSIONS

The bioerosion patterns observed in patch reef environments in Belize suggest that an inside-out model of bioerosion is most applicable. Internal bioerosion, primarily from boring sponge is rapidly destroying coral rubble, with little additional bioerosion from scraping grazers. This inside-out model is in contrast to outside-in bioerosion that has been recorded by most other experimental studies. Additional studies are needed to determine if an inside-out model is more applicable to typical reef settings with abundant branching and foliose corals with high surface area and partial protection from scraping herbivores.

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