Results of long-term bioerosion study: Belize patch reefs

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Abstract. Bioerosion rates were tracked for up to 8 years on patch reefs in central Belize using natural and experimental substrates. Mortality from bleaching in 1998 provided the start of a natural experiment in which *Acropora cervicornis* and *Agaricia tenuifolia* were collected at 1-2 year intervals for 8 years. In addition, experimental substrates (conch shells) deployed along a depth gradient (1-12m) were retrieved at 1, 3, and 5 year intervals. Macroboring bioerosion rates were initially highly linear (5-6%/yr), and inversely related to depth. After 3-4 years macroboring bioerosion slowed and average maximum intensity tended toward approximately 40%. Individual substrates had a threshold of around 50% which may reflect the maximum gallery density for *Cliona* or the collapse and disappearance of more highly bored substrates. Wide spread coralline algae encrustation and the persistence of corallite surface texture suggests that external bioerosion from grazing was negligible. These results differ from previous studies that have found grazing bioerosion to be an order of magnitude or more greater than macroboring. This study highlights the greater importance of boring than grazing in several Caribbean reef habitats and the need to re-evaluate the relative impacts of inside-out vs outside-in bioerosion on coral reefs.

Key words: Belize, Bioerosion, Bleaching, Boring, Grazing

Introduction

In order to understand coral reef accretion, it is important to keep in mind that to a first approximation most biological coral growth is ultimately lost from the reef structure via bioerosion and transport (Glynn 1997). This is evident on apparently healthy reefs that have little accretion over geologic time (Smithers et al. 2006), in reef cores where fast growing corals do not result in faster reef accretion than slower growing corals (Gischler 2008), and in nutrient rich areas where bioerosion predominates over fast coral growth (Edinger et al. 2000).

Despite the importance of bioerosion to reef formation, there are few quantitative studies of bioerosion, especially in the Caribbean. Studies on bioerosion rates in the Pacific and Indian Oceans suggest that in most cases external bioerosion from scraping herbivores such as parrotfish and sea urchins far exceeds internal bioerosion by macroborers such as sponges and bivalves generally by more than an order of magnitude (Table 1).

The emerging outside-in, rather than inside-out paradigm for reef bioerosion is an important consideration for geologists who focus primarily on macroboring and microboring rather than grazing bioerosion (e.g., Perry and Hepburn 2008), and only recently have attempts been made to reconstruct grazing in the rock record (Lescinsky 2008).

The outside-in paradigm for reef bioerosion, however, is derived from studies that used sawed blocks of *Porites* that were bolted to the reef (Kiene and Hutchings 1994; Chazottes et al. 2002; Osorno et al. 2005). Results from these studies may be most applicable to flat, exposed reef-rock surfaces and they may be less applicable to other types of reef substrate and environments. Previously reported low macroboring rates are also at apparent odds with studies on experimental substrates (Neumann 1966, Schonberg and Wilkinson 2001) and naturally bleached corals (Sheppard et al. 2002; Schuhmacher et al. 2005) that document rapid sponge bioerosion. The grazing paradigm also does not hold for all reefs. Boring outpaced grazing at nearshore sites on the Great Barrier Reef (Table 1), and on the Belize patch reefs reported here.

Methods

Natural Experiment

Coral bleaching in 1998 killed healthy *Acropora cervicornis* and *Agaricia tenuifolia* stands on Wee Wee Cay (16.620 N x 88.090W) and Peter Douglas Cay (16.700 N x 88.170W) in southern Belize approximately nine miles off the east coast of the mainland in the Stann Creek District (Aronson et al. 2000, Paul Shave, pers. com.). Beginning two years after bleaching, coral pieces were haphazardly collected on snorkel from dead stands

along the north ridge of each cay. Collections were made after 2, 3, 4, 6, and 8 years (November or December of 2000, 2001, 2002, 2004, 2006). *Agaricia* patches were located just below the lip of the windward rise (3-4m) while *Acropora* dominated on the ridge tops (2-3m). Corals stands were obvious at the beginning of the study with many long (>20cm) pieces of *Acropora* and in-place *Agaricia* with many blades. By the end of the study, the colonies were largely obscured, especially because of coral resurgence on Wee Wee Cay beginning in 2006. Coral pieces retrieved at the end were smaller and many were detached rubble.

Experimental deployments: Conchs
Conch shells (*Strombus gigas*) harvested live for food and without macroboring were deployed along a depth gradient at 1.5m, 6m and 12m along the north face of Wee Wee patch reef (approximately 100 yards west of Wee Wee Cay). Only shells with a mature flared lip, and without

encrustation (or with minor encrustation removed) were used. The 12m site was near the base of the slope above a flat plain of carbonate mud. Some shells were partially buried by fine sediment during the course of the study. Thirty or more shells were deployed at each of the three depth stations to allow collection of 10 shells each after 1 year (2002), 3 years (2004) and 5 years (2006). Shells were then sawed to remove the center section of the mature apertural lip for analysis.

Bioerosion Analysis
For corals, 20 pieces per sample (80 total: 2 species at 2 sites), per time interval were sectioned using a rock saw. For conch lips, 10 pieces per sample (30 total, 10 at 3 depths), per time interval were sectioned. Each piece was cut into three sections which were analyzed for bioerosion. Each section was digitally photographed and overlaid by a grid of points. Bioerosion proportion was determined by the number of points located over borings divided by the total points (>100). Microboring was not examined in this study.

Table 1: Results of studies that calculated both internal and external bioerosion. External generally exceeds internal bioerosion by an order of magnitude except in nearshore Great Barrier Reef (GBR) settings.

Location	Duration (months)	Internal bioerosion (kg m^{-2} yr^{-1})	Internal:external bioerosion	Reference
French Polynesia	24	.02-.14	1: 2.5-86 (av. 16)	Pari et al. 1998
	60	.02-1.04	1: 1.4-74 (av. 18)	Pari et al. 2002
Reunion	12	.006-.05	1: 61-263, (av. 130)	Chazottes et al. 2002
Lizard Island	60-84	.06-.24	1: 5.8-10.3	Kiene and Hutchings 1994
GBR nearshore	36-48	.25-.39	1: .16-.55	Osorno et al. 2005, Tribollet
GBR offshore	36-48	.04-.13	1: 2.6-112 (av. 27)	and Golubic 2005
Galapagos	15	.6-2.4, (0.6%/yr)	1:9.5	Reaka-Kudla et al. 1996
Belize	36	(6%/yr)	<<1	This study

Results
Natural Experiment
Over the eight years of study, dead branching colonies of *Acropora* and *Agaricia* became increasingly fragmented and in some cases overgrown, although former stands remained easy to locate and sample. Coral surfaces were often partially encrusted by coralline algae (Fig. 1). On unencrusted surfaces, original corallite topography, such as the raised polyp rims in *Acropora* was generally maintained There was little to no evidence of scrape marks from grazing bioeroders.

Macroboring was almost entirely from several ichno-taxa of boring sponge (undifferentiated in the data). Worm and bivalve borings were rarely encountered. Over the first 4 years, average macroboring bioerosion of the coral rubble proceeded at about 6%/year in a highly linear fashion (Fig. 2-3, Table 2). Rates decreased

towards the end of the study. Variation between the three sections per sample and between samples was substantial but did not obscure overall trends.

Between sites there was a small but significant (ANOVA <.001) difference with Wee Wee having slightly greater total bioerosion over most of the study, even though after the first 3 years the overall rates (slopes of best fit line) were similar.

Bioerosion rates between *Agaricia* and *Acropora* were similar (6%/yr). Higher absolute "bioerosion" in *Acropora* in Fig. 3 results from the inclusion of the initial porosity of the coral skeleton. Unbored *Acropora* skeleton has initial growth pores that occupy a varying amount of the cut surface depending on the age of the branch and the angle of the cut. We used 5% initial porosity (an average of several measurements) as our initial condition (y-intercept).
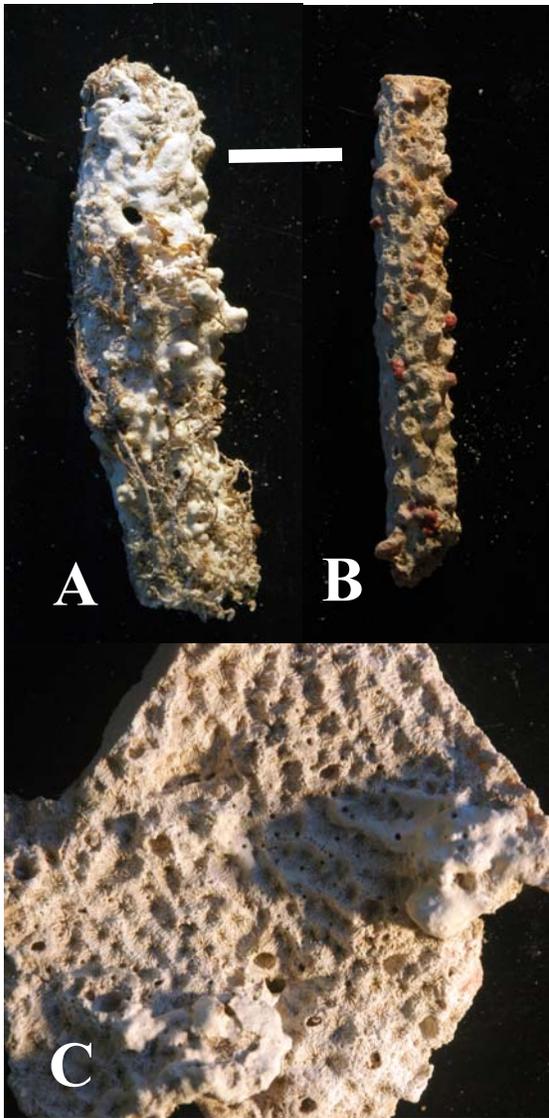
Figure 1: Encrustation and surface texture of substrates. *A. cervicornis*, 6 yrs (A) has knobby coralline algae and lacks evidence of grazing bioerosion. *A. cervicornis,* 8 yrs (B), partial retains corallite collars with limited encrustation by *Homotrema rubrum*. *A. tenuifolia*, 6 yrs (C), preserves original corallite topography. Scale bar is 1 cm.
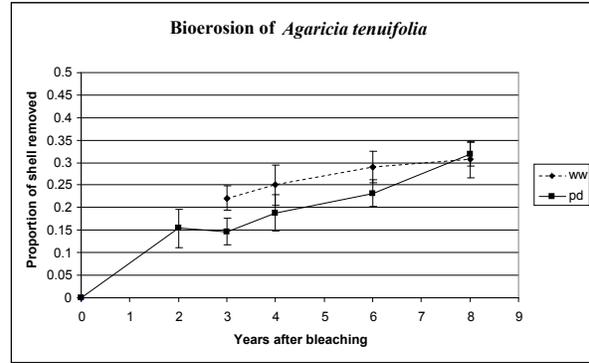

Figure 2: Bioerosion over 8 years for *Agaricia tenuifolia* killed in the 1998 bleaching. Mean values and 95% confidence intervals for Wee Wee Cay (ww) and Peter Douglas Cay (pd). Bioerosion has a nearly constant rate over the first 4 years of 5-6%/year. .
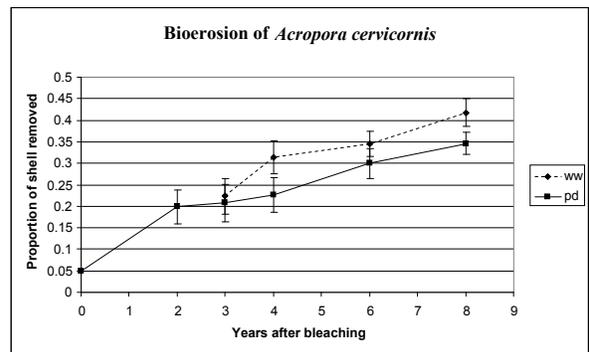

Figure 3: Bioerosion over 8 years for *Acropora cervicornis* killed in the 1998 bleaching. Mean values and 95% confidence intervals for Wee Wee Cay (ww) and Peter Douglas Cay (pd). *Acropora cervicornis* has a living porosity of 5-10% (depending on age, angle of cut); 5% is used here for the y-intercept.

Experimental Substrates

For the first 3 years, experimental conch shells were macro-bored at around 9%/yr at the two shallower depths, a rate higher than those of natural substrates at similar depth. There was no significant difference between bioerosion at the two shallower stations, but the deepest station (12m), bioerosion decreased to about a half (4.4%/yr).

Table 2: Bioerosion rates (proportion of skeleton removed per year) as measured as the slope of best fit line of the average of both sites. R^2 values for linear regression lines are high over 3+ years suggesting a tight correlation between time and macroboring intensity.

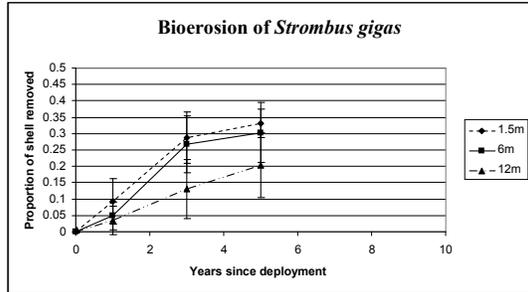|	Bioerosion Rate:	R^2: 3 yrs	R^2: 4 yrs
Agaricia	.063	.97	.95
Acropora	.058	.94	.96
Strombus (1.5m)	.096	.999	
Strombus (6m)	.092	.97	
Strombus (12m)	.044	.996	

Figure 4: Bioerosion over 5 yeas for experimentally deployed *Strombus gigas* shells. Over the first 3 years the bioerosion rate is linear at about 9%/yr for <6m and 4.4%/yr for 12m sample. Mean values with 95% confidence intervals.

Discussion

Direct comparisons of the rates reported here (6-9%/yr in shallow water) with those from previous studies are difficult because bioerosion rates are generally reported as a function of weight loss per reef surface area (kg m^{2}yr^{-1}). This metric is easily applied to small flat experimental plates but is more difficult to apply to complex 3-D substrates or where the vertical extent of boring is not known.

In this study, bioerosion of 6% yr^{-1} at a density of about 1 g/cm^3 (Boucher et al. 1998) corresponds to a weight loss of 60kg m^2 yr^{-1} for a 1m cube and .6kg m^2 yr^{-1} for a 1m^2 slab 1cm thick. To correct for surface area of the coral we can divide this number in half for tabular colonies with erosion on two sides (ex. *Agaricia*, *Strombus* shell) or for cylindrical colonies (e.g., *A. cervicornis*) a number depending on diameter (1cm: .25, 2cm: .5, 4cm: 1). To relate colony surface area to reef planar area, an additional multiplication factor would be needed since the former may be many times the latter.

Given the assumptions inherent in the conversion, we suggest that 6% yr^{-1} translates to around .3 kg m^2 yr^{-1}, and rates 4-5x greater are appropriate if related to planar reef surface. Within this range of rates, macroboring bioerosion on the Belize shelf is considerably higher than reported in most previous studies (Table 1), except where living sponges were attached directly to substrates (e.g., Neumann 1966, Rutzler 1975).

An important conclusion of the study is that bioerosion rates were surprisingly linear and similar between sites and substrate types (Fig. 5). For example, after 3-4 years, best fit lines had R^2 values .95 or greater for all three substrate types (*Agaricia*, *Acropora,* and *Strombus*). There was no time lag in the onset of macroboring has been suggested in some previous studies (Bromley et al. 1990).

Using linear bioerosion rates as a tool for estimating removal time for dead corals, or as a proxy for post-mortem exposure requires two important caveats. The first is that an upper limit to macroboring probably exists. Boring sponges have characteristic gallery patterns and may switch to lateral extension after excavating about 50% of the substrate (Rutzler 1975). Bored substrates also become increasingly fragile and will eventually collapse into smaller pieces that would be omitted from collections. For example after 5 years, several conch shells were missing parts and collapsed during retrieval.

A second consideration is that bioerosion is greatly slowed by burial. On reefs, vast differences in bioerosion and other taphonomic metrics occur between substrates resting on the seafloor, and those located above it on racks (Lescinsky et al. 2002). Intervals of burial and excavation may mix substrates of very different ages. For example, mollusc shells of similar preservation may be hundreds of years different in age in some settings (Meldahl et al. 1997).

The results of this study also call for a re-evaluation of the outside-in paradigm for reef bioerosion. Although previous studies (Table 1) have found grazing to be an order of magnitude greater than macroboring this is not the case for branching corals on Belize patch reefs. Grazing rates, although not measured directly are apparently minimal because coral surface texture is retained and there are thick coatings of coralline algae. In addition, if outside-in bioerosion rates were comparable to macroboring, our small substrates, would have disappeared entirely over the course of the study.

It is likely that we grazing bioerosion dominates macroboring bioerosion in many reef settings worldwide, though our results may also reflect in-part low grazing bioerosion in the Caribbean. As pointed out by Bellwood and Choat (1990) the Pacific has a diverse complement of excavating parrotfish but in the Atlantic *Scarus* species are all functional scrapers and only *Sparisoma viride* (stoplight parrotfish) is a significant bioeroder. In addition, bite size and bioerosion are related to fish size, and *S. viride* is dwarfed in size by the most important bioeroders in the Pacific, such as *Bolbometopon* which accounts for 88% of the bioerosion on outer reefs (Hoey and Bellwood 2008). Regional die-off of *Diadema* sea urchins would also lower grazing bioerosion in the Atlantic. Overfishing on the Belize reefs is probably not a direct cause because *S. viride* is abundant there (Rotjan and Lewis 2006, Brown-Saracino et al. 2007).

While regional processes may contribute to the differences described here, differences in methods were also likely important. The substrates in this study were small plates and branches of colonies that have numerous cryptic surfaces that would be difficult for large parrotfish to feed on. Similarly, invertebrate grazers such as sea-urchins may stay primarily on reef-rock and avoid branching corals and rubble (e.g., Bak

1990). Bioerosion of branching corals and corals with complex colony form, therefore, probably proceeds very differently than bioerosion of massive corals. When viewed from the perspective of the whole-reef, this is very important since branching corals are fast growing, dominate many shallow reef zones, and comprise most reef rubble. Macroboring probably also dominates in reef zones with low grazing, such as deeper water (Fox and Bellwood 2007), and throughout the reef in crypts which may comprise as much as 75% of the reef surface area and support diverse suspension feeding communities (Richter and Wunsch 1999).

In conclusion, bioerosion on the patch reefs of Belize occurs primarily through macroboring rather than grazing. This may in part result from differences of grazing bioeroders in the Caribbean, but it is also probable that inside-out bioerosion is a dominate force on most reefs in many zones. With the exception of large dead coral heads and smooth reef rock, boring may dominate in other situations such as where branching coral and rubble are abundant and in deeper water and crypts where grazing is greatly diminished.

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