

**PROCEEDINGS OF THE 13th SYMPOSIUM
ON THE GEOLOGY OF THE BAHAMAS
AND OTHER CARBONATE REGIONS**

**Edited By
Lisa E. Park and Deborah Freile**

**Production Editor
Lisa E. Park**

**Gerace Research Centre
San Salvador, Bahamas
2008**

Front Cover: Rice Bay Formation, looking southwest along Grotto Beach. Photograph by Sandy Voegeli.

Back Cover: Dr. John Milliman, The College of William and Mary. Keynote Speaker for the 13th Symposium. Photograph by Sandy Voegeli.

**Produced at
The Department of Geology and Environmental Sciences, The University of Akron**

**© Copyright 2008 by Gerace Research Center.
All rights reserved. No part of this publication
may be reproduced or transmitted in any form
or by any means, electric or mechanical,
including photocopy, recording, or any
information storage and retrieval system,
without permission in written form.**

ISBN 0-935909-82-6

BIOEROSION AND ENCRUSTATION ON CURAÇAO PLEISTOCENE REEFS: EVALUATING GRAZING IN THE FOSSIL RECORD

Halard Lescinsky
Department of Life and Earth Sciences
Otterbein College
Westerville, OH 43081
hlescinsky@otterbein.edu

ABSTRACT

Coral reef bioerosion studies on experimental substrates through time find that grazing bioerosion is an order of magnitude greater than macroboring bioerosion. Geologists working on fossil reefs, on the other hand, have focused primarily on boring bioerosion, largely ignoring grazing which can be more difficult to measure. Here, I assess the relative effects of grazing, macroboring, and encrustation in a well preserved Pleistocene reef, Curaçao, Netherlands Antilles. Taphonomic data from windward reef crest, back-reef flat, lagoon, and leeward reef crest facies all suggest that grazing bioerosion was very low. There is a low incidence of surface pitting on the reef, and surface features such as the corallite collars of *Acropora* are well preserved. Boring is estimated to have been <10%, which is similar to rates reported in modern reefs. Encrustation, primarily by coralline algae, is pervasive, occurring in crusts up to 30 mm thick on *Acropora palmata* trunks, and encasing *A. cervicornis* rubble that is sometimes only preserved via bioimmuration on the inner surface of algal rinds. The absence of grazing probably reflects high live coral cover on the living reef, and an overestimation of the importance of grazing in many coral reef settings.

INTRODUCTION

Reefs form where carbonate framework is produced faster than it is removed by either physical transport or the erosive effects of organisms. When Neumann (1966) first proposed the term "bioerosion" for this latter process, he emphasized that both scraping (external) and boring (internal) bioerosion were important to the reef--but the subsequent geological study of bioerosion

has focused almost exclusively on the study of borers (e.g., Palmer and Plewes 1993; Perry, 1996, 2000; Weidlich, 1996; Vogel et al., 1987). This is no doubt in part because boring traces are preserved as discrete voids within carbonate substrate and are easy to quantify in fossils. Quantifying the removal of material from the exterior of a surface, as occurs in grazing, is more problematic since successive grazing events remove the evidence of previous events and thus have the primary effect of decreasing substrate size.

The current geological focus on internal bioerosion is at odds with most experimental studies of bioerosion on modern reefs that have found that the intensity of grazing bioerosion is an order of magnitude or more greater than macroboring (Kiene and Hutchings, 1994; Chazottes et al., 1995; Pari et al., 1998). Although, quantifying grazing in fossil reefs is probably inherently impossible if grazing is intense, it is relatively simple if grazing is low. I propose that grazing on fossil reefs can be evaluated using original corallite topography, since external scraping will quickly obliterate any characteristic corallite morphology. This paper addresses grazing prevalence across several different facies of a Pleistocene fossil reef in Curaçao. The observed low rates of grazing bioerosion in the Pleistocene of the Caribbean suggest a need to re-evaluate experimental results, at least as they apply to the Caribbean prior to human impact.

Geological Setting

Curaçao, Netherlands Antilles, lies approximately 60 km north of Venezuela and is composed of a Cretaceous diabase core that was subsequently covered around the margins by carbonate reef deposits. Slow regional uplift (.06

m/1000 yr over the last 1-200 kyr, Schellmann et al., 2004) has resulted in 5 raised carbonate terraces around most of the island (Figures 1, 2). The top of the Lower Terrace (de Buissonjé, 1974) sits 10-12 m above sea level and is composed of a lower Cortalein Unit (216 Ka) and an upper Hato Unit (122 Ka) (Schellmann et al., 2004). The semi-arid climate results in little diagenetic alteration (Bries et al., 2004); and the infrequency of hurricanes has resulted in a high percentage of the corals remaining in life position and comparatively little rubble making up the reef interior (Meyer et al., 2003). The reef corals and constituent grains suggest that there has been little mixing within environments and that several well preserved reef facies are exposed (Pandolfi and Jackson, 2001; Pandolfi et al., 1999). Together, previous work (and this study) suggests that Curaçao fossil reefs preserve a high level of ecological integrity and will give an accurate reflection of coral reef processes that occurred within the living reef community.

METHODS

Bioerosion information was collected on the Curaçao Pleistocene (123 Ka) reef within 4 reef facies: windward reef crest, windward back reef, windward lagoon, and leeward reef flat. Two representative sites of each facies were chosen within the Hato Unit along the northwest end of Curaçao (Figures 3, 4, Table 1). The top of the Hato Unit forms the distinct Lower Terrace whose oceanward edge is marked by a sea cliff that rises from about 10 m below sea level to about 10 m above sea level. Because there is no recent reef along the windward coast (van Duyl, 1985), large waves pound the terrace, making its edge largely inaccessible. The fossil reef interior is only accessible at infrequent “bocas” that cut perpendicular to shoreline and expose cross-sectional views of the reef interior up to 100 m long in cliffs along both sides of the cut. Although bocas occur at mouths of intermittent stream channels, their origin remains a “problem” (Scheffers, 2004).

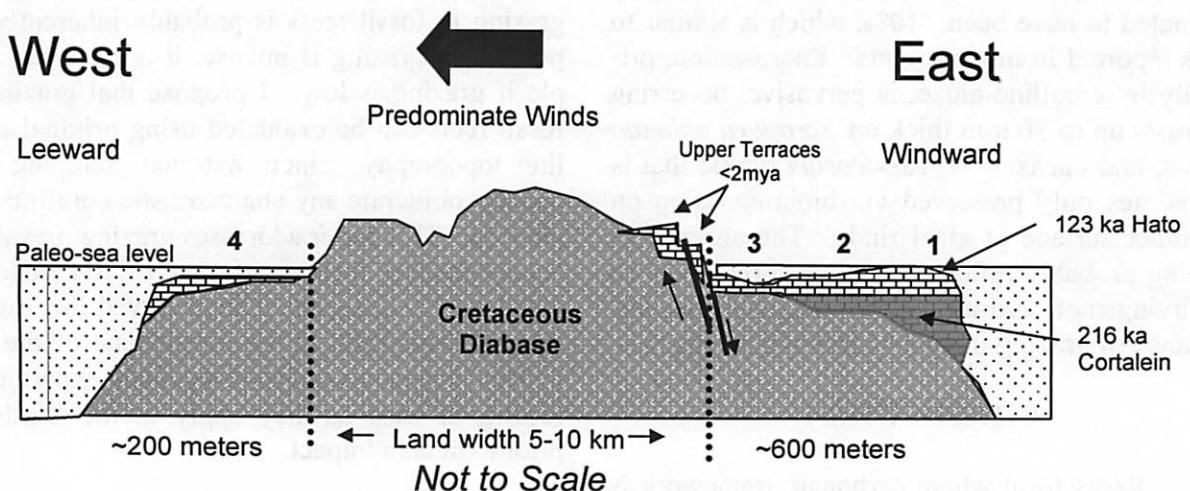


Figure 1. Generalized cross-section through the north end of Curaçao during the Pleistocene. Note that Pleistocene reefs and limestones rest on the Cretaceous volcanic bedrock in several discrete terraces. The Lower Terrace is composed of the upper Hato Unit (123 Ka) and the underlying Cortalein Unit (216 Ka). Windward reef development is far more extensive than leeward. Facies examined include 1) windward reef crest, 2) windward reef flat, 3) lagoon, and 4) leeward reef crest. Subsequent uplift has elevated the Hato Unit (and upper Cortalein) above modern sea level.



Figure 2. Pleistocene reef terraces, Curaçao. View southwest from coast, 5 km north of airport. Photograph taken from the top of Lower Terrace (123 Ka) approximately 10 m above sea level. Limestones of the Middle Terrace 1 are 400 Ka (Schellmann et al., 2004) and ages of higher terraces are poorly constrained.

Windward reef facies occur along Curaçao's eastern shore and consist of a well-developed *Acropora palmata* crest that preserves many large spectacular colonies in life position (Figure 3A). Landward of the crest is an apparently lower energy reef flat facies in which dome-shaped colonies of massive coral (i.e. *Siderastrea*, *Diploria*, *Montastrea annularis*) and large colonies of the extinct organpipe species of *Montastrea* (Pandolfi et al., 2002) are preserved (Figure 3B-D). Between the windward reef and the volcanic shoreline, lagoon deposits are sometimes preserved. These facies have a carbonate mud matrix and preserve highly encrusted coral rubble (Figure 3E). Numerous large conch (*Strombus gigas*) shells (Figure 3F) suggest ancient seagrass beds.

Leeward reef deposits are preserved on the western side of Curaçao and represent a well developed leeward reef flat containing *in situ* fine branching corals such as *Acropora cervicornis* and *Pocillopora cf. palmata* (Figure 3G, H), and various massive coral heads (e.g., *Diploria*, *Montastrea*).

In each of the reef facies, taphonomic/bioerosion information was collected for 20 samples in each coral-form category, as limited by coral occurrence.

Growth form categories were chosen to allow comparisons between facies with different species composition. The two *Acropora* species (*A. palmata* and *A. cervicornis*) were deemed significantly different from other morphologies and were therefore examined as their own categories. For *A. palmata*, separate data was collected for upright colonies and rubble in order to examine the effect of breakage and transport on taphonomy. All *A. cervicornis* were considered to be potentially rubble because of the difficulty in determining life position for this coral. Massive corals were primarily hemispherical domes including *Diploria strigosa*, *Diploria labyrinthiformis*, *Colpophyllia natans*, *Montastrea cavernosa*, and *Siderastrea siderea*. *Montastrea annularis*, a lumpy massive species, was also included here. The branching coral category included primarily organ pipe *Montastrea* in windward sections and organpipe *Montastrea*

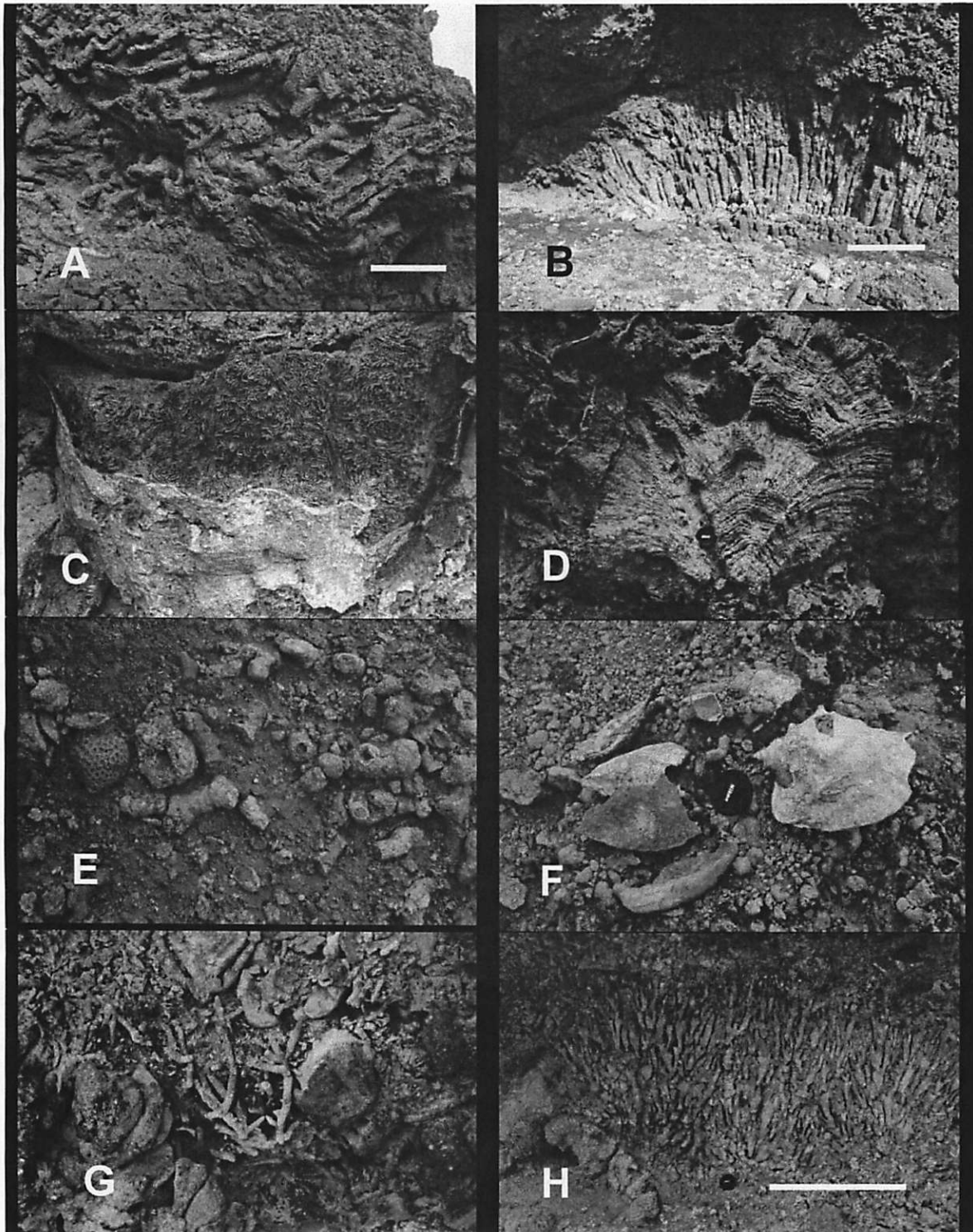


Figure 3. Examples of four Curaçao reef facies. A and B, windward reef crest facies : A) In situ *A. palmata*, B) Large organ pipe *Montastrea* colony. C and D) windward back reef facies: C) Coralline algae crust on *Diploria strigosa*, D) *Montastrea annularis* with macroboring. E and F) windward lagoon/sea grass facies: E) heavily encrusted *Porites* rubble, F) Numerous *Strombus gigas*. G and H) Leeward reef flat facies. In situ *A. cervicornis* (G) and *Pocillopora* (H). Scale bar 1 m, Lens cap 7 cm.

and *Pocillopora* in leeward sections.

At each site, a 30 m transect line was laid out horizontally on the outcrop and corals of particular growth forms were examined along the transect. If less than 20 colonies of a particular growth form were encountered, additional colonies were sought within 1 m above and below the transect, or a second transect at the same height was positioned on the opposite wall of the Boca in an effort to reach 20 colonies. Specimens of *A. cervicornis* were collected and returned to lab for analysis.

Each coral colony was first examined for its orientation in 15 degree intervals (life position = 0, on side=90). Next, the average thick-

ness of encrustation (almost entirely by coralline algae) was recorded in mm, and the % cover of bioerosion was estimated from the cross sectional area in outcrop, and by searching the exposed colony surface. This measure is considered a minimum estimate, since encrustation and lack of exposure makes macroboring difficult to estimate in some situations. Finally, the external surface of the coral was examined for signs of pitting that could have been attributed to grazing and external bioerosion. The percent cover of the pitted or irregular surface was estimated and recorded.

Table 1. Study site with four reef facies. Letters in parentheses refer to site letters in Figure 4.

Facies	Locality	Growth Forms
WW Crest	Boca Un (C)	<i>A. palmata</i> , in situ, N=20 <i>A. palmata</i> , rubble, N=20 domes, N=20 branching (<i>Montastrea</i>), N=20 <i>A. cervicornis</i> , N=16
	Boca Degu (A)	<i>A. palmata</i> , in situ, N=20 <i>A. palmata</i> , rubble, N=20 domes, N=20
Back Reef	Boca Un (C)	branching (<i>Montastrea</i>), N=20 domes, N=12 <i>A. palmata</i> , rubble, N=20 <i>A. cervicornis</i> , N=16
	Boca Degu (A)	branching (<i>Montastrea</i>), N=16 domes, N=16
	Boca Plate (B)	<i>A. cervicornis</i> , N=20
Lagoon	Boca Mansalina (B)	<i>Porites</i> , <i>A. cervicornis</i> , N=10
Leeward	Punta Halvedag (F)	<i>A. palmata</i> , in situ, N=20 <i>A. palmata</i> , rubble, N=24 domes, N=23 branching, N=13
	Playa Lagun (E)	<i>A. palmata</i> , rubble, N=22 domes, N=20 branching, N=21
	Wamaloa (D)	<i>A. cervicornis</i> , N=15

In the lab, *A. cervicornis* specimens were assigned a taphonomic grade based on their surface texture (5= pristine, 4= corallite collars present, 3= corallite collars mostly gone, surface texture more or less smooth, cylindrical, 2= corallum wall eroded/pitted on one side, 1= pitting on more than one side). Specimens were then cross-sectioned in three cuts and the average percent of skeleton missing was recorded. Maximum thickness of encrustation (coralline algae) was also measured in cross-section and considered a minimum estimate, since encrustation and lack of exposure makes macroboring difficult to estimate in some situations. Finally, the external surface of the coral was examined for signs of pitting that could have been attributed to grazing and external bioerosion. The percent cover of the pitted or irregular surface was estimated and recorded.

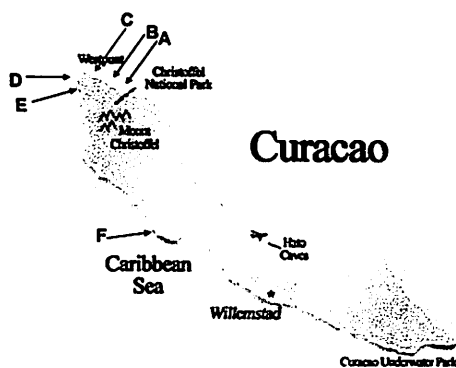


Figure 4. Study sites along northwest end of Curaçao. Letters refer to sites in Table 1.

RESULTS

Colony Orientation

80-94% of coral colonies in windward and leeward reef settings were preserved in up-

right position (Figure 5). The high *in situ* rate for corals was true for massive coral heads and large branching colonies such as organ pipe *Montastrea*. Even examples of *in situ* vertically oriented *A. cervicornis* were seen in outcrop (Figure 3G).

Encrustation

Encrustation by coralline algae was the rule at all sites (Figure 6). More than 80% of the colonies of most coral types were encrusted with coralline algal crusts between 3 and 10 mm (Figure 7). The exception was *in situ* *A. palmata* colonies in the reef crest zone that were coated, on average, by crusts 30-40 mm thick. Rubble from *A. palmata* and *A. cervicornis* were not more heavily encrusted than in *in situ* colonies.

One interesting result of the intense encrustation of most corals is that in some settings the coralline crust is better preserved than the coral and at times the coral itself has been lost. In these cases the coral's presence can be inferred from the encrusting algae's internal surface which is in effect an internal mold of the coral surface (Figure 8). This effect is termed bioimmuration (Taylor, 1990).

Boring

Most coral substrates examined did not have extensive boring bioerosion (Figure 9). Less than 20% of specimens of most facies and growth forms showed any boring, and most specimens that were bored had less than 10% bioerosion. The highest incidence of boring occurred in *A. palmata* rubble, and the least occurred in branching corals.

A. cervicornis rubble, measured in cross-section also showed a relatively high incidence of boring bioerosion (Figure 10), although rates of bioerosion were low (<10%).

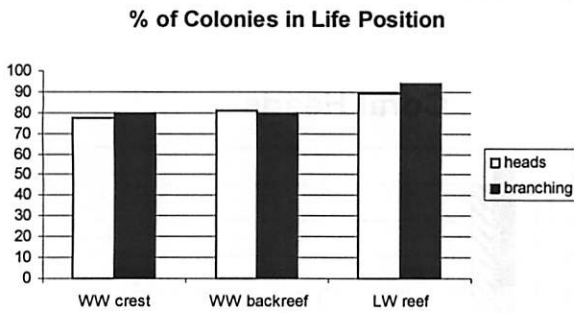


Figure 5. Orientation of massive coral heads and branching colonies. Very few were toppled, suggesting little storm reworking.

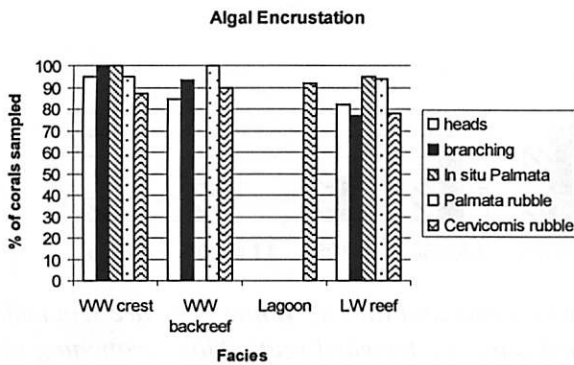


Figure 6. Percentage of coral colonies of various types that were encrusted with coralline algae. In all environments, most substrates were encrusted.

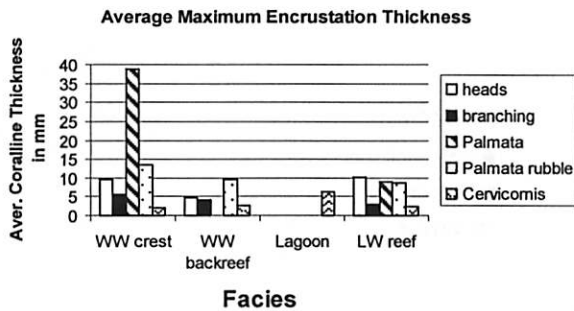


Figure 7. Algal thicknesses on various substrates and in various facies. Thicknesses (in mm) are the average of the maximum thicknesses of each coral piece.

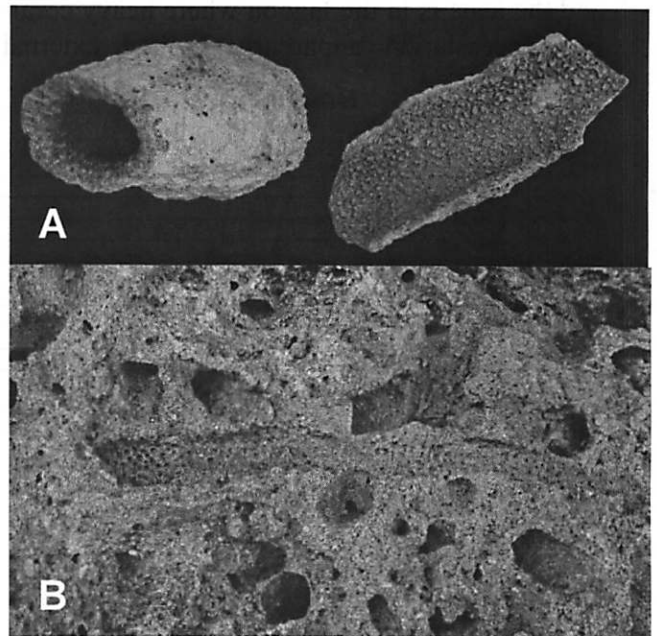


Figure 8. Examples of bioimmuration. A) Coralline algal ring remaining after *A. cervicornis* is dissolved (left), inside view of ring showing impressions of corallite necks (right). B) Impression of *A. cervicornis* left in coralline algae in the outcrop.

External Bioerosion

There was little evidence for the removal of the outer wall of the coral colonies as would be expected through scraping and biting during grazing or physical abrasion. The incidence of pitting of the external coral wall was low (< 20%, Figure 11). *In situ A. palmata* were the least pitted and leeward coral heads had the greatest frequency of pitting, although even here the pitting was generally over only a small proportion of the coral surface.

Taphograde analysis of *A. cervicornis* also suggests a low incidence of grazing (Figure 12). Grades 4 and 5 preserve the fragile corallite collars and thus indicate little external bioerosion. Grade 3 likewise shows some original surface texture and contains no pitting of the surface. Grades 1 and 2 indicate external erosion from either biological or physical (e.g., abrasion) processes. The greatest incidence of pitting is 40% in the windward reef crest setting,

and the least is in the lagoon where heavy coral-line encrustation apparently limited external

bioerosion.

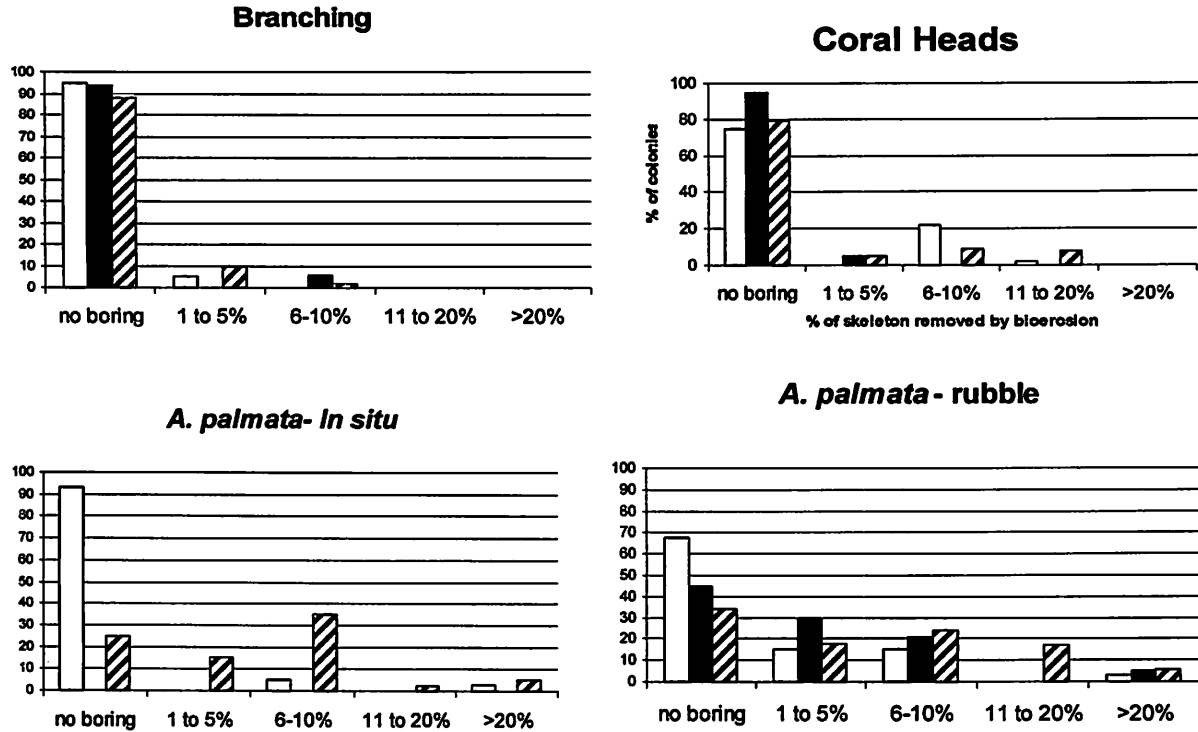


Figure 9. Boring incidence and intensity in various growth forms and facies. White bars are windward reef crest, black bars are windward back reef, and striped bars are leeward reef. Most branching and head colonies have > 80% of specimens without evidence of internal boring. Those that were bored typically had <10% bioerosion. *A. palmata* rubble had a higher incidence of bioerosion, but it was still low.

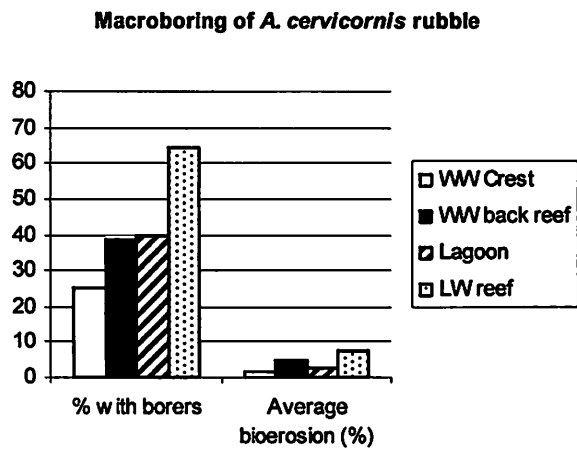


Figure 10. Boring in *A. cervicornis* rubble, examined in cross-section. Rubble from leeward reefs had a greater incidence of boring than other facies, but the % of bioerosion was <10% in all facies.

Geological Biases

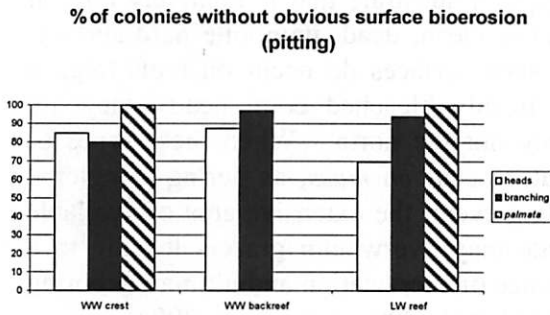


Figure 11. Incidence of external bioerosion on in various substrates and facies.

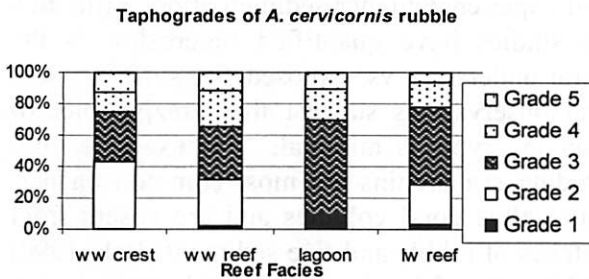


Figure 12. Taphograde analysis of *A. cervicornis* rubble. Grades 3-5 (pristine) preserve surface texture and indicate little external bioerosion.

DISCUSSION

Little external (grazing) erosion of most coral colonies was evident from the low incidence of surficial pitting and the preservation of fine corallite morphology (e.g., the thin tubes of *Acropora* polyps). This data, coupled with the near ubiquitous encrustation by coralline algae suggest that grazing bioerosion was rare in Curaçao Pleistocene reefs.

Possible explanations for why these results are apparently at odds with the results of most experimental studies may include the loss of grazing evidence in the fossil record, differences in setting from previous studies, and an over-estimation of the importance of grazing bioerosion in previous experimental studies.

It is unlikely that the Curaçao Pleistocene provided a highly biased measure of grazing excavation because the coral surfaces were so well preserved. Post-mortem reworking, burial, and diagenesis may all degrade coral surface texture, creating a potential taphonomic bias towards greater, not lesser, external bioerosion. In addition, although external scraping can destroy the evidence of previous grazing bioerosion, the lack of highly bored surfaces suggests that substrates were not reduced in size until ultimately being removed from the fossil record.

Some types of grazing bioerosion are more difficult to evaluate and will probably be generally overlooked in fossil studies. For example, many parrotfish take bites of live coral skeleton, and this bioerosion is rapidly masked by coral regeneration (Henry and Hart, 2005). The magnitude of this type of external bioerosion has not been quantified but is expected to be small since corallivory by Caribbean parrotfish is less than 10 bites/m²/day, and makes up generally <1% of parrotfish bites (Rotjan and Lewis, 2006).

Bioerosion of coralline algae crusts is also difficult to evaluate in the fossil record. While the net rate of coralline algal growth on the reef was positive, this does not imply an absence of algal grazing; parrotfish and echinoids would certainly remove some of the gross coralline algae production. While it is possible to evaluate coral bioerosion in fossil studies, it is difficult or impossible to estimate bioerosion of coralline algae or other secondary substrates in fossil studies.

Importance of Grazing Bioerosion

Low rates of grazing in this fossil study could simply reflect that the living reef had a very high proportion of live coral cover, and most external bioeroders (with the exception of some parrotfish, as mentioned above) scrape substrates other than live coral. On the other hand, the high incidence and thickness of coralline algae encrustation on corals in all

environments suggest that the colonies were exposed for a period of time prior to burial. The absence of substantial grazing during that interval requires a different explanation. I suggest that grazing is less important than has been generally reported.

The presumed high importance of grazing vs. boring bioerosion can be attributed to studies that took cut blocks of *Porites* and fastened them to hard reef substrates and monitored the experimental blocks through time (e.g., Kiene and Hutchings, 1994; Chazottes et al., 1995; Pari et al., 1998). Studies that have used more natural substrates have received less attention but have found that boring, rather than grazing, is generally greater. For example, naturally killed acroporid colonies showed little evidence of external bioerosion after 9 months, except for what was attributed to wave breakage in fragile plate colonies (Musso, 1992). Coral bleaching has also provided "natural" experiments of bioerosion of entire coral colonies. Results from Belize (Lescinsky, 2004) and the Indian Ocean (Sheppard et al., 2002; Zahir, 2002; Schuhmacher et al., 2005) have found boring to be intense after 1-5 years, and that coralline encrustation, rather than surficial erosion was observed.

It is unclear why cut-block and "natural" bioerosion studies have yielded such different results, although differences in the type of substrates examined may play a part. Whereas "natural" studies have focused primarily on branching colonies and coral rubble, the cut-block studies have focused on reef framework independent of individual coral colonies. This study, however, examined various coral growth forms in several different shallow facies and found few differences, suggesting that the observed patterns were generally applicable across the Pleistocene reef. Deeper reef zones were not preserved, but can be expected to have had even lower rates of grazing bioerosion, based on the well-documented trend towards decreasing grazing bioerosion with depth (e.g., Kiene and Hutchings, 1994; Bruggemann et al., 1996).

It is possible that cut-block studies overestimate grazing bioerosion because they focus

on a type of substrate that is relatively rare on the reef--a clean, dead, immobile hard surface. While such surfaces do occur on reefs (e.g., a single freshly bleached coral head), they are probably not the norm. When these types of substrates occur *en mass*, as during a regional bleaching event, the extensive area of available substrate may overwhelm grazers leading to a prevalence of encrustation and ultimately boring (Sheppard et al., 2002; Lescinsky, 2004).

In reefs with high live coral cover, such as the Pleistocene reef in this study, it is probable that much of the coral death occurs in lower, older parts of the colony that are shaded and experience higher sedimentation. Although no studies have quantified bioerosion in the coral understory vs. exposed flat surfaces, several observations suggest that grazing bioerosion in crypts is minimal. For example, bioeroding sea urchins are most common on partially alive coral colonies and are absent from patches of rubble and fine sediment (Bak, 1990) and in parrotfish, bioerosion rate is strongly tied to fish size. Smaller parrotfish that might be better able to reach reef recesses account for little to no bioerosion until an ontogenetic diet shift around 20 cm in length for common Caribbean species (Bruggemann et al., 1996). Larger individuals have more frequent, deeper bites and are responsible for most of the bioerosion, but are limited to feeding on more open surfaces.

Macroboring Bioerosion

Macroboring bioerosion, in contrast, will be favored in more cryptic settings, where early recruits are not scraped away. The rates of bioerosion noted in this study (generally <10%) are comparable to annual rates previously reported for bioerosion studies of entire reef corals (e.g., 8%, Lescinsky, 2004; 4-14%, Zahir, 2002, 1-8%, Musso, 1992), and are also within the range of natural macroboring rates reported on reef substrates in different environments where macroboring intensity has been shown to be related to productivity and burial (e.g., Risk et al., 1995; Holmes et al., 2000; Lescinsky et al., 2002). The observed rates of bioerosion, are

comparable to those on modern reefs and substrates that have been exposed for about a year.

Are Curaçao Reefs Unusual?

Curaçao reefs are unusual in their ecological integrity. Unlike many reefs that are composed primarily of stabilized rubble (Blanchon et al., 1997), the Curaçao reefs are composed largely of in place coral colonies with little breakage. In addition, Curaçao reefs probably had very high rates of live coral cover, judging from corallite surface texture, although this deserves further quantification--perhaps using microborer assemblages as markers of post mortem exposure.

High live coral cover in the Pleistocene reef is at odds with current reef conditions throughout most of the Caribbean, that is due in part to recent anthropogenic causes (Gardner et al., 2003). Sea-level transgression during the Pleistocene also would have contributed to rapid reef accretion and perhaps to overall live coral cover, although in recent reefs, live coral cover is dependent on physical disturbance and ecological factors (e.g., bioerosion) that would have functioned independent of the rate of sea-level rise.

CONCLUSIONS

Pleistocene coral reefs of Curaçao are unusually intact ecologically and form a good basis for evaluating external bioerosion from grazers in the fossil record. The data presented here show that grazing bioerosion in each of the four coral types and four facies examined was low, while boring bioerosion was comparable to that described on modern reefs. Previously observed high rates of grazing bioerosion in modern studies is in part a design bias and in part reflects anthropogenic changes to live coral cover in modern reefs. Low grazing, as observed in the Curaçao Pleistocene reef is probably a reflection of normal bioerosion patterns in a healthy (high percentage live coral cover) reef.

ACKNOWLEDGMENTS

I thank Adophe Debrot and the rest of the CARMABI Staff for logistical support in Curaçao and Otterbein College's White Fund, and Sabbatical-Leave Program for funds to conduct this research.

REFERENCES

- Bak, R.P.M., 1990, Patterns of echinoid bioerosion in two Pacific coral reef lagoons: Marine Ecological Progress Series, v. 66, p. 267-272.
- Blanchon, P., Jones, B., and Kalbfleisch, W., 1997, Anatomy of a fringing reef around Grand Cayman: storm rubble, not coral framework: Journal of Sedimentary Research, v. 67, p. 1-16.
- Bries, J.M., Debrot, A.O., and Meyer, D.L., 2004, Damage to the leeward reefs of Curaçao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999: Coral Reefs, v. 23, p. 297-307.
- Bruggemann, J.H., van Kessel, A.M., van Rooij, J.M., and Breeman, A.M., 1996, Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode, and habitat use: Marine Ecological Progress Series, v. 134, p. 59-71.
- Buissonjé P.H. de, 1974, Neogene and Quaternary Atlas of Aruba, Curaçao, and Bonaire (Netherlands Antilles): Foundation for Scientific Research in Surinam and the Netherlands Antilles, v. 78, Utrecht, 291 p.

- Chazottes, V., LeCampion-Alsumard, T., and Peyrot-Clausade, M., 1995, Bioerosion rates on coral reefs: interactions between macroborers, microborers, and grazers (Moorea, French Polynesia): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 113, p. 189-198.
- Gardner T.A., Cote, I.M., Gill, J.A., Grant, A., and Watkinson, A.R., 2003, Long-term region-wide declines in Caribbean corals: *Science*, v. 301, p. 958-960.
- Henry, L.A., and Hart, M., 2005, Regeneration from injury and resource allocation in sponges and corals- a review: *International Review of Hydrobiology*, v. 90, p. 125-158.
- Holmes, K. E., Edinger, E., Hariyadi, Limmon, H.G., and Risk, M.J., 2000, Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs: *Marine Pollution Bulletin*, v. 40, p. 606-617.
- Kiene, W.E., and Hutchings, P.A. 1994, Bioerosion experiments at Lizard Island, Great Barrier Reef: *Coral Reefs*, v. 13, p. 91-98.
- Lescinsky, H.L., 2004, Bioerosion in the Caribbean: using coral bleaching as a natural experiment, *in* Lewis, R.D., and Panuska, B.C., eds. *Proceedings of the Eleventh Symposium on the Geology of the Bahamas and other Carbonate Regions: San Salvador, Bahamian Field Station*, p. 25-34.
- Lescinsky, H.L., Edinger, E., and Risk, M., 2002, Mollusc shell encrustation and bioerosion rates in a modern epeiric sea: taphonomy experiments in the Java Sea, Indonesia: *Palaios*, v. 17, p. 171-191.
- Meyer, D.L., Bries, J.M., Greenstein, B.J., and Debrot, A.O., 2003, Preservation of *in situ* reef framework in regions of low hurricane frequency: Pleistocene of Curaçao and Bonaire, southern Caribbean: *Lethaia*, v. 36. p. 273-286.
- Musso, B.M., 1992, Rates of skeletal degradation following death in three species of *Acropora*: *Proceeding of the Seventh International Coral Reef Symposium, Guam*, v. 1, p. 413-418.
- Neumann, A. C., 1966, Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*: *Limnology and Oceanography*, v. 11, p. 92-108.
- Palmer, T., and Plewes, C., 1993, Borings and bioerosion in fossils: *Geology Today*, v. 9, p. 138-142.
- Pandolfi, J.M., Llewellyn, G., and Jackson, J.B.C., 1999, Pleistocene reef environments, constituent grains, and coral community structure: Curaçao, Netherlands Antilles: *Coral Reefs*, v. 18, p. 107-122.
- Pandolfi, J.M., and Jackson, J.B.C., 2001, Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles: *Ecological Monographs*, v. 71, p. 49-67.
- Pandolfi, J.M., Lovelock, C.E., and Budd, A.F., 2002, Character release following extinction in a Caribbean reef coral species complex: *Evolution*, v. 56, p. 479-501.
- Pari, N., Peyrot-Clausade, M., LeCampion-Alsumard, T., Hutchings, P.A., Chazottes, V., Golubic, S., LeCampion, T., and Fontaine, M.F., 1998, Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) after two years exposure: *Marine Ecology Progress Series*, v. 166, p. 119-130.

- Perry, C.T., 1996, Distribution and abundance of macroborers in an upper Miocene reef system, Mallorca, Spain: Implications for reef development and framework destruction: *Palaios*, v. 11, p. 40-56.
- Perry, C.T., 2000, Macroboring of Pleistocene coral communities, Falmouth Formation, Jamaica: *Palaios*, v. 15, p. 483-491.
- Risk, M. J., Sammarco, P. W., and Edinger, E. N., 1995, Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef: *Coral Reefs*, v. 14, p. 79-86.
- Rotjan, R.D., and Lewis, S.M., 2006, Parrotfish abundance and selective corallivory on a Belizean coral reef: *Journal of Experimental Marine Biology and Ecology*, v. 335, p. 292-301.
- Scheffers, A., 2004, Tsunami imprints on the Leeward Netherlands Antilles (Aruba, Curaçao, Bonaire) and their relation to other coastal problems: *Quaternary International*, v. 120, p. 163-172.
- Schellmann, G., Radtke, U., Scheffers, A., Whelan, F., and Kelletat, D., 2004, ESR dating of coral reef terraces on Curaçao (Netherlands Antilles) with estimates of younger Pleistocene sea level elevations: *Journal of Coastal Research*, v. 20, p. 947-957.
- Schuhmacher, H., Loch, K., Loch, W., and See, W.R., 2005, The aftermath of coral bleaching on a Maldivian reef- a quantitative study: *Facies*, v. 51, p. 80-92.
- Sheppard, C.R.C., Spalding, M., Bradshaw, C. and Wilson, S., 2002, Erosion vs. recovery of coral reefs after 1998 El Nino, Chagos Reefs, Indian Ocean: *Ambio*, v. 31, p. 40-48.
- Taylor, P. D., 1990, Preservation of soft-bodied and other organisms by bioimmuration a review: *Palaeontology*, v. 33, p. 1-17.
- van Duyl, F.C., 1985, Atlas of living reefs of Curaçao and Bonaire (Netherlands Antilles). Foundation for Scientific Research in Surinam and the Netherlands Antilles, 117, Utrecht, 37 pp.
- Vogel, K., Golubric, S., Brett, C.E., 1987, Endolith associations and their relation to facies distribution in the Middle Devonian of New York State, USA: *Lethaia*, v. 20, p. 263-290.
- Weidlich, O., 1996, Bioerosion in Late Permian Rugosa from reefal blocks (Hawasina Complex, Oman Mountains): Implications for reef degradation: *Facies*, v. 35, p. 133-142.
- Zahir, H., 2002, Assessing bioerosion and its effect on reef structure following a bleaching event in the Maldives, *in* Linden, O., Souter, D., Wilhelmsson, D., and Obura, D., *Coral Degradation in the Indian Ocean, Status Report 2002, CORDIO: Department of Biology and Environmental Science, University of Kalmar, Sweden*, p. 135-138.

