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## Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia)

V. Chazottes<sup>a</sup>, T. Le Campion-Alsumard<sup>b,c</sup>, M. Peyrot-Clausade<sup>b,c</sup>

<sup>a</sup> UA CNRS 1208, Université d'Aix-Marseille I, Centre de Sédimentologie et de Paléontologie, Place V. Hugo  
13331 Marseille, France

<sup>b</sup> UA CNRS 41, Université d'Aix-Marseille II, Station Marine d'Endoume, Centre d'Océanologie de Marseille,  
13007 Marseille, France

<sup>c</sup> Antenne du Museum National d'Histoire Naturelle et de l'Ecole Pratique des Hautes Etudes, B.P.1013 Papetoai,  
Moorea, French Polynesia

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### Abstract

A two-year experimental study of bioerosion at Moorea Island, French Polynesia, clearly demonstrated the importance of microborers in the initial stages of the establishment of infaunal boring communities. Rates of erosion by micro- and macroborers and by grazers were estimated from measurements of carbonate removal from experimental substrates, using Image Analysis. The studied substrates have been exposed for 2, 6, 12 and 24 months. After 2 months of exposure, the only borers present in the substrates were cyanobacteria and one chlorophyte (*Phaeophila* sp.) and their bioerosion rate was estimated at  $0.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ . In the course of the 2 years of exposure, recruitment of macroborers occurred and their estimated rates of erosion increased during this period from 2.15 to  $90 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ . Carbonate removal by grazers was the dominant agent of erosion, responsible for 89% of the total bioerosion:  $2.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ , as recorded in substrates exposed for 2 years. The measurable rates of bioerosion by microborers apparently decreased with the time of exposure from 0.6 to  $0.2 \text{ kg m}^{-2} \text{ yr}^{-1}$ , but these values are underestimations which need to be corrected by including the intensity of microboring in substrate layers removed by grazing. Bioerosion is dependent on numerous environmental factors such as depth, light availability, and nutrient supply. A good knowledge of bioerosional processes in modern environments could highlight bioerosion significance in the fossil record.

### 1. Introduction

The initial successional stages of bioerosion of recently killed corals have been investigated by Davies and Hutchings (1983), Hutchings and Bamber (1985), Peyrot-Clausade et al. (1992), Kiene and Hutchings (in press). These studies have documented the distribution and abundance of macro- and microborers and the role of grazers in the process of bioerosion. Various exposed carbon-

ate substrates have also been studied to determine the nature and extent of microbial infestation by endolithic organisms: blocks of calcium carbonate rocks (marble and limestone) have been studied by Bromley et al. (1990), and substrates prepared from shells and inorganic calcite have been used by Le Campion-Alsumard (1975), Golubic et al. (1975), Perkins and Tsentas (1976), Kobluk and Risk (1977), May and Perkins (1979), May et al. (1981) and Golubic et al. (in press.). However,

the possible interactions between micro and macro-borers and grazers on coral substrate have not been investigated.

The aim of this study was to document the succession of microborers over time and to determine their boring rates and their relative contribution to total bioerosion, which also includes macroboring and grazing. Image Analysis method was applied for the first time.

## 2. Material and methods

### 2.1. Study area

The experiments were carried out on the Tiahura transect located on the north-west barrier reef of Moorea, French Polynesia, ( $17^{\circ}30'S$  and  $149^{\circ}50'W$ ), (Fig. 1). The Tiahura area is well documented from the bionomic point of view. Many studies have been conducted along this transect which are relevant to this study, including studies of fish communities (Galzin and Pointier, 1985), availability of algal turf for herbivorous fish (Harmelin-Vivien et al., 1992), bioerosion of dead corals *in situ* habitats (Hutchings and Peyrot-Clausade, 1988; Peyrot-Clausade et al., 1992),

bioerosion of experimental exposed substrates (Peyrot-Clausade et al., submitted), skeletal grains of sediment (Vénec Peyré, 1987) and rates of grazing by echinoids (Bak, 1990).

The Tiahura reef flat extends over 850 m (Fig. 1). The fringing reef extends more than 250 m, with a depth not exceeding 1.5 m. The dominant coral genera present are *Synarea*, *Psammocora* and *Acropora*. From 50 to 100 m from the shore, algae cover 25–30% of the substrate, and this algal zone is dominated by *Halimeda*, *Padina* and *Turbinaria*. The barrier reef flat is approximately 400 m wide with a water depth of 2.5 m. The coral community in this region is characterized by large patches of *Porites*, *Pocillopora*, *Acropora* and *Montipora* and the algal community by *Turbinaria* and *Porolithon* on the seaward margins of this reef flat.

Tiahura area is exposed to NW winds from January to March and receives oceanic water continually across the reef into the lagoon, at a velocity of between  $0.06 \text{ m s}^{-1}$ – $0.10 \text{ m s}^{-1}$  (Leenhardt, 1988) and exits the lagoon via the passes. Tides are semi-diurnal with an amplitude of less than 0.4 m. An outbreak of the crown-of-thorns starfish *Acanthaster planci* occurred between 1979 and 1982 and damage from cyclones in 1983 greatly reduced the percentage of living coral along the transect.

### 2.2. Sampling design and analytical procedures

Large heads of live *Porites lobata* were collected on the barrier reef flat and cut into regular blocks about  $10 \times 10 \times 5 \text{ cm}$ . Blocks showing evidence of boring were discarded. Organic material was removed by soaking the blocks in sodium hypochlorite, rinsed and dried in the sun. The blocks were affixed on 2 large patch reefs of dead *Porites* which were situated close to each other, using aqua cement. A total of 8 blocks per patch reef were laid in November 1986 and 2 replicate samples were collected after 2, 6, 12 and 24 months exposure, although only 1 block was processed for each time period.

After the relevant exposure period the blocks were collected and fixed in buffered 5% solution of formaldehyde in seawater. Blocks were cut into

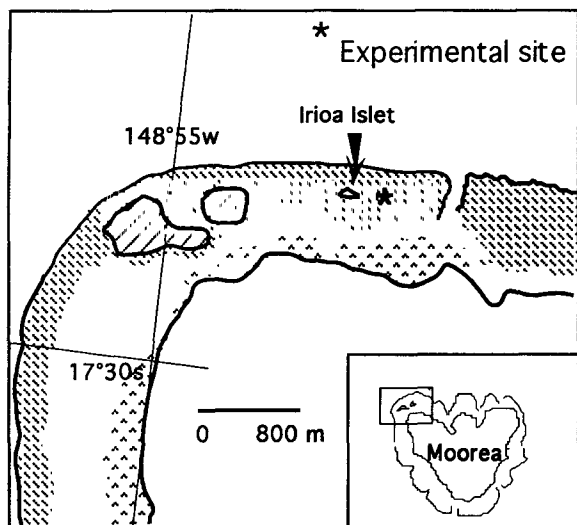


Fig. 1. Location map of the Moorea reef studied and location of the experimental site (the asterisk refers to the location of the experimental site).

2 halves, one half was used for quantitative analysis of micro- and macroborers, and the other half for determining the rates of  $\text{CaCO}_3$  loss by grazing and boring by both macro- and microborers.

The half block used for a quantitative analysis of the micro- and macroborers was subdivided into 2 parts. One part (60–90 cm<sup>3</sup> in volume) was used for determining the number of the major groups of macroborers present. This subsample was split up into small fragments in order to extract the macroborers. The obtained values were then converted to numbers per dm<sup>3</sup>. The second part of this half-block was used to investigate the distribution and species composition of the microborers using light or scanning electron microscopy (SEM), and resin embedded sections for studying the endoliths *in situ*. The samples used for study by light microscopy were prepared by dissolving the substrate using Pereny's solution (4 vol. 10% nitric acid, 3 vol. 0.5% chromic acid, 3 vol. 90% ethanol). The specimens for SEM and resin embedding were fixed in 2.5% glutaraldehyde in seawater and cacodylate buffer and postfixed in 2% osmium tetroxide prior to embedding in polymerizing resin and decalcifying using Pereny's solution. The resin casts obtained were then examined with the SEM from the surface of the substrate down to the limit of endolith penetration.

In order to estimate the rates of loss of  $\text{CaCO}_3$  by both grazing and (micro and macro) boring, the half-block intended for bioerosion quantification was cut into 6 slices 5 mm in thickness and photographed after organic matter destruction by

chlorax. Image analyses of these photographs together with those taken by SEM were made using the computer programme Carto-PC, operated on an HP 9000 computer. The losses of  $\text{CaCO}_3$  attributable to grazing (external bioerosion) and boring by both macro- and microborers (internal bioerosion) were distinguished. Grazing was estimated by comparing image analyses of the exposed blocks with the known original dimensions of the blocks. Internal bioerosion was estimated from boring volumes measured by Image Analysis method. An average coral density of 1.4 was used in calculations. An analysis of the porosity of the samples was carried out using the mercury-injection method (Guillaume and Carrio-Schaffhauser, 1985).

### 3. Results

#### 3.1. Macroborers

Several groups of macroborers were found including polychaetes, sipunculans and vermetids. Polychaete worms were the initial agents of macroboring and they were responsible for all the macro-erosion which was present after 2 months:  $2.15 \times 10^{-3} \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  (Table 1). Polychaete densities were 46 ind/dm<sup>3</sup> after 2 months of experiment and 89 ind/dm<sup>3</sup> after 6 months. The density of polychaetes continued to increase with increasing time of exposure: 122 ind/dm<sup>3</sup> present after 1 year and 1231 ind/dm<sup>3</sup>

Table 1

Bioerosion rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) estimated from boring and grazing volumes (expressed in % of initial block volume) calculated by Image Analysis Method

Internal bioerosion					External bioerosion grazing		Total bioerosion rates (kg m <sup>-2</sup> yr <sup>-1</sup> )
Exposure length	Macroboring		Microboring				
	volumes (%)	rates (kg m <sup>-2</sup> yr <sup>-1</sup> )	volumes (%)	rates (kg m <sup>-2</sup> yr <sup>-1</sup> )	volumes (%)	rates (kg m <sup>-2</sup> yr <sup>-1</sup> )	
2 months	0.1 × 10 <sup>-2</sup>	0.2 × 10 <sup>-2</sup>	0.39	0.57	0.26	0.37	0.94
6 months	0.6 × 10 <sup>-2</sup>	0.3 × 10 <sup>-2</sup>	0.42	0.20	1.99	0.96	1.16
12 months	9.4 × 10 <sup>-2</sup>	2.2 × 10 <sup>-2</sup>	0.62	0.14	7.42	1.74	1.90
24 months	76.0 × 10 <sup>-2</sup>	9.0 × 10 <sup>-2</sup>	1.68	0.20	19.85	2.33	2.62

after 2 years (Fig. 2). Sipunculans first appeared after 6 months but were restricted to a microfracture which would have facilitated their penetration into the substrate. Thus they were not taken into account for this exposure period. After 12 months of exposure, their density was 10 ind/dm<sup>3</sup> and after 2 years 233 ind/dm<sup>3</sup>. Vermetids appeared only after 2 years of exposure with a density of 50 ind/dm<sup>3</sup>. No evidence of boring by sponges or bivalve molluscs was found in any of the blocks.

Rates of substrate loss ascribed to boring by macroborers were determined for each exposure period but they were not apportioned to the particular macroboring agents. The rate of loss of CaCO<sub>3</sub> attributable to these macroborers increased from  $0.2 \times 10^{-2}$  kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> after 2 months to  $9 \times 10^{-2}$  kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> after 2 years (Table 1). Their boring contribution to the total bioerosion recorded in the 2 months-exposed block is 0.2% (Fig. 3) and only reaches 3.4% in the 2 years-exposed block.

### 3.2. Microborers

The initial infestation of the coral blocks by microborers was rapid. After 2 months of exposure, 22.4% of the block surface was colonised by microborers. However this level of infestation did not increase greatly with increasing exposure time, so that after 6 months the level was still 22.5%.

After 1 year it was 29.6% and after 2 years of exposure 30.8%.

The composition of the endolithic assemblages changed with the increasing exposure time. The initial infestation by endolithic microborers involved 2 cyanobacterial species *Mastigocoleus testarum* and *Plectonema terebrans*, and one chlorophyte *Phaeophila* sp. After 2 months of exposure, cyanobacteria were still abundant whereas *Phaeophila* occurred in low densities and was only found at this time. After 6 months, the cyanobacteria were still present, with the addition of the chlorophyte *Ostreobium*. Three categories of pore sizes could be recognised in the 6 month block after using the Mercury-injection method to determine porosity, these were: pores 2–6 µm in diameter, probably produced by *Plectonema*, others of 8–15 µm, probably produced by *Mastigocoleus* and a group 20–40 µm which were produced by *Ostreobium*. After 12 months of exposure, the density of this endolithic flora had increased but was restricted to the surface of the substrate and penetrated only to a depth of 0.77 mm. After 24 months of exposure, *Ostreobium* tended to become the dominant microborer and this species increased the depth of penetration to 2.73 mm. The highest measurable rate of loss of CaCO<sub>3</sub> ( $0.6 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) attributable to boring by the endolithic algae occurred after the first 2 months of exposure (Table 1). Subsequently, estimated rates of bioero-

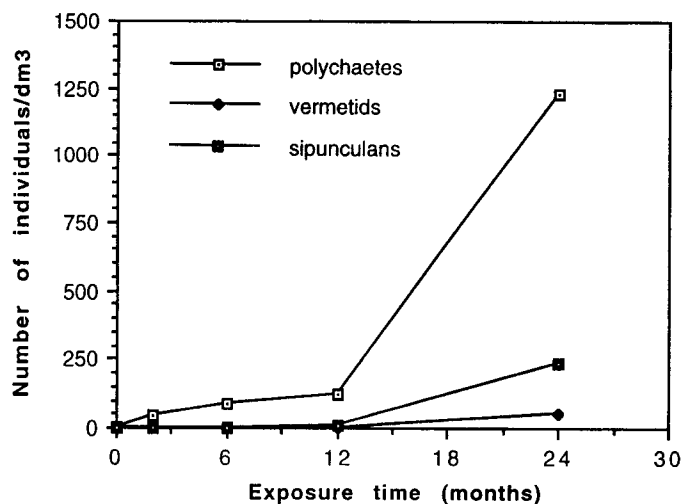


Fig. 2. Density of macroborers (ind/dm<sup>3</sup>) in experimental substrates.

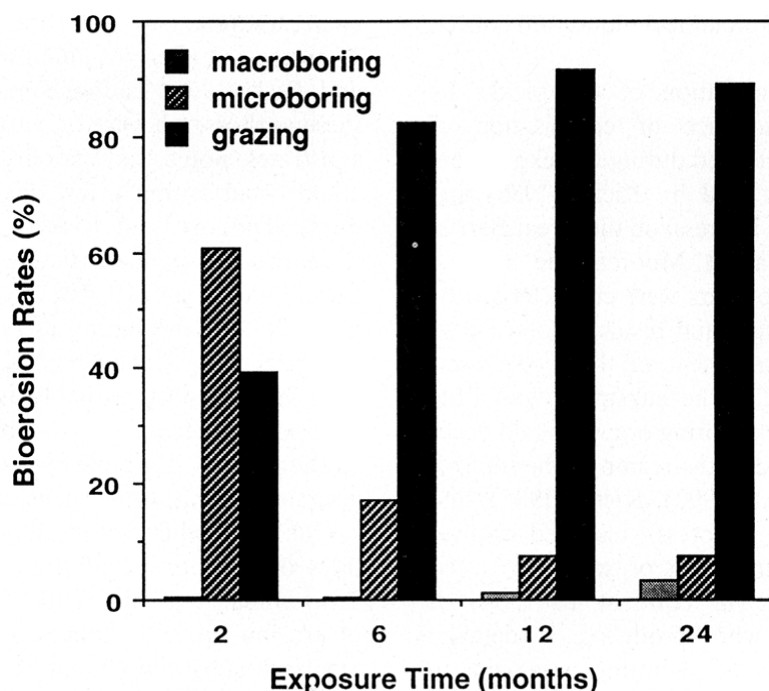


Fig. 3. Relative contribution of bioeroders to total bioerosion over the length of exposure.

sion decreased and then became stable ( $0.2 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) with increasing exposure periods.

### 3.3. Grazers

The experimental substrates exposed longer than 6 months exhibited high grazing traces. Grazer organisms at Moorea are urchins, herbivorous fishes (scarid fish) and few molluscs. Four urchin species were present in Tiahura transect. *Echinometra mathaei* was the most numerous ( $7.4 \text{ m}^{-2}$ ), followed by *Diadema savignyi* ( $4.8 \text{ m}^{-2}$ ), then *Echinothrix diadema* ( $0.6 \text{ m}^{-2}$ ) and *Echinostrephus molaris* ( $0.2 \text{ m}^{-2}$ ) (Bak, 1990). The density of herbivorous fishes has been estimated at 61 ind/100  $\text{m}^2$  (Harmelin Vivien and Galzin, pers. comm., 1990).

The quantities of  $\text{CaCO}_3$  removed by grazers were estimated from the loss of substrate by comparing the block volumes before and after exposure. Rates of grazing increased with increasing exposure from  $0.37 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  after 2 months to  $2.33 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  after 2 years (Table 1). After one year of exposure, 7.4% of the

initial block volume were removed by grazers and 19.8% after 2 years (Table 1). Grazer organisms were responsible for 39.3% of total recorded bioerosion after 2 months of exposure and for 88.9% after 2 years (Fig. 3).

## 4. Discussion

### 4.1. Bioeroders and estimated bioerosion rates

In previous publications, external and internal bioerosion were estimated using point-count analysis or direct measurements of volume and weight changes (Sammarco and Risk, 1990; Kiene and Hutchings, in press). Image Analysis method, introduced in this study, allowed for an integrated quantification of microbioerosion and gave more comparable results for internal and external bioerosion.

Previous studies have not distinguished between the rates of boring by macroborers and microborers (Kiene and Hutchings, in press; Peyrot-Clausade et al., submitted) because the treatment

of the latter required special techniques introduced in this study.

Regarding the colonisation of the blocks by macroborers, the sequence of colonisation of macroborers which occurred during this experiment was similar to that found by Kiene (1988) and Kiene and Hutchings (in press) on the Great Barrier Reef. In Australia, as in Moorea, the samples exposed for up to two years were characterised by a lack of boring sponges and bivalve molluscs; we presume that the recruitment of these organisms would have occurred if the substrates had been exposed longer, as these boring organisms do occur in coral heads sampled in the region of the transect (Peyrot-Clausade et al., 1992). Kiene (1985), and Kiene and Hutchings (in press), recorded bivalves and sponges only after 3 years of exposure.

These findings are in contrast to those of McCloskey (1970) who produced a detailed scheme of the succession of boring organisms in which sponges were the initial agents of macroboring, appearing after the endolithic algae but before polychaetes. We suggest that the reason for this apparent discrepancy may be that our study dealt with experimentally exposed, newly available substrates, whereas McCloskey examined *in situ* natural habitats, the age of which (i.e. time since death of coral) were unknown. It should also be noted that all experimental studies of bioerosion have demonstrated the spatial and temporal variations in recruitment of boring organisms (Hutchings et al., 1992; Kiene 1988; Kiene and Hutchings, in press).

On the Great Barrier Reef, Kiene (1988), showed a high variability in bioerosion rates in relation with space and time. He found rates varying for grazing between 0.01–1.69 kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> and for boring between 0.01–0.19 kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup>. For similar exposure length, the estimated grazing and boring rates are higher at Moorea. This can be explained by the fact that the samples of the Great Barrier reef were grazed only by scarids and few molluscans. On Moorea, on the contrary, urchins occurred in high densities and were the dominant grazers. Moreover, it must be noted that the microborer activity has not been estimated in Kiene's study.

Endolithic microborers (especially cyano-

bacteria) are known to be among the initial agents of bioerosion (Perkins and Tsentas, 1976; Kobluk and Risk, 1977; Tudhope and Risk, 1985). All these authors, who used a variety of experimental substrates, noted that endolithic algal infestations could occur within a few days of exposure (4–9 days). Tudhope and Risk (1985) estimated that the carbonate sediment dissolution by microborers was about 350 g CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup>. Our estimation for endolithic infestation after 2 months of exposure was 570 g CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> (Table 1). This high value results probably from a difference of porosity between our coral blocks and the substrates used by Tudhope and Risk (grain sand and aragonitic non porous shells).

Our study while not investigating the initial few days of recruitment of these organisms, showed the dominance of microborers over all other agents of erosion up to 2 months of exposure of newly available substrate (Table 1), and has confirmed the finding of previous studies which utilised non-coral reef substrates such as calcite, iceland spar, shells. We demonstrated that microendolithic organisms are responsible for more than 50% of the total bioerosion recorded during the initial stages of bioerosion (Fig. 3).

Phototrophic microborers, such as cyanobacteria and algae penetrate the substrate to their compensation depths (where photosynthesis equals respiration) which approximate 1 mm, depending on species. For example, *Ostreobium* requires less light for growth than cyanobacteria and can therefore penetrate deeper into the substrate where light levels are low (Le Campion-Alsumard, 1979), increasing the depth of penetration to 2.73 mm after 24 months of exposure. Thus it appears that the depth of penetration is largely determined by the species composition of the microflora rather than by the length of exposure. After 6 months, although macroorganisms become dominant bioeroders, microendolithic organisms remain an important component of the bioeroding community through their interaction with grazers.

Phototrophic endoliths ensure a renewable food source for the grazers, while the grazing inhibits the settlement of epilithic macro- and microphytes which compete with the endolithic organisms for substrate (Golubic and Schneider, 1979). On the

other hand, it is the presence of these boring algae which makes the substrate attractive to grazers (Schneider and Torunski, 1983; Bellwood and Choat, 1990). The compensation depth for the endolithic algae (as defined above) depends on the intensity of grazing, as the process of grazing continuously removes the substrate and extends the depth to which the algae can penetrate. The constant removal of substrate by grazing organisms will result in an underestimation of the rates of boring by endolithic algae as grazing removes substrate infested by boring algae. In our study, the substrates were not heavily grazed (see Table 1) until after they had been exposed for more than 2 months; this may explain why microboring rates were higher after 2 months of exposure ( $0.57 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) than after 2 years of exposure, ( $0.20 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ), (Table 1). In fact, after 2 months of exposure, the bioerosion rates relevant to microalgae must be considered as “residual” rates, after removal by grazing.

It should also be noted that none of the experimental substrates exhibited any accretion by coralline algae or other encrusting organisms. This is in contrast to the findings of Peyrot-Clausade et al. (submitted) who recorded net accretion after 6 months at several sites in French Polynesia including a site at Moorea on the same transect but on the fringing reef. This may be a result of the varying intensities of grazing along the transect, as suggested by Peyrot-Clausade et al. (submitted). Harmelin-Vivien and Peyrot-Clausade (pers. comm., 1989) counted on the barrier reef  $86.82 \pm 12.05$  herbivorous fish per  $100 \text{ m}^2$ ,  $12.65 \pm 7.60$  individual of urchins per  $\text{m}^2$  and 13

herbivorous gastropods in  $10 \text{ dm}^3$  of coral substrate. In contrast, on the fringing reef, only  $41.2 \pm 14.5$  herbivorous fish per  $100 \text{ m}^2$  and  $2.5 \pm 1.5$  urchins per  $\text{m}^2$  were present. These data suggest that grazing pressures are much higher on the barrier reef than on the fringing reef at Moorea and could therefore be a limiting factor in calcareous algae development on the barrier reef.

Our study has shown that extensive bioerosion of *Porites* as experimental substrate occurred over the 2-year study period. What are the potential meanings for the entire reef of these bioerosion rates? Obviously one cannot extrapolate from the rates of erosion calculated for one particular substrate to the transect as a whole, as it seems likely that the rates will vary between substrates. However, some data are available on the abundance of the *Porites* substrates on the same transect at Tiahura. 32% dead and 19% live *Porites* have been recorded on this transect (G. Faure, pers. comm., 1988). Using these figures and assuming that the rates of bioerosion of *Porites* calculated from our study are similar for all such colonies, we calculated that the rates of bioerosion could reach  $0.84 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  after 2 years for dead *Porites* substrates on the Tiahura Barrier Reef Flat (Table 2). These are minimal rates for this site. Other coral substrates present in the area are probably also subjected to similar degradation processes but their contribution to the reef bioerosion rates are not yet established.

On the other hand, constructional processes also occur on coral reefs. Accretion rates of *Porites* skeleton on the Tiahura barrier reef flat have been estimated by Guillaume (1990) over 2 years (from

Table 2

Bioerosion rates of dead *Porites* substrates of Tiahura reef flat estimated from experimental data and temporal variations of the ratio “skeletal production rate/bioerosion rate” of dead *Porites* substrates on Tiahura reef flat

Exposure length	Bioerosion rates of experimental substrates ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Bioerosion rates of dead <i>Porites</i> on Tiahura reef flat ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Production rate/bioerosion rate
2 months	0.94	0.30	8.33
6 months	1.16	0.37	6.76
12 months	1.90	0.61	4.10
24 months	2.62	0.84	2.98

1986 to 1988) at about  $13 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ . Extrapolating from this figure to Faure's data (19% of living *Porites*), the production rate would be of  $2.5 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  on Tiahura Reef Flat. Thus at least for *Porites* habitats on the barrier reef flat at Moorea, the rate of  $\text{CaCO}_3$  production exceeds the rate of loss of  $\text{CaCO}_3$  by bioerosional processes (Table 2). This is consistent with the results of Le Campion-Alsumard et al. (1993) who found on the same study site a net calcification of  $0.45 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ .

#### 4.2. Geological relevance

Relating the effects of bioerosion to particular organisms or particular fossil traces has been the subject of several studies. For example, bioerosion by macroborers (especially by boring clionid sponges and their fossil trace *Entobia*) has been compared in recent and fossil coral material (Bromley and D'Alessandro, 1990). Bromley (1975) compared Mesozoic and Cenozoic trace fossils to recent echinoids bioerosion data. Palmer (1982) attempted to review the changes in hard-ground communities (including borers) from the Cambrian to the Cretaceous. High fossilization potential of endolithic microorganisms and their microborings has been amply demonstrated. Fossil endoliths have been reported from Mesoproterozoic (Zhang and Golubic, 1987), Neoproterozoic (Knoll et al., 1986) and Paleozoic strata (Campbell, 1980), whereas their fossil traces (microborings) are abundant throughout the Phanerozoic (Hessland, 1949; De Meier, 1969; Gatrall and Golubic, 1970; Golubic et al., 1975). The preparation technique using polymerizing resins to cast boring networks has been developed for modern (Golubic et al., 1970), as well as for fossil borings (Golubic et al., 1979, 1980, 1983) which enables a direct comparison between them. SEM studies of resin-cast borings have been carried out for the Triassic limestones (Schmidt, 1990), different facies of the Upper Jurassic (Glaub, 1988), Upper Cretaceous (Hofmann and Vogel, 1992), and the older Tertiary (Radtke, 1991). However, in evaluating fossil microborings, early and late diagenetic changes must be taken in consideration. Borings appear to be preferential

sites of carbonate precipitation from interstitial waters (Bathurst, 1966, 1971; Scherer, 1974). Consequently, a large proportion of fossil borings may contain lithified fill or cement that are difficult to remove. In such cases, borings may not be successfully cast, and need to be evaluated by using petrographic thin sections.

In the present study, we focus particularly on microborings. Whereas previous studies of microborings were concerned mainly with specific microbial boring patterns, depicting size, form and penetration depth, exploring primarily their paleoecological and paleobathymetric applicability (e.g. Budd and Perkins, 1980), our study has focussed on successional patterns in bioeroder communities, and followed the patterns of interaction between microbioeroders and grazers (see Schneider, 1976). We have also obtained reliable quantitative estimates of bioerosion using computer analysis of microscopic images. Quantification procedures relating the activities of borers (both macro- and microborers) and grazers were introduced, providing for the first time data of their estimated bioerosion rates and relative contributions to the overall bioerosion. It is expected that these data will provide a better basis for comparisons with the fossil record.

Some recent studies of modern coral reefs focused more specifically on the influence of environmental factors on bioerosion processes. For example, it is known that coral reefs are generally well adapted to nutrient deficient conditions (Hallock, 1988). If nutrients become abundant, the reefal carbonate producers tend to become outcompeted by filamentous and fleshy algae (Cuet et al., 1988; Naim, 1993; Montaggioni et al., 1993). Bioeroding organisms, on the other hand, seem to increase in abundance with increasing availability of nutrients, further exacerbating the negative effect of eutrophication on reef construction. Our study of the oligotrophic Tiahura reef may, therefore, serve as a baseline study for future evaluation of the relationship between bioerosion and eutrophication.

Our results suggest that significant differences in bioeroder assemblages occur not only over geological time and from environment to environment, but also in relation to the substrate "maturity", i.e.



since the substrate became first available for endolith infestation. The present study shows that bioerosion changes significantly in the course of substrate exploitation both in nature and intensity. For example, the observed amount of substrate removed by algae indicates only the 'residual' removal rates, expressing merely how much the microalgae are able to keep up with the grazing pressure. Bioerosion by grazers is difficult to quantify in fossil substrates because the amount of carbonate removed by grazers cannot be measured. In addition to preserved grazing traces, the assessment of 'residual' bioerosion by endolithic algae may, therefore, constitute an indirect measure of grazing intensity. This assessment may provide more quantifiable information than other indirect means of bioerosion estimates in the fossil record, such as increased substrate porosity (Kanwisher and Wainwright, 1967), or grain size distribution of bioerosional products (Fütterer, 1974; Hunter, 1977; Schneider, 1976; Schneider and Torunski, 1983).

## References

- Bak, R.P.M., 1990. Patterns of echinoid bioerosion in two pacific coral reef lagoons. *Mar. Ecol. Progr. Ser.*, 66: 267–272.
- Bathurst, R.G.C., 1966. Boring algae, micrite envelopes and lithification of molluscan biosparites. *Geol. J.*, 5: 15–32.
- Bathurst, R.G.C., 1971. Carbonate sediments and their diagenesis. *Sedimentology*, 12: 620 pp.
- Bellwood, D.R. and Choat, J.A., 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ. Biol. Fishes*, 28: 189–214.
- Bromley, R.G., 1975. Comparative analysis of fossil and recent echinoid bioerosion. *Palaeontology*, 18 (4): 725–739.
- Bromley, R.G. and D'Alessandro, A., 1990. Comparative analysis of bioerosion in deep and shallow water, Pliocene to recent, Mediterranean Sea. *Ichnos*, 1: 43–49.
- Bromley, R.G., Hanken, N.M. and Asgaard, U., 1990. Shallow marine bioerosion: preliminary results of an experimental study. *Bull. Geol. Soc. Den.*, 38: 85–99.
- Budd, D.A. and Perkins, R.D., 1980. Bathymetric zonation and palaeoecological significance of microborings in Puerto Rican shelf and slope sediments. *J. Sediment. Petrol.*, 50: 881–894.
- Campbell, S.E., 1980. *Palaeoconchocelis starmachii*, a carbonate boring microfossil from the Upper Silurian of Poland (425 million years old): implications for the evolution of the Bangiaceae (Rhodophyta). *Phycologia*, 19: 25–36.
- Cuet, P., Naim, O., Faure, G. and Conan, J.Y., 1988. Nutrient-rich groundwater impact on benthic communities of La Saline fringing reef (Reunion Island, Indian Ocean): preliminary results. *Proc. 6th. Int. Coral Reef Symp. Aust.*, 2: 207–212.
- Davies, P.J. and Hutchings, P.A. (1983). Initial colonization, erosion and accretion on coral substrates. Experimental results, Lizard Island, Great Barrier Reef. *Coral Reefs*, 2: 27–35.
- De Meijer, J.J., 1969. Fossil non-calcareous algae from insoluble residues of algal limestones. *Leidse Geol. Meded.*, 44: 235–239.
- Fütterer, D.K., 1974. Significance of the boring sponge *Cliona* for the origin of fine grained material of carbonate sediments. *J. Sediment. Petrol.*, 44 (1): 79–84.
- Galzin, R. and Pointier, J.P., 1985. Moorea island, Society Archipelago. In: C. Gabri   et al. (Editors), *Proc. 5th Int. Coral Reef Congr.*, Antenne Museum-EPHE, Moorea, French Polynesia, 1: 73–102.
- Gatrall, M. and Golubic, S., 1970. Comparative study on some Jurassic and recent endolithic fungi using scanning electron microscope. In: T.P. Crimes and J.C. Harper (Editors), *Trace Fossils. Geol. J. Spec. Iss.*, 3: 167–178.
- Glaub, I., 1988. Mikrobhrspuren in verschiedenen Faziesbereichen des Oberjura Westeuropas (vorl  ufige Mitteilungen). *N. Jahrb. Geol. Pal  ontol. Abh.*, 177 (1): 135–164.
- Golubic, S. and Schneider, J., 1979. Carbonate dissolution. In: P.A. Trudinger and D.J. Swaine (Editors), *Biogeochemical Cycling of Mineral-Forming Elements*. Elsevier, Amsterdam, pp. 107–129.
- Golubic, S., Brent, G. and Le Campion-Alsumard, T., 1970. Scanning electron microscopy of endolithic algae and fungi using a multipurpose casting-embedding technique. *Lethaia*, 3: 203–209.
- Golubic, S., Campbell, S.E. and Spaeth, C., 1983. *Kunsttharzausg  sse Fossiler Mikroben-Bohrg  nge*. Pr  parator, 29: 197–200.
- Golubic, S., Hoffman, E.J. and Campbell, S.E., 1979. Study of fossil microbial borings: a new approach. In: *Am. Assoc. Pet. Geol. Annu. Meet.*, Abstr., p. 94.
- Golubic, S., Kiene, W.B., Radtke, G. and Vogel, K., in press. Investigations of endolithic colonization in corals and other substrates by microboring organisms. *Proc. 7th Int. Coral Reef Symp.*, Guam, 1992.
- Golubic, S., Knoll, A.H. and Ran, W., 1980. Morphometry of Late Ordovician microbial borings. *Tech. Summa. Abstr. AAPG Bull.*, 64: 713.
- Golubic, S., Perkins, R.D. and Lukas, K.T., 1975. Borings microorganisms and microborings in carbonate substrates. In: R.W. Frey (Editor), *The Study of Trace Fossils*. Springer, New York, pp. 229–259.
- Guillaume, M., 1990. Growth and calcium carbonate production of massive *Porites* (Barrier reef of French Polynesia). In: X. Ricard (Editor), *Proc. Congr. Int. Soc. Reef Studies*. Univ. Pacifique, Noumea, pp. 87–90.
- Guillaume, M. and Carrio-Schaffhauser, E., 1985. Non influence of depth on porosity of *Porites lutea* skeleton in Reunion Island (West Indian Ocean). *Proc. 5th Int. Coral Reef Symp.*, 6: 193–197.
- Hallock, P., 1988. The role of nutrient availability in bioerosion:

- consequences to carbonate buildups. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 63: 275–291.
- Harmelin-Vivien, M.L., Peyrot-Clausade, M. and Romano, J.C., 1992. Transformation of algal turf by echinids and scarid fishes on French Polynesian coral reefs. *Coral Reefs*, 11 (1): 45–50.
- Hessland, I., 1949. Investigations of the Lower Ordovician of the Siljan District, Sweden, II. Lower Ordovician penetrative and enveloping algae from the Siljan District. *Geol. Inst. Univ. Uppsala Bull.*, 33: 409–428.
- Hofmann, V.K. and Vogel, K., 1992. Endolithische Spurenfossilien in der Schreiebkreide (Maastricht) von Rügen (Norddeutschland). *Z. Geol. Wiss.*, 20 (1/2): 51–65.
- Hunter, I.G., 1977. Sediment production by *Diadema antillarum* on a Barbados fringing reef. In: D.L. Taylor (Editor), *Proc. 3th Int. Coral Reef Symp.*, Miami, 2: 105–109.
- Hutchings, P.A. and Bamber, E., 1985. Variability of bioerosion rates at Lizard Island, Great Barrier Reef, preliminary attempts to explain these rates and their significance. *Proc. 5th Int. Coral Reef Symp.*, 5: 333–338.
- Hutchings, P.A. and Peyrot-Clausade, M., 1988. Macro-boring communities of *Porites*: a biogeographical comparison. *Proc. 6th Int. Coral Reef Symp.*, 3: 263–268.
- Hutchings, P.A., Kiene, W.E., Cunningham, R.B. and Donnelly, C., 1992. Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculans, and bivalve molluscs) in *Porites* at Lizard Island, Great Barrier Reef. *Coral Reefs*, 11: 23–32.
- Kanwisher, J.W. and Wainwright, S.A., 1967. Oxygen balance in some reef corals. *Biol. Bull.*, 133: 378–390.
- Kiene, W.E., 1985. Biological destruction of experimental coral substrates at Lizard Island (Great Barrier Reef). *Proc. 5th Int. Coral Reef Symp.*, 5: 339–344.
- Kiene, W.E., 1988. Biological destruction on the Great Barrier Reef. Thesis. *Aust. Nat. Univ.*, 361 pp.
- Kiene, W.E. and Hutchings, P.A., in press. Long-term bioerosion of experimental substrates from Lizard Island, Great Barrier Reef. *Proc. 7th Int. Coral Reef Symp.*, Guam.
- Knoll, A.H., Golubic, S., Green, J. and Swett, K., 1986. Organically preserved microbial endoliths from the Late Proterozoic of East Greenland. *Nature*, 321: 856–857.
- Kobluk, D.R. and Risk, M.J., 1977. Rate and nature of infestation of carbonate substrates by a boring alga, *Ostreobium* sp., *J. Exp. Mar. Biol. Ecol.*, 27: 107–115.
- Le Campion-Alsumard, T., 1975. Etude expérimentale de la colonisation d'éclats de calcite par les cyanophycées endolithes marines. *Cah. Biol. Mar.*, 16: 177–185.
- Le Campion-Alsumard, T., 1979. Les cyanobactéries marines endolithes. *Bull. Soc. Bot. Fr. Actual. Bot.*, 1: 99–112.
- Le Campion-Alsumard, T., Romano, J.C., Peyrot-Clausade, M., Le Campion, J. and Paul, R., 1993. Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia). *Mar. Biol.*, 115: 685–693.
- Leenhardt, X., 1988. Hydrodynamisme des lagons d'atoll et d'île haute en Polynésie française. Thesis. *Mus. Nat. Hist. Nat.*, Paris.
- May, J.A. and Perkins, R.D., 1979. Endolithic infestation of carbonate substrates below the sediment-water interface. *J. Sediment. Petrol.*, 49: 357–378.
- May, J.A., MacIntyre, I.G. and Perkins, R.D., 1981. Distribution of microborers within planted substrates along a barrier reef transect, Carrie Bow Cay, Belize, Smithsonian. *Contrib. Mar. Sci.*, 12: 93–107.
- McCloskey, L.R., 1970. The dynamic of community associated with a scleractinian coral. *Int. Rev. Ges. Hydrobiol.*, 55(1): 13–81.
- Montaggioni, L.F., Cuét, P. and Naim, O., 1993. Effect of nutrient excess on a modern fringing reef (Reunion Island, Western Indian Ocean). Geological implications. *Proc. Global Aspects of Coral Reefs. Health, Hazards and History*, Miami, pp. N27–N33.
- Naim, O., 1993. Seasonal responses of a fringing reef community to eutrophication (Reunion Island, Western Indian Ocean). *Mar. Ecol. Progr. Ser.*, 99: 137–151.
- Palmer, T., 1982. Cambrian to Cretaceous changes in hard-ground communities. *Lethaia*, 15: 309–323.
- Perkins, R.D. and Tsentas, C.I., 1976. Microbial infestation of carbonate substrates planted of the St Croix shelf, West Indies. *Geol. Soc. Am. Bull.*, 87: 1615–1628.
- Peyrot-Clausade, M., Hutchings, P.A. and Richard, G., 1992. The distribution and successional patterns of macroborers in marine *Porites* at different stages of degradation on the barrier, Tiahura, Moorea, French Polynesia. *Coral Reefs*, 11: 161–166.
- Peyrot-Clausade, M., Le Campion-Alsumard, T., Hutchings, P.A., Payri, C., Le Campion, J. and Fontaine, M.F., submitted. Comparison of rates and agents of reef bioerosion in lagoons of high islands and atolls (French Polynesia) — the first six months. *Coral Reefs*.
- Radtke, G., 1991. Die mikroendolithischen Spurenfossilien im Alt-Tertiär West-Europas und ihre palökologische Bedeutung. *Cour. Forsch.-Inst. Senckenberg*, 138: 1–150.
- Sammarco, P.W. and Risk, M.J., 1990. Large-scale patterns in internal bioerosion of *Porites*: cross continental shelf trends on the Great Barrier Reef. *Mar. Ecol. Progr. Ser.*, 59: 145–156.
- Scherer, M., 1974. The influence of two endolithic microorganisms on the diagenesis of recent coral skeletons. *N. Jahrb. Geol. Paläontol. Monatsh.*, 9: 557–566.
- Schmidt, H., 1990. Mikrobohrspuren in Fossilien der Triassischen Hallstätter Kalke und ihre bathymetrische Bedeutung. *Facies*, 23: 109–120.
- Schneider, J., 1976. Biological and inorganic factors in the destruction of limestone coasts. *Contrib. Sedimentol.*, 6: 1–112.
- Schneider, J. and Torunski, H., 1983. Biokarst on limestone coasts, morphogenesis and sediment production. *Mar. Ecol.*, 4(1): 45–63.
- Tudhope, A.W. and Risk, M.J., 1985. Rate of dissolution of carbonate sediments by microboring organisms, Davies Reef, Australia. *J. Sediment. Petrol.*, 55: 440–447.
- Vénec-Peyré, M.T., 1987. Boring foraminifera in French Polynesian coral reefs. *Coral Reefs*, 5: 205–212.
- Zhang, Y. and Golubic, S., 1987. Endolithic microfossils (cyanophyta) from early Proterozoic stromatolites, Hebei, China. *Acta Micropaleontol. Sin.*, 4: 1–12.