

# Bioerosion of experimental substrates on high islands and on atoll lagoons (French Polynesia) after two years of exposure

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**ABSTRACT:** Rates of bioerosion by grazing and boring were studied in lagoons of 2 high islands (3 sites) and 2 atolls (2 sites each) in French Polynesia using experimental carbonate substrates (blocks of *Porites lutea* skeleton). The substrate loss versus accretion was measured after 6 and 24 mo of exposure. The results show significant differences between pristine environments on atolls and environments on high islands subjected to different levels of eutrophication and pollution due to human activities. Whereas experimental substrates on the atolls maintain a balance between accretion and erosion or exhibit net gains from accretion (positive budget), only 1 site on a high island exhibits significant loss of substrate by net erosion (negative budget). The erosional patterns set within the first 6 mo of exposure were largely maintained throughout the entire duration of the experiment. The intensity of bioerosion by grazing increases dramatically when reefs are exposed to pollution from harbour waters; this is shown at one of the Tahiti sites, where the highest average bioerosional loss, up to 25 kg m<sup>-2</sup> yr<sup>-1</sup> (6.9 kg m<sup>-2</sup> yr<sup>-1</sup> on a single isolated block), of carbonate substrate was recorded.

**KEY WORDS:** Bioerosion · Experimental substrates · Coral reefs · French Polynesia

## INTRODUCTION

Coral reefs are dynamic systems characterized by a delicate balance between reef growth and reef destruction, the latter primarily caused by bioerosion of coral substrate by grazing and boring organisms (Hutchings 1986). Excessive bioerosion weakens the structure of the reef framework and makes it more susceptible to damage by cyclones and storms (Harmelin-Vivien 1994), by El Niño events (Glynn 1994, Eakin 1996), and by coral predators such as the Crown-of-Thorns starfish (Musso 1997). Direct and indirect impact of bioerosion on coral reef structures, both recent and ancient, has been widely recognized

(Bromley 1975, Bromley & D'Alessandro 1990, Fiege 1993, Glynn 1997). However, only limited information is available on agents and rates of bioerosion. Experimental studies on bioerosion rates in the Indo-Pacific region have been carried out on the Great Barrier Reef, Australia at Lizard Island (Hutchings et al. 1992, Kiene & Hutchings 1994a, b, Musso 1997) and One Tree Island (Kiene 1985, 1988) and on Britomart Reef (Sammarco et al. 1987), which includes a cross-shelf transect (Sammarco & Risk 1990). Other studies were carried out on the reefs of Moorea, French Polynesia (Chazottes et al. 1995), and at Réunion Island, Indian Ocean (Chazottes 1996). Reaka-Kudla et al. (1996) have recently undertaken experimental studies on a highly degraded reef at Champion Island in the Galapagos. Most of these quantitative studies have

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revealed variations within a single reef system. These variations need to be evaluated in their respective regional contexts before they can be incorporated into generalized coral reef budgets.

Therefore, in 1990 we initiated a study of regional variations in bioerosion on high island and atoll coral reefs in French Polynesia. The preliminary results, following 6 mo of exposure of *Porites* skeleton blocks, revealed considerable differences between sites (Peyrot-Clausade et al. 1995b). High densities of algal turf at one polluted site were found to be correlated with large numbers of *Echinometra mathaei* and with extremely high rates of bioerosion, primarily caused by these sea urchins. From our preliminary results the following questions arose: (1) How does bioerosion vary over time? (2) Is the contrast between atolls and high islands found after 6 mo (Peyrot-Clausade et al. 1995a) maintained after longer exposure? (3) Are these results different from those obtained elsewhere on similar experimental substrates?

This paper presents the results of bioerosion after 2 yr of exposure of coral blocks. It discusses the changes in rates and agents of bioerosion over time, both within and between sites and compares our results with those obtained elsewhere.

## MATERIALS AND METHODS

**Location and description of study sites.** Seven sites were selected: 3 on the fringing reefs of high islands [2 on Tahiti (17°40' S, 149°30' W) and 1 on Moorea (17°30' S, 149°50' W), Society Archipelago] and 4 (2 on each atoll) on lagoon pinnacles on 2 atolls [Takapoto (14°30' S, 145°20' W) and Tikehau (15°00' S, 148°10' W), Tuamotu Archipelago, French Polynesia] (Fig. 1). All sites were located in water depths of 1 to 2 m. Full details of the 7 study sites are given in Peyrot-Clausade et al. (1995b); brief descriptions are given in the following.

(1) Faaa, Tahiti, is located in Papeete harbour at the mouth of the Tiparui River, which carries large quantities of terrigenous sediments and domestic sewage during the annual rainy season (Fraizier et al. 1985). (2) Atimaono, Tahiti, is a patch reef 100 m offshore, well away from urban populations. This site has numerous live coral colonies, a diverse assemblage of other colonial reef organisms (Gabié et al. 1986) and good

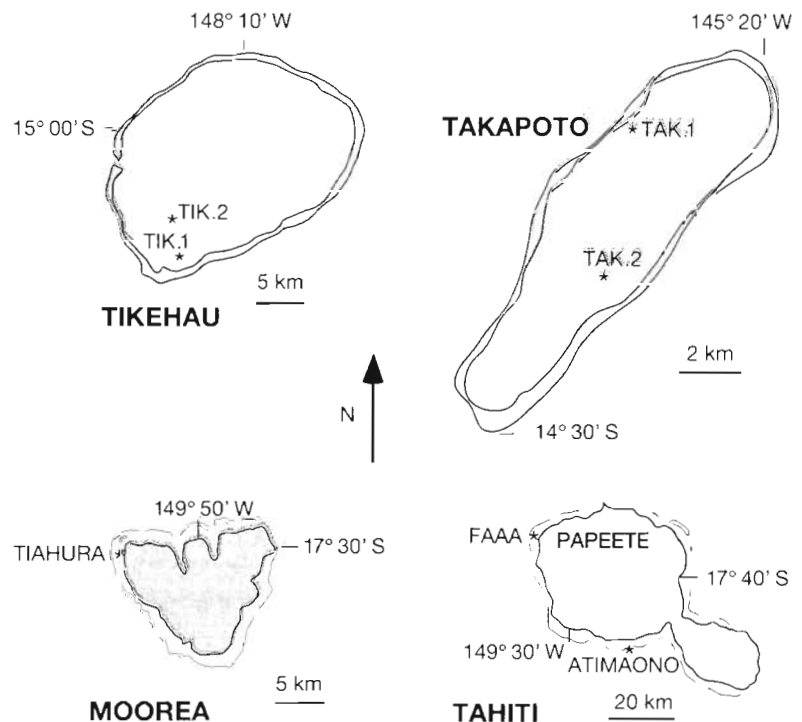


Fig. 1. Location of sampling sites on 2 atolls and 2 high islands in French Polynesia

water quality (see Cariès 1991 and Hutchings et al. 1994). (3) Tiahura is a fringing reef at Moorea located about 50 m offshore. For a description of the coral communities in this area, see Bouchon (1985). Gabié et al. (1988) and Adjeroud (1996) reported that water quality was consistently good in the area, although Wolanski et al. (1993) showed that under certain weather conditions a build up of nutrients may occur in the area from the discharge of nearby resort developments.

Takapoto is a closed elongated atoll with many lagoonal pinnacles. Salvat & Richard (1985) described the lagoonal coral communities and reported salinity levels varying from 35.5 to 36.1 ppt in the course of 1979. The waters are oligotrophic (Charpy 1996). (4) Tak. 1 was selected at the north end of the Takapoto lagoon in the Takai area. The experimental substrates were placed on the leeward side of a pinnacle. (5) Tak. 2 was selected in the mid part of the Takapoto lagoon at the Teavatika hoa, a small channel through which exchanges of oceanic and lagoonal water occur during storm conditions.

Tikehau is an almost circular atoll with one pass (Harmelin-Vivien 1985, Peyrot-Clausade 1989). The coral communities on the lagoonal pinnacles are zoned according to depth and exposure and were described by Faure & Laboute (1984) and Harmelin-Vivien (1985). Water quality was reported as oligotrophic (Charpy 1996). (6) Tik. 1 was selected at leeward side of a pin-

nacle at the southern end of the lagoon, close to a functional *hoa*. (7) The Tik. 2 site was selected at the leeward side of a pinnacle located more to the centre of the lagoon, but closer to the main village than site Tik. 1

**Experimental substrates.** Large live colonies of *Porites lutea* collected earlier at the Great Barrier Reef were used as the source of substrates for exposure experiments. The skeletons without endolithic boreholes were cut into regular sized blocks ( $8 \times 4 \times 4$  cm) using a band saw. Each block was soaked in sodium hypochlorite to remove organic matter, rinsed in freshwater for several days and dried. Dry weight and linear measurements were taken, and each block was provided with a unique number. The surfaces of all blocks were uniformly cut and layers with coral polyps removed. A representative piece of each colony was stored for reference. The density of each block was determined by the relationship between the dry weight and the block volume. Blocks were attached *in situ* with aqua cement to large heads of dead *Porites lutea*. The dead *Porites* colonies were cut flat before mounting of the blocks. Twenty blocks were placed on each site in November 1990 to be removed sequentially after exposure periods of 6 mo (Peyrot-Clausade et al. 1995b) and 24 mo. For each period, 5 replicates were collected from each of the 7 sites. For the present study, blocks were collected in November 1992 after 2 yr of exposure.

**Treatment after exposure.** After exposure, each block was fixed in a buffered 3% solution of formaldehyde in seawater. Any remaining aqua cement on the block was easily removed with a hammer and chisel. The blocks were cut in half and one half was cut vertically into 1 cm slices. For each block at least 2 slices were analysed. Additional slices were occasionally available for further analyses. Thus, at least 10 slices per site were obtained for analysis. The slices were photographed and the photographs scanned. Image analyses was performed on the scanned images using the program Optilab.

The rates of accretion were determined from scanned photographs of the slices. The surface area covered with crustose coralline algae and the mean thickness of accretion were measured by image analysis, which allowed the volume of coralline algal accretion per slice to be calculated. Using a density of  $1.26 \text{ g cm}^{-3}$  for calcareous algae (Laubier 1962), the mass and rate of accretion could be estimated.

The rates of external erosion by grazing were also determined from scanned photographs of the slices. The perimeter of and surface area under the encrusting organisms on each slice were measured using image analyses. The volume of the remaining substrate was calculated for each 1 cm thick slice from the measured surface areas. The difference between initial and final volumes represents the volume of the slice lost during exposure. Using the density value

measured for each block prior to exposure, the rate of calcium carbonate loss by external erosion expressed as  $\text{kg m}^{-2} \text{ yr}^{-1}$  could be estimated.

The rates of internal erosion by macroborers were calculated on the basis of carbonate volume removed (see above), which was determined from outlines of borings visible on scanned slices and evaluated using image analysis.

The rates of net erosion were determined from accretion minus erosion (external plus internal) for each slice; the average rate for each block was determined and the mean and standard deviations (based on at least 10 values) were calculated for each site. The data are presented as net rates of change of calcium carbonate in  $\text{kg m}^{-2} \text{ yr}^{-1}$ .

The total organic matter (epilithic and endolithic flora and fauna) resident in the block, which is potential food for the grazers, was estimated on the basis of several  $1 \text{ cm}^3$  cubes cut from the exposed surfaces of 1 slice per block. These  $1 \text{ cm}^3$  samples were rinsed with deionized water and dried to constant mass at  $60^\circ\text{C}$ . Dry samples were heated to  $550^\circ\text{C}$  for 5 h to remove organic matter, and weighed. For each slice, 8 cubes were selected, 2 from the top surface and 3 from each side, and the results were expressed as  $\text{mg cm}^{-3}$  (mean  $\pm$  standard deviation). A previous study (Peyrot-Clausade et al. 1995b) had shown that using 4 cubes selected at random provided a relatively large error (20%) of the mean (see Bliss 1967 and Sachs 1982) for both epilithic and endolithic algal biomasses. The method used by Peyrot-Clausade et al. (1995b) for calculating the organic biomass from decalcified dry mass per unit area was found to be an underestimate, and after different statistical tests a correction factor of 3.5 was needed to convert these figures to be comparable with those obtained by organic matter combustion, as used in our study for blocks exposed for 2 yr (see Table 1).

Biomass and density of macroborers were determined on the other half of the block which remained unsliced. This half was treated with a mixture of formalin and hydrochloric acid (for details see Hutchings & Weate 1978) to dissolve calcium carbonate, which facilitates the removal of all the macroborers (Hutchings 1981). Polychaetes, sipunculans and vermetid molluscs were counted and wet weighed (in mg to 3 decimal places) just after blotting. The wet weight was converted to mg per  $100 \text{ cm}^3$ .

The number of sea urchins *Echinometra mathaei* present at each site was estimated from counts of individuals in 20 random quadrats of  $0.25 \text{ m}^2$  made in November 1992 at the time of collection of blocks. These densities were compared with those present at the sites after 6 mo of exposure (Peyrot-Clausade et al. 1995b).

**Statistical analyses.** The univariate data display (box plots) developed by Tukey (Frigge et al. 1989) was

used. Each sample is represented as a box, divided at the median, and 2 whiskers; the box length is the interquartile range and the whisker ends correspond to the first and the last decile. All the observations beyond these limits are plotted individually.

A series of 1-way analyses of variance (ANOVAs) was carried out to investigate the variation in the net rates of erosion (accretion minus erosion) among blocks within a site and among the sites (Bliss 1967).

Subsequently a series of 1-way ANOVAs was also carried out to investigate the effects of site on various parameters (rates of accretion, external erosion, internal erosion, organic matter present in the surface 1 cm layer of the substrate, composition and biomass of infaunal communities) after 2 yr of exposure. Two-way ANOVAs with equal replication (cross classification) were then carried out on each of the above parameters obtained after 6 mo and 2 yr of exposure to investigate the effects of site and length of exposure. Multiple comparison of means according to Student-Newman-Keuls (SNK) test (Zar 1984) were used to determine which of these means were significantly different from each other. In both sets of ANOVAs the mean values for each block were used.

The classification of the blocks exposed for 2 yr was made using the Ward method (Euclidean distance on standardised data; Saporta 1978), and confirmed by centroid clustering (Roux 1985). The parameters considered were rates of accretion, external erosion, internal erosion, organic matter, biomass of polychaetes and sipunculans; their contribution to each cluster (class) was established as in Principal Component Analysis (PCA) (Roux 1985).

Using 2-way ANOVA, the interaction between the factors (sites and periods) was analysed and illustrated by means of diagrams. For each site the difference between mean values obtained after 6 mo and 24 mo was established with 95 % confidence interval.

All the analyses were performed on log transformed data to reduce the skewed distribution of the original data and the homoscedasticity using the statistical packages Super Anova 1.11 (1991), Statview 4.5 (1996) and Stat-Itcf (1991).

## RESULTS

### Rates of accretion

The mean rates of accretion varied among sites, the maximum value of  $1.13 \pm 0.54 \text{ kg m}^{-2} \text{ yr}^{-1}$  was recorded at Tik. 1 and the minimum value of  $0.18 \pm 0.19 \text{ kg m}^{-2} \text{ yr}^{-1}$  at Faaa (Table 1). A 1-way ANOVA revealed that significant differences ( $p = 0.0008$ ) occurred among the sites (Table 2). A SNK test showed that the rate of accretion was significantly higher at Tik. 1 (where the

Table 1. Means  $\pm$  SD of accretion and erosion rates, organic matter, polychaete and sipunculan densities and biomass, and sea urchin *Echinometra mathaei* densities after 24 mo (this study) and 6 mo (Peyrot-Clausade et al. 1995b) exposure

Site	Months of exposure	Rate of accretion ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of external erosion ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of internal erosion by macroborens ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of net erosion (accretion-erosion) ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Total organic matter (dry weight) ( $\text{mg cm}^{-2}$ )	Polychaete density (ind. $100 \text{ cm}^{-2}$ )	Polychaete biomass (wet weight) ( $\text{mg } 100 \text{ cm}^{-2}$ )	Sipunculan density (ind. $100 \text{ cm}^{-2}$ )	Sipunculan biomass (wet weight) ( $\text{mg } 100 \text{ cm}^{-2}$ )	<i>Echinometra mathaei</i> density (ind. $\text{m}^{-2}$ )
Moorea	24	$0.65 \pm 0.42$	$-0.89 \pm 1.24$	$-0.13 \pm 0.05$	$-0.38 \pm 1.31$	$38.0 \pm 8.9$	$193 \pm 85$	$200 \pm 130$	$13 \pm 10$	$30 \pm 20$	$4.8 \pm 10.6$
	6	$0.14 \pm 0.40$		$-0.18 \pm 0.10$	$-0.040$	23.4	$80 \pm 31$		$3 \pm 3$		$10 \pm 4.8$
Faaa	24	$0.18 \pm 0.19$	$-6.87 \pm 2.16$	$-0.08 \pm 0.06$	$-6.77 \pm 2.19$	$37.6 \pm 12.7$	$378 \pm 173$	$150 \pm 60$	$5 \pm 7$	$40 \pm 30$	$210 \pm 60.4$
	6		$-10.38 \pm 8.73$	$-0.07 \pm 0.02$	$-10.450$	11.9	$7 \pm 6$		0		$110 \pm 75.6$
Atimaono	24	$0.22 \pm 0.19$	$-0.63 \pm 0.50$	$-0.08 \pm 0.05$	$-0.49 \pm 0.63$	$37.5 \pm 9.1$	$78 \pm 60$	$160 \pm 100$	$51 \pm 37$	$200 \pm 180$	$8 \pm 10.6$
	6		$-1.20 \pm 1.36$	$-0.02 \pm 0.02$	$-1.22$	19.9	$21 \pm 16$		$2 \pm 3$		$11.2 \pm 13.2$
Tik. 1	24	$1.13 \pm 0.54$	$-0.36 \pm 0.10$	$-0.14 \pm 0.09$	$0.63 \pm 0.73$	$37.1 \pm 9.2$	$68 \pm 18$	$40 \pm 10$	0	$40 \pm 10$	0
	6	$0.55 \pm 0.80$		$-0.03 \pm 0.04$	0.52	23.4	$9 \pm 8$		$0.2 \pm 0.5$		0
Tik. 2	24	$0.97 \pm 0.59$	$-0.86 \pm 0.45$	$-0.14 \pm 0.25$	$-0.03 \pm 0.73$	$36.7 \pm 11.3$	$39 \pm 19$	$40 \pm 20$	$1 \pm 1$	$50 \pm 10$	0
	6	$0.06 \pm 1.30$		$-0.26 \pm 0.51$	$-0.20$	24.5	$4 \pm 3$		$0.4 \pm 0.5$		0
Tak. 1	24	$0.43 \pm 0.04$	$-0.33 \pm 0.20$	$-0.02 \pm 0.02$	$0.08 \pm 0.17$	$32.67 \pm 6.9$	$13 \pm 9$	$30 \pm 20$	$1 \pm 1$	$10 \pm 10$	0
	6	$0.94 \pm 0.30$		$-0.13 \pm 0.24$	0.81	11.9	$19 \pm 16$		$1 \pm 1$		0
Tak. 2	24	$0.51 \pm 0.13$	$-0.59 \pm 0.56$	$-0.05 \pm 0.05$	$-0.13 \pm 0.53$	$31.2 \pm 6.5$	$16 \pm 8$	$10 \pm 10$	$2 \pm 4$	$30 \pm 20$	0
	6		$-0.30 \pm 0.70$	$-0.08 \pm 0.14$	$-0.38$	18.9	$3 \pm 2$		0		0

blocks gained about 16 % of their original volume) than at the Tahiti sites (Faaa and Atimaono) (Fig. 2). The other 4 sites (Moorea, Tak. 1 and 2 and Tik. 2) had intermediate overlapping values. The variability within sites was particularly low in Takapoto (Fig. 3).

### Rates of external erosion

Estimated rates of  $\text{CaCO}_3$  loss by external erosion were highest at Faaa ( $6.87 \pm 2.16 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) and lowest at Tak. 1 ( $0.33 \pm 0.20 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) (Table 1). A 1-way ANOVA revealed that significant differences ( $p = 0.0001$ ) occurred among sites (Table 2). A SNK test showed that the amount of external erosion was significantly higher at Faaa (where the blocks lost about 50 % of their original volume) than at the other 6 sites (Fig. 2). A 1-way ANOVA excluding the site at Faaa showed that no significant differences in rates of external erosion occurred among the other 6 sites ( $p = 0.5282$ ). In addition, the variability within each site was low except at Moorea and particularly at Faaa, as shown by box plots (Fig. 3).

Table 2. One-way ANOVA among sites. Data were rates of accretion, external and internal erosion, net erosion, organic biomass and density and biomass of polychaetes and sipunculans. The original data were transformed before analysis, according to the logarithmic transformations  $\log x$  or  $\log(x+1)$  to ameliorate distribution skewness and homoscedasticity

Source of variation	df	MS	F	p
<b>Accretion</b>				
Site	6	0.186	5.619	0.0008
Residual	26	0.003		
<b>External erosion</b>				
Site	6	7.073	5.712	0.0001
Residual	26	1.236		
<b>Internal erosion</b>				
Site	6	0.007	1.050	0.4167
Residual	26	0.007		
<b>Net erosion</b>				
Site	6	36.345	26.016	0.0001
Residual	26	1.397		
<b>Organic matter</b>				
Site	6	0.209	3.479	0.0026
Residual	26	0.6		
<b>Polychaete density</b>				
Site	6	8.082	19.452	0.0001
Residual	26	0.415		
<b>Polychaete biomass</b>				
Site	6	3.545	5.868	0.0006
Residual	26	0.604		
<b>Sipunculan density</b>				
Site	6	8.571	11.430	0.0001
Residual	26	0.750		
<b>Sipunculan biomass</b>				
Site	6	0.018	3.706	0.0001
Residual	26	0.005		

From the photographs taken at the end of the exposure series at Faaa, it was possible to measure the decrease of coral patches where blocks were attached (Peyrot-Clausade et al. 1995a). The rate of carbonate removal was estimated from these photographs at  $25.14 \pm 2.40 \text{ kg m}^{-2} \text{ yr}^{-1}$ .

### Rates of internal erosion by macroborers

Boring activities by macrofaunal animals were highest at the 2 sites at Tikehau ( $0.14 \pm 0.09$  and  $0.14 \pm 0.25 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) and lowest at the 2 sites at Takapoto ( $0.02 \pm 0.02$  and  $0.05 \pm 0.05 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) (Table 1). However no significant differences among the sites ( $p = 0.4167$ ) were revealed by the 1-way ANOVA (Table 2). The variability within each site was limited, as shown on the box plot, except at Tik. 2 (Fig. 3). The box plots show that at 5 sites out of 7 the median is not superposed with the mean, confirming the asymmetrical distribution of these data.

### Rates of net erosion (accretion minus external and internal erosion)

Variations in the net rates of erosion (balance between losses due to erosion and gains due to accretion) were tested. The variance in erosion rates among blocks was at least 7 times greater than the variation within blocks (as determined from the individual slices from one block). Similarly the variance of rates of net erosion among sites was 1.7 times greater than the variability within sites.

The balance between rates of erosion (both by grazers and borers) and accretion varied significantly among sites ( $p = 0.0001$ ), with erosional processes prevailing at all sites except at Tak. 1 and Tik. 1 (Table 2). The highest net rate of loss was recorded at Faaa with an estimated net loss of  $6.77 \pm 2.19 \text{ kg m}^{-2} \text{ yr}^{-1}$ , while Tak. 1 and Tak. 2 exhibited small mean net gains of  $0.08 \pm 0.17$  and  $0.63 \pm 0.73 \text{ kg m}^{-2} \text{ yr}^{-1}$ , respectively.

It is obvious that the SNK test showed that only Faaa was significantly different from the other sites (Fig. 2). The box plots (Fig. 3) show that the other 6 sites vary slightly around a balance between accretion and erosion.

### Total organic matter

The amount of organic matter (consisting mainly of algae, sponges, micropolychaetes and sipunculans) was highest at Moorea ( $38.0 \pm 8.9 \text{ mg cm}^{-3}$ ) and lowest at Tak. 2 ( $31.2 \pm 6.5 \text{ mg cm}^{-3}$ ) (Table 1). A 1-way ANOVA

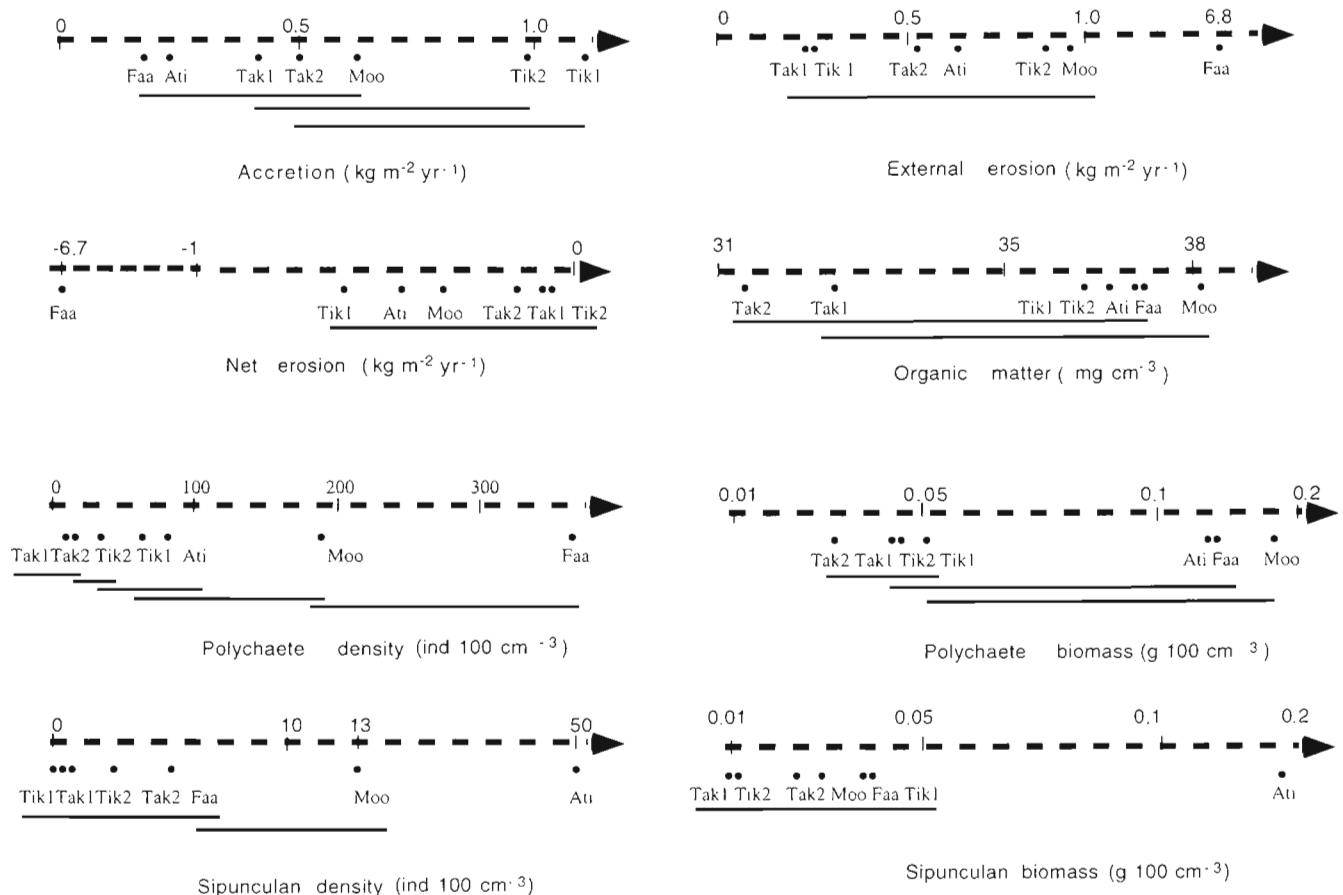


Fig. 2. Student-Newman-Keuls multirange test applied to the data analysed in Table 2. Significance level,  $\alpha = 0.05$ . Sites are ranked by mean; means sharing the same underline are not significantly different. Faa: Faaa; Ati: Atimaono; Moo: Moorea

revealed that the amount of organic biomass differed significantly among sites ( $p = 0.0026$ ) (Table 2). A SNK test showed the highest value for Moorea and the lowest for Tak. 2 (Fig. 2), the other sites exhibiting intermediate overlapping values. Box plots revealed a low variability within sites (Fig. 3).

#### Density and biomass of macroborers

Polychaetes represented by 9 species (species lists will be published separately) dominated the macroborer communities, in terms of the number of individuals (Table 1). A 1-way ANOVA revealed that a significant difference ( $p = 0.0001$ ) occurred among the sites (Table 2) with regard to the density of polychaetes present. A SNK test based on polychaete densities indicated that the 2 sites at Takapoto were grouped and differed significantly from Moorea and Faaa, with the other sites overlapping (Fig. 2). Box plots indicated very high values and variability in the density of polychaetes on high island sites Faaa, Moorea and Atimaono (Fig. 3).

A 1-way ANOVA showed that the biomass of polychaetes differed significantly among the various sites ( $p = 0.0006$ , Table 2), with the highest biomass being recorded at Moorea ( $200 \pm 130 \text{ mg } 100 \text{ cm}^{-3}$  of block) and the lowest at Tak. 2 ( $10 \pm 10 \text{ mg } 100 \text{ cm}^{-3}$  of block). A SNK test based on the biomass of polychaetes showed that Moorea was significantly higher than Tak. 1 and 2 and Tik. 2. The other sites exhibited intermediate overlapping values. Most polychaetes were very small; thus their biomass was very low despite high densities found locally (in Moorea:  $193 \pm 85 \text{ ind. } 100 \text{ cm}^{-3}$  of block).

Six species of sipunculans were present in the samples. A 1-way ANOVA revealed a significant difference ( $p = 0.0001$ ; Table 2) among sites with regard to the density of sipunculans present. A SNK test based on the density of sipunculans present showed Atimaono was significantly highest with  $51 \pm 37 \text{ ind. } 100 \text{ cm}^{-3}$  of substrate (Table 1), and that the atoll sites were low and grouped together with Faaa, Moorea being intermediate (Fig. 2).

A box plot revealed the great variability in the distribution of sipunculans among replicates on high island



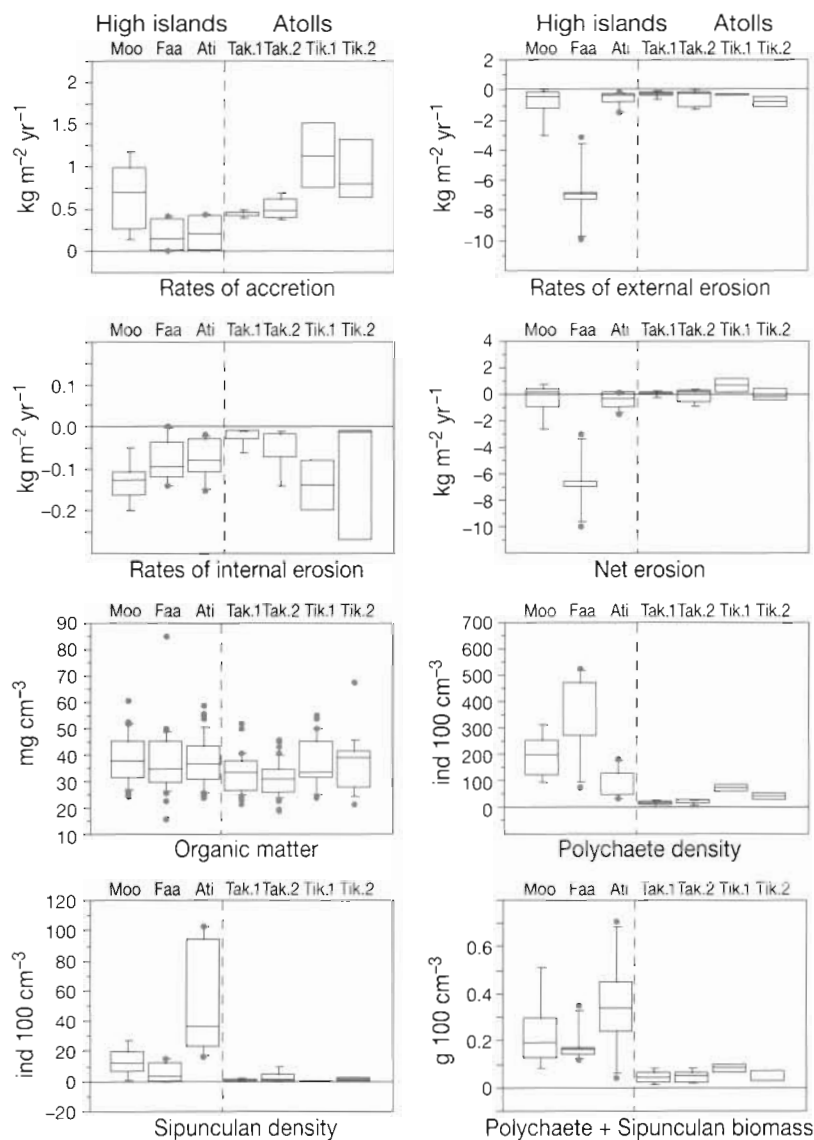


Fig. 3. Box plots of calculated rates of accretion and erosion, total organic matter accumulated in the exposed substrates, densities and biomass of polychaetes and sipunculans after 2 yr of exposure. (●) Outlier. Site abbreviations as in Fig. 2

sites (Fig. 3) particularly for Atimaono, which had positive skewness.

A 1-way ANOVA of the biomass of sipunculans revealed differences among sites ( $p = 0.0001$ ; Table 2), and a SNK test showed that Atimaono was significantly different from the others sites (Fig. 2), with the highest biomass of sipunculans recorded ( $200 \pm 180 \text{ mg } 100 \text{ cm}^{-3}$  of block).

A box plot based on total biomass of polychaetes and sipunculans indicated high values and more variability within sites of high islands (Fig. 3).

Vermetid molluscs were only abundant on 2 blocks at Moorea, with densities of 4 and 17 ind.  $100 \text{ cm}^{-3}$ . No other group of molluscs was found.

Only 2 blocks, 1 at each of the 2 sites at Tikehau, were infested by the sponge *Cliona vastifica* and rates of internal bioerosion were much higher in these blocks than in other samples ( $0.2$  and  $0.5 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) but not sufficient to induce a difference among sites.

### Density of sea urchins

The sea urchins *Echinometra mathaei* were present only at the high island sites (Table 1). A 1-way ANOVA showed that Faaa with its high density of sea urchins ( $210 \pm 60.4 \text{ ind. m}^{-2}$ ) was significantly different from sites at Moorea and Atimaono ( $p = 0.0001$ ).

### Classification of sites

The results of the cluster analysis revealed 5 groups of blocks (Fig. 4). An analysis of the factors contributing to these groupings revealed that for Group 1 (blocks from Moorea and Atimaono, together with 1 block from Faaa) the most important variable was the biomass of polychaetes and sipunculans, which contributed 84 % to the clustering. For Group 2 (blocks from Moorea, Atimaono, Tak. 2 and Tik. 1 and 2) 47 % was contributed by organic matter content, 33 % by net rates of accretion and 13 % by external erosion. For Group 3 (Faaa) the most important variable, contributing 83 % to the clustering, was the external erosion with extremely high rates, and

Group 4 (blocks from Tak. 1, Tak. 2 and Tik. 2) is characterized by similar contributions from rates of internal erosion and biomass of polychaetes and sipunculans (about 30 % each), and also a smaller contribution from the organic matter present. Group 5 (consisting of just 1 block from Tik. 2) was characterized by a single factor, contributing 94 %, which was the extremely high rate of internal bioerosion caused by the boring sponge *Cliona*. It should be noted that none of the sites had replicates that all clustered together, indicating variation within all sites. Two groups were restricted to atoll sites (Groups 4 and 5) and another 2 were composed only of high island sites (Groups 1 and 3). Only one group contained both high island and atolls replicates.

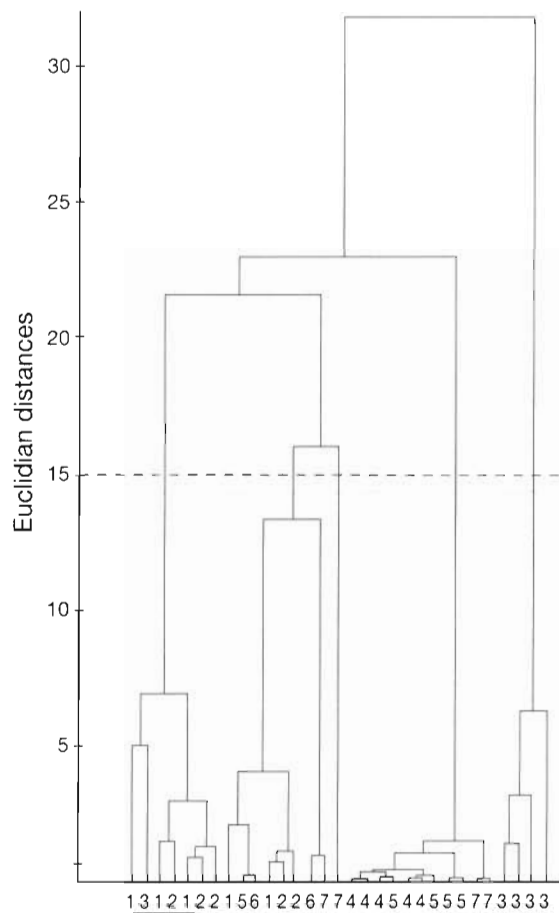


Fig. 4. Dendrogram of cluster analysis results using the Ward method. Each site is represented by all its blocks. Site 1, Mooorea; 2, Atimaono; 3, Faaa; 4, Takapoto-1; 5, Takapoto-2; 6, Tikehau-1; 7, Tikehau-2. The dashed line indicates the cut-off level chosen to separate the groups

#### Comparison between 6 mo and 2 yr of exposure

Comparing the results from Peyrot-Clausade et al. (1995b) and those presented here (Table 1) a 2-way ANOVA (Table 3) indicated that the net rates of erosion exhibited significant interaction between sites and sampling periods ( $p = 0.0065$ ). However, Table 3 shows that there is no significant difference between sampling periods ( $p = 0.0970$ ). The diagram established from the difference between mean values from each period for each site revealed that the difference found among sites ( $p = 0.0001$ ) was due essentially to Faaa samples (Fig. 5a). The rate of internal bioerosion exhibited no significant difference between the 2 sampling periods and among sites.

The amount of organic matter present at the 7 sites exhibited significant differences (Table 3) for sites ( $p = 0.0001$ ) and for sampling times ( $p = 0.0001$ ) with a significant interaction ( $p = 0.0001$ ). At all sites the amount

Table 3. Two-way ANOVA (nested mixed model) on the net rates of erosion, organic biomass and density and biomass of polychaetes and sipunculans for the 7 sites and the 2 sampling periods (6 mo and 2 yr). The original data were transformed before analysis, according to the logarithmic transformations  $\log x$  or  $\log(x+1)$ , to ameliorate distribution skewness and homoscedasticity

Source of variation	df	SS	MS	F	p
<b>Internal erosion</b>					
Site	6	0.144	0.024	0.718	0.6369
Sampling period	1	0.004	0.004	0.129	0.7206
Site $\times$ period	6	0.073	0.012	0.369	0.8991
Residual	51	1.707	0.033		
<b>Net erosion</b>					
Site	6	517.497	86.250	63.941	0.0001
Sampling period	1	3.856	3.858	2.858	0.0970
Site $\times$ period	6	27.669	4.612	3.419	0.0065
Residual	51	68.794	1.349		
<b>Polychaete density</b>					
Site	6	58.639	9.773	16.151	0.0001
Sampling period	1	45.724	45.724	75.562	0.0001
Site $\times$ period	6	21.696	3.616	5.976	0.0001
Residual	51	30.861	0.605		
<b>Sipunculan density</b>					
Site	6	37.076	6.179	11.909	0.0001
Sampling period	1	11.905	11.905	22.944	0.0041
Site $\times$ period	6	15.214	2.536	4.887	0.0001
Residual	51	26.464	0.519		
<b>Organic matter</b>					
Site	6	6.952	1.159	14.252	0.0001
Sampling period	1	28.844	28.844	3.552	0.0001
Site $\times$ period	6	4.821	0.804	9.884	0.0001
Residual	51	24.632	0.081		

of organic matter increased with time, and this was particularly evident at Faaa and Tik. 1 (Fig. 5b).

The densities of polychaetes (Table 3) varied significantly among sites and between sampling periods with a significant interaction ( $p = 0.0001$ ). At all sites, the number of polychaetes was significantly higher after 2 yr than

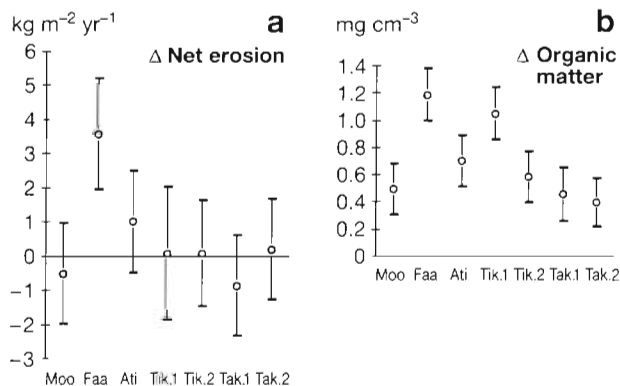


Fig. 5. Interactions between sites and sampling periods. The differences between mean values after 2 yr and 6 mo and the 95% confidence intervals are shown for each station for (a) net rate of erosion (only Faaa shows a significant interaction) and (b) total organic matter (where there are significant interactions for all the sites)



after 6 mo. The densities of sipunculans were significantly different (Table 3) for both factors (sites and sampling periods) with a significant interaction ( $p = 0.0001$ ). The densities of sea urchins varied significantly with site ( $p = 0.0001$ ) but not with sampling time ( $p = 0.5324$ ); these had with a significant interaction ( $p = 0.0027$ ).

## DISCUSSION

### Agents of bioerosion

Subsequent to damage and death of the coral colony, the exposed surfaces become available to colonization by epilithic and endolithic flora and fauna, followed by a suite of grazing organisms which feed on such substrates. Various organisms are known to remove substantial quantities of carbonate while grazing on dead coral substrates, including echinoids, scarid fishes and gastropods (Hutchings 1986, Harmelin-Vivien et al. 1992, Bellwood 1995a, b, Van Treeck et al. 1996). The calculated total rates of net carbonate removal on the 7 sites under study here range between 0.03 (Tik. 2) and  $6.77 \text{ kg m}^{-2} \text{ yr}^{-1}$  (Faaa).

At Faaa, where overfishing has occurred and water quality is severely degraded (Fraizier et al. 1985), rates of loss of block mass by grazing were estimated at  $10.38 \pm 8.70 \text{ kg m}^{-2} \text{ yr}^{-1}$  after 6 mo of exposure. This rate of substrate removal slowed down to annual value of  $6.87 \pm 2.16 \text{ kg m}^{-2} \text{ yr}^{-1}$  after 2 yr. By then the blocks stuck out on their isolated platforms, while the grazers continue to remove the reef around them and change its topography. This site also had the highest density of *Echinometra mathaei* ( $210 \pm 60.4 \text{ m}^{-2}$ ) of any of the study sites, suggesting that these sea urchins are responsible for the high rates of substrate loss. The corrected values for *in situ* total carbonate removal by grazing at Faaa of up to  $25 \text{ kg m}^{-2} \text{ yr}^{-1}$  are closely comparable with high rates reported in a recent study of Reaka-Kudla et al. (1996), who used similar techniques at Champion Island of the Galapagos, on a reef that was severely impacted by the 1982-1983 El Niño Southern Oscillation event (Macintyre et al. 1992, Glynn 1994). Their estimated rates of substrate loss were  $25.4 \text{ kg m}^{-2} \text{ yr}^{-1}$ . They also found that in the 14 mo of their bioerosion experiments the 3-dimensional topography of the reef changed dramatically. They suggested that grazing by sea urchins as well as several species of herbivorous fish was responsible for the extremely high rates of substrate loss. Similar studies by Bak (1990) in

Table 4. Review of the results obtained in experimental bioerosion (blocks of *Porites* spp. skeleton) studies in the world. Averages rates of net erosion are given for the atoll and high islands sites in this study

Location	Duration of experiment	Rate of accretion ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of external erosion (grazing) ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of internal erosion (macroboring) ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of internal erosion (microboring) ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of total erosion ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Rate of net erosion (accretion - erosion) ( $\text{kg m}^{-2} \text{ yr}^{-1}$ )	Source
French Polynesia, 7 sites	6 mo	0.06 to 0.94	-0.30 to -10.38	-0.02 to -0.26	Not measured	Not measured	0.81 to -10.45	Peyrot-Clausade et al. (1995b)
French Polynesia, 7 sites	24 mo	0.22 to 1.12	-0.33 to -6.87	-0.02 to -0.14	Not measured	-0.35 to -6.95	0.62 to -6.77	This study
French Polynesia, outer barrier at Moorea	2 mo	Not measured	-0.37	$-0.2 \times 10^{-2}$	-0.57	-0.94	Atolls + 0.18	Chazottes et al. (1995)
	6 mo		-0.96	$-0.3 \times 10^{-2}$	-0.20	-1.16		
	12 mo		-1.74	$-2.2 \times 10^{-2}$	-0.14	-1.90		
	24 mo		-2.33	$-9.0 \times 10^{-2}$	-0.20	-2.62		
Island, Indian Ocean	12 mo	Not measured	-1.51 to -4.31	-0.05 to -0.47	-0.23 to -0.69			Chazottes (1996)
Capricorn group, Great Barrier Reef, Australia, several sites within the group	6 mo	0.09 to 0.97			Not measured	-0.04 to -0.61		Kiene (1988)
	12 mo	0.00 to 0.63				-0.25 to -1.71		
	18 mo	0.00 to 1.04				0.00 to -5.91		
	24 mo	0.00 to 2.15				-0.11 to -9.11		
Lizard Island, GBR, Australia	3.5 yr	Not measured			Not measured	-0.41 to -2.71		Kiene (1985)
Lizard Island, GBR, Australia	4 yr	Not measured	-0.08 to -0.68	-0.05 to -0.20	Not measured	-0.22 to -1.75		Kiene & Hutchings (1994a)
Lizard Island, GBR, Australia	7-9 yr	Not measured	-0.35 to -2.46	-0.06 to -0.24	Not measured	-0.57 to -2.52		Kiene & Hutchings (1994b)
Champion Island, Galapagos Islands	14.8 mo	0.08 to 0.11	-22.8	-2.4	Not measured	-25.4		Reaka-Kudla et al. (1996)
Gulf of Aqaba	2 yr		-1.88 to -2.74					Van Treeck et al. (1996)

French Polynesia have shown that the sea urchins can consume  $12.5 \text{ g of CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ , which is equivalent to  $4.51 \text{ kg m}^{-2} \text{ yr}^{-1}$ . Few scarids were observed at the high island sites except on Moorea, where they are abundant (Peyrot-Clausade et al. 1995b).

At the atoll sites, where no sea urchins were present, scarids were probably responsible for the losses observed ( $0.33 \pm 0.20$  to  $0.86 \pm 0.45 \text{ kg m}^{-2} \text{ yr}^{-1}$ ). At Lizard Island, Great Barrier Reef, a 'healthy' reef, rates of loss due to external grazing were estimated at  $0.59 \pm 0.25$  to  $2.52 \pm 0.38 \text{ kg m}^{-2} \text{ yr}^{-1}$ , and were due almost entirely to scarids (Kiene & Hutchings 1994a, b). Kiene & Hutchings (1994a) postulated that lower levels of grazing by scarids at deeper sites at Lizard Island were related to lower levels of algal content in the substrate. Bruggeman et al. (1996) showed that the highest bioerosional rates by scarids occurred on shallow reefs ( $7 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) and decreased with reef depth.

Losses of substrate are caused not only by grazers, but also by macroborers. We suggest that rates of loss attributed to macroborers in this study ( $0.02 \pm 0.02$  to  $0.14 \pm 0.25 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) are probably underestimated. This is because a part of the burrow is removed by grazing and it is difficult to differentiate the holes made by small polychaetes from structural cavities of the coral skeleton on the scanned images. It is also difficult to distinguish between algal filaments and small burrows in the surface layers of the blocks. We found many small polychaetes in the algal residue after acid dissolution of substrate blocks. Currently, we are not aware of any better method of estimating rates of substrate loss attributable to boring by macrofauna, as they often live in burrows that are much larger than themselves. In addition, many of the smallest polychaetes have short life cycles and thus several generations may have occupied a block exposed for 2 yr (Hutchings et al. 1992). The composition of polychaete populations in this study changed over time with an increasing number of longer lived members of the family Eunicidae.

### Interactions

Bioerosion in the coral reef environment is the result of complex interactions between accretion, grazing and internal erosion. Evidence of all 3 activities is present in the current experimental series; however, their individual contributions are difficult to assess on the basis of 2 time profiles of collection and evaluation (6 mo and 2 yr). In our evaluation, therefore, the result of this interaction is presented as cumulative net erosion, i.e. residual volume of accreted substrate minus internal and external substrate loss, with reference to the original volume and weight of the exposed blocks.

The initial colonization of exposed blocks is microbial; penetration of carbonate substrates by microbial endoliths occurs within weeks (Chazottes et al. 1995). In the shallow tropical waters at Moorea, the relative contribution of phototrophic microbial endoliths to total bioerosion after 2 mo was 60 %, amounting to a removal rate of  $0.6 \text{ kg m}^{-2} \text{ yr}^{-1}$  of carbonate. These primary producers are the principal initial food source for grazers. Their downward growth orientation and fast recovery rates permit a rapid progression of total carbonate removal (Schneider & Torunski 1983) from 0.9 to  $2.6 \text{ kg m}^{-2} \text{ yr}^{-1}$  at Moorea (Chazottes et al. 1995).

The accretion by epilithic crustose rhodophytes becomes established later. It protects the substrate and counterbalances external erosion by grazing. Thus, net removal of the exposed substrates occurs prior or intermittent to the periods when the substrate is covered by encrusting algae. For example, Faaa, which had the highest level of net loss from grazing, also had the lowest level of algal accretion. A similar study carried out on a Caribbean reef (Hackney et al. 1989) showed that the crusts of coralline algae survived greater grazing intensities than turfs, suggesting that the former are better adapted to resist grazing. In our study, the atoll sites, in general, showed a higher rate of accretion by crustose algae, probably due to the absence of sea urchins, than the sites on high islands, almost completely compensating for grazing pressure.

Apparently, high levels of grazing do not prevent the establishment of large infaunal populations which contribute to internal substrate erosion. For example, high external erosion rates on high islands are correlated with high levels of infaunal biomass and density. In addition, it is conceivable that internal erosion sufficiently weakens the substrate, which may, in turn, enhance grazing efficiency. Generally, high levels of suspended organic matter at the high island sites favors growth of infaunal suspension feeders in blocks, which is in sharp contrast to the low biomass and densities of suspension feeders in oligotrophic waters of atolls.

Similar and relatively even distribution of total organic content in the exposed blocks throughout the range of studied sites, despite clear differences in trophic levels of the surrounding waters, is surprising. This finding indicates that the overall rates of organic production and consumption may be different but balanced.

### Patterns of erosion

Carbonate budgets of experimental substrates in atoll lagoons after 2 yr seem to be balanced. So Tik. 2 and Tak. 2, exhibiting negative budgets after 6 mo ( $-0.20$  and  $-0.38 \text{ kg m}^{-2} \text{ yr}^{-1}$ ), respectively, and Tak. 1,

exhibiting a positive budget after 6 mo ( $0.81 \text{ kg m}^{-2} \text{ yr}^{-1}$ ), tend to reach equilibrium after 2 yr (erosion balanced by accretion).

There is a large difference in carbonate budget between atolls and high islands after 2 yr. At Moorea the negative budget is more marked after 2 yr ( $-0.38 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) than it was after 6 mo ( $0.04 \text{ kg m}^{-2} \text{ yr}^{-1}$ ). At Faava, however, it should be noted that the net loss tends to decrease with time (length of exposure) from  $-10.45 \text{ kg m}^{-2} \text{ yr}^{-1}$  after 6 mo against to  $-6.77 \text{ kg m}^{-2} \text{ yr}^{-1}$  after 2 yr. This site, distinguished from the others by the highest net rate of loss after 6 mo of exposure, maintained a marked negative budget after 2 yr.

The pattern set within the first 6 mo of exposure (Peyrot-Clausade et al. 1995b) was maintained after 2 yr (this study). Kiene & Hutchings (1994a, b) found that patterns of bioerosion (grazing and boring) established at a particular site within the same reefal system (Lizard Island, Great Barrier Reef) after 2 yr of exposure were generally maintained for the following 5, 7 and 9 yr.

This study revealed unusually low rates of internal erosion by macroborers. This is consistent with the virtual absence of boring sponges in the studied blocks. Similar conditions were also observed at Lizard Island, Australia (Kiene 1988). Clionid sponges are known to be the most efficient borers (Rose & Risk 1985).

A summary of data from recent works that used a similar experimental approach to this study is presented in Table 4. Spencer (1992) also tabulated rates of grazing and boring by a variety of organisms. The table shows that variations exist between areas; however, all figures except for those from highly degraded reefs (Faava and Galapagos) are within the same order of magnitude. Low bioerosion rates have been largely found whatever the geological history of the site or the population of organisms responsible for grazing and boring. However, high rates of bioerosion may be a good measure of disturbances in coral reef functioning due to sewage (Faava) or to natural events such as El Niño (Galapagos). Perhaps this means that we can start defining baselines for rates of bioerosion and accretion for healthy reefs and using them to assess the condition of a reef.

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