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Initial bioerosion and bioaccretion on experimental substrates in high island and atoll lagoons (French Polynesia)

Bioerosion
Coral reef
Grazing
French Polynesia

Bioérosion
Récif corallien
Broutage
Polynésie Française

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ABSTRACT

In order to estimate the losses of $CaCO_3$ from bioerosion (grazing and boring), experimental coral substrates were laid in the lagoons of high islands and atolls in French Polynesia. After six months of exposure, the sites could be divided into those exhibiting net bioerosion and those exhibiting net accretion. Of the five sites exhibiting net bioerosion (grazing and macroboring greater than accretion), three were located off high islands and two in atoll lagoons. The average net rate of bioerosion was greatest at Faaa in Papeete Bay, Tahiti (10.45 $kg.m^{-2}.yr^{-1}$). Of the two sites exhibiting net accretion, the greatest rate of gain (0.81 $kg.m^{-2}.yr^{-1}$) was recorded at the eastern site in Takapoto lagoon. Recorded differences in the composition and distribution of macroborers, microborers and the algal turf appeared to be related to the presence or absence of grazing sea urchins (*Echinometra mathaei*). It is suggested that the high densities of algal turf recorded at Faaa are a result of elevated nutrients at this site, originating in the sewage discharge from nearby residential and industrial sites.

RÉSUMÉ

Bioérosion et bioaccrétion sur substrat expérimental : six premiers mois d'exposition (Polynésie Francaise).

Des modèles expérimentaux constitués de blocs de *Porites* sain ont été mis en place sur différents sites de la Polynésie française (dans des lagons d'îles hautes et d'atolls). On a pu estimer la quantité de $CaCO_3$ enlevé au substrat par les organismes brouteurs et les organismes macroperforants récoltés après six mois d'exposition. Dans cinq des sept sites, la bioérosion est supérieure à l'accrétion et la bioérosion maximale (10,45 $kg.m^{-2}.an^{-1}$) se trouve sur le site de Faaa (port de Papeete). Le plus grand taux d'accrétion a été obtenu à Takapoto (0,81 $kg.m^{-2}.an^{-1}$). Des différences dans la composition et la distribution des microperforants, des macroperforants ont été mises en évidence, en relation avec la présence ou l'absence du broutage par les oursins *Echinometra mathaei*. Cette étude suggère que le développement important du feutrage algal à Faaa et l'érosion active provenant du broutage sont liés aux apports de nutriments dans ce secteur.

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INTRODUCTION

Although it is one of the major processes affecting the structure of coral reefs (Hutchings, 1986), only limited information is available on the rates and agents of bioerosion (which consists of both external erosion by grazing and internal erosion by boring). Experimental studies have been carried out within one reefal system on the Great Barrier Reef, Australia, at Lizard Island (Hutchings *et al.*, 1992; Kiene and Hutchings 1994 *a*, *b*), at One Tree Island (Kiene, 1985, 1988) and at Britomart Reef (Sammarco *et al.*, 1987); in French Polynesia at Moorea, (Peyrot-Clausade *et al.*, 1995; Chazottes *et al.*, 1995); and in La Réunion (Chazottes, 1994). But to date no studies have been undertaken to compare rates and agents of bioerosion on different reefs within the same geographical area. In the present study, this gap was filled by selecting two high islands and two atolls within the single area of French Polynesia. The data obtained may be important for developing management plans for such areas, which need to take account of information on rates of growth as well as of destruction in order to predict the long term viability of the reefs in question.

For the experiments in French Polynesia, recently killed colonies of *Porites* were cut into regular-sized blocks. Similar experimental substrates were used by Kiene (1988), Hutchings *et al.* (1992), Pari *et al.* (1993), Kiene and Hutchings (1994 *a*, *b*), Chazottes (1994), Peyrot-Clausade *et al.* (1995) and Chazottes *et al.* (1995). Use of these substrates makes it possible to know the exact age of the internal bioeroding communities, whereas in natural substrates *in situ* total bioerosion and changes in the internal structure of bioeroding communities occur over various periods of time.

This paper presents the initial results (six months of exposure, from November 1990 to April 1991) of a long-term series of experiments which began in November 1990.

MATERIAL AND METHODS

Experimental substrates

Experimental substrates (blocks cut from living *Porites* colonies) were attached to large heads of dead colonies (Peyrot-Clausade *et al.*, 1995, Fig. 1), the upper surface of which had been eroded to form a flattened horizontal surface. The experimental substrates took the form of regular-sized (8 × 4 × 4 cm) blocks cut with a band saw; each block was measured after soaking in sodium hypochlorite, rinsed and dried in sun to constant weight after soaking in fresh water for several days to remove salt and any possible organic material. This assumes that all the organic matrix is destroyed. Representative pieces of each coral colony used were retained and the porosity of each colony was determined using the techniques employed by Guillaume (1984). The density of each colony could then be estimated from the porosity and the known density of aragonite (Guillaume, 1988), and thus the density of the blocks cut from each coral colony was determined. The blocks were laid on one large colony of dead *Porites* per site in a known order and fixed with aqua cement to the coral substrate in such a way that only one surface of the block was attached. At each site, 20 blocks were cemented for removal after exposure periods of 6 months, 2, 5 and 10 years with five replicates being collected after each exposure period. From the top surface of each block a stainless steel bolt and washer were screwed into the coral substrate to provide a reference point for determining the original height of the block, thus allowing an estimation of the net losses and gains due to grazing and accretion to be made. The stainless steel washer and bolt were removed after the blocks had been collected following exposure.

In this preliminary study, no attempt was made to investigate variations in rates and agents of bioerosion (both by boring and grazing) within a reef, but it should be noted that in the atolls two pinnacles were selected on each lagoon.

Study sites

Seven sites were selected, three on the fringing reefs of high islands (Tahiti (2) and Moorea (1)) and four on lagoon pinnacles in the lagoons of two atolls (Takapoto and Tikehau) in French Polynesia (Fig. 1). All sites were located in water depths of 1-2 m.

In Tahiti (17° 40' S and 149° 30' W), one of the sites, Faaa, was 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). Detailed investigations in this area have shown that the most serious pollution is from detergents (78 mg. l^{-1}), the concentration of which was directly related to population densities. The Faaa site was located on the fringing reef, which was severely degraded with few live coral colonies present. The dead coral substrate was covered with dense populations of sea urchins (*Echinometra mathaei*) and severely eroded. The experimental substrates were attached to one of the few remaining dead colonies of *Porites*. The other site in Tahiti was located at Atimaono, on the southern part of the island, well away from urban populations. A patch reef about 100 m offshore and adjacent to the main navigation channel was selected, consisting of numerous live coral colonies and a diverse assemblage of other colonial reef organisms (Gabrié *et al.*, 1986). Water quality was high in the area (Caries, 1991), although clarity may be fairly low, especially during the rainy season.

On Moorea, the site selected was on the fringing reef of the Tiahura transect (17° 40' S and 149° 30' W) (Fig. 1), located about 50 m offshore and landward of the navigation channel. The site was on a small patch reef surrounded by numerous other patch reefs. The patch reefs all had 30-40 % live coral cover as well as other colonial reef organisms present. For a description of these coral communities, see Bouchon (1985). Gabrié *et al.* (1988) have

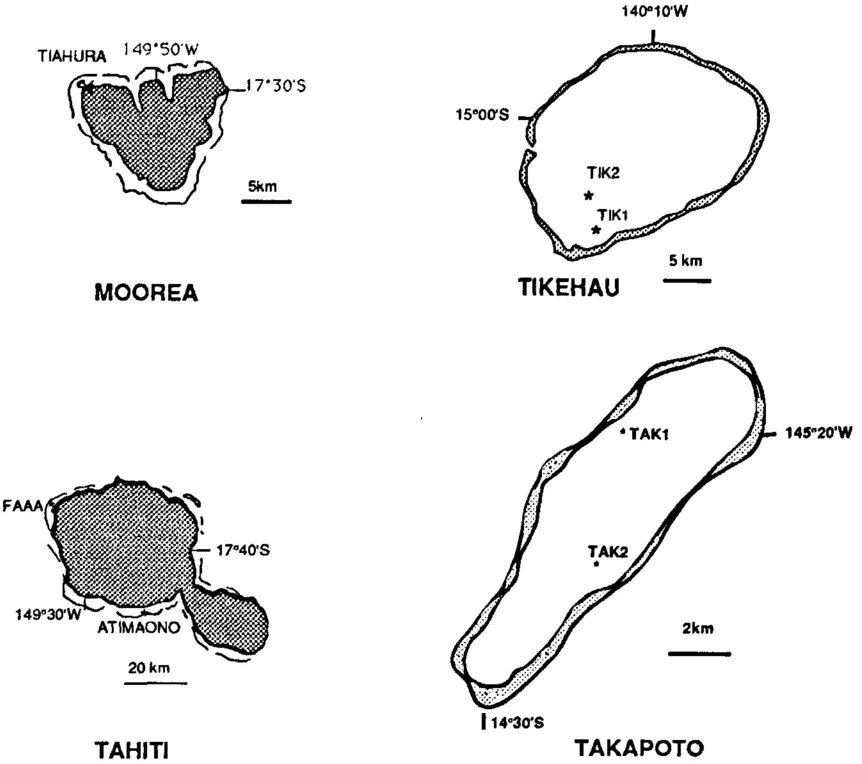

Figure 1

Location of sampling sites.

investigated the water quality in this area, showing it to be consistently high. However, a more recent study by Wolanski *et al.* (1993) has shown that with certain weather patterns there may be a build-up of discharged nutrients in the area.

At Takapoto, which is a closed elongated atoll at 14° 30' S and 145° 20' W, two lagoonal pinnacles were selected, one at the northern end in the Takai area (Tak 1), and the other opposite the Teavatika hoa (Tak 2) (a small channel through which exchanges of oceanic and lagoonal water occur during storm conditions) (Fig. 1). The pinnacles, rising from the floor of the lagoon which has a mean depth of 23 m and a maximum depth of 60 m, had numerous live coral colonies but represented by few species, as well as four dominant species of deeply embedded bivalves (Salvat and Richard, 1985). Water quality was good although oligotrophic (Martin, unpublished data) and salinity levels varied during the year from 35.5 to 36.1 $g.l^{-1}$ (Salvat and Richard, 1985). Experimental substrates were laid on the leeward side of both pinnacles.

At Tikehau, which is an almost circular atoll with one pass (Harmelin-Vivien, 1985; Peyrot-Clausade, 1989) at 15° S and 148° W, two lagoonal pinnacles were selected, one at the northern end (Tik 1) close to a functional hoa near the main village and the other in the centre of the lagon (Tik 2) (Fig. 1). Maximum depth of the lagoon is 35-40 m, and water quality was good (Charpy-Roubaud *et al.*, 1990). The coral communities on the pinnacles were zoned according to depth and exposure and were described by Faure and Laboute (1984) and Harmelin-Vivien (1985). Experimental substrates were laid on the leeward side of both pinnacles. Unfortunately, precise data on nutrient loading was unavailable for most of the sites.

Analytical procedures

After exposure, each block was fixed in a buffered 5 % solution of formaldehyde in seawater. The remaining aqua cement was easily removed from the previously attached surface with a hammer and chisel. The volume of the block was determined by water displacement after blocking off the pores by thin polythene film and each block was cut in half. One half of each block was randomly selected and used for a quantitative analysis of the macroborers; the other was used for studying the microborers and determining the net amounts of bioerosion (both boring and grazing) and accretion which had occurred.

One half of each block was sliced into several sections 1 cm in width, one of which was used for the analysis of the microborers; the other sections were point-counted throughout their surface with a millimetre grid, under a binocular microscope (Schaefer, 1970) in order to measure the amount of substrate eroded by macroborers and the net changes to the original surfaces of the block due to accretion. The percentages of removed substrate, according to the method of Webel *et al.* (1966), were processed by arcsine transformation and compared using the Kruskal-Wallis test (heteroscedasticity). The change in the original volume of the block (*i.e.* the sum of the losses due to internal boring together with losses of the surface area as a result of grazing or boring or a combination of both processes) was converted, using the density of the blocks, to net changes in weight during the exposure period. These figures were themselves converted to net rates of change of calcium carbonate ($kg.m^{-2}.yr^{-1}$) and apportioned to the various processes. An experimental mesure of calcareous algal density (from volume and $CaCO_3$ weight) allowed us to estimate it at 5.01 g.cm^{-3} (*i.e.* grazing, boring and accretion).

The slice used to determine the composition and density of the microborers was then cut into a number of squares measuring 1 cm^2 in surface and 1 cm in depth. The number of cubes which needed to be examined in order to give a reliable estimate (95 % confidence limits) of the algal biomass present was determined by taking the five sample blocks from Moorea, selecting six cubes from each block and determining the algal biomass of each cube. A one-way analysis of variance (random model) was then performed on the results and the residual variance (σ^2) was found to equal 0.012; σ^2_A equalled 0.0124, n = 4 for the number of cubes per block and p = 3 blocks per site for a relative error of 20 % of the mean (Bliss, 1967; Sachs, 1982). Therefore these sample sizes were used and four cubes were selected at random from the slice used for determining the algal biomass of both epilithic and endolithic flora, which was estimated as decalcified dry mass per unit area. Four 1 cm^2 samples were decalcified from each block by the method described below and the material collected on filter paper, rinsed with deionized water and dried to constant mass at 60 °C. The remaining material is only algal. The other cubes were used to study the composition of the microborer community by light microscopy after substrate dissolution by Perenyi's solution (3 vol. of 0.05 % chromic acid, 4 vol. of 10 % nitric acid, 3 vol. of 90 % alcohol); samples had been previously fixed in a buffered 5 % solution of formaldehyde in sea water.

For the study of the macroborers, the other half of each block was plunged in an acid solution of formalin and hydrochloric acid (for details see Hutchings and Weate, 1978) to dissolve the calcium carbonate and facilitate the removal of all the macroborers (Hutchings, 1981). Polychaetes, sipunculans and vermetid molluscs were counted, identified and wet-weighed. The average numbers of borers present at each site were calculated and these were converted to numbers per dm^3 using the volume of the blocks after exposure.

The number of *Echinometra mathaei* present at each site, except for Takapoto where the data of Bak (1990) were used, were estimated from counts of individuals in 20 random quadrats of 50 cm^2.

As two blocks had come unstuck at the Atimaono site, all the statistical tests were realized with three blocks taken at random.

A number of one-way analyses of variance were carried out to determine the effects of site on net changes in weight of the blocks and density of macroborers. Friedman's test was then used to compare the amount of borings recorded from all sections of each block to assess the within block and within-site variations (Dagnelie, 1975).

A two-way analysis of variance (nested mixed model) was performed to investigate the relationship between the biomass of algae present within and between sites. Two a posteriori tests were used to determine which of these means were significantly different (Student-Newman-Keuls test; Zar, 1984) or more simply the greatest. (Gupta test, in Dagnelie, 1975).

In order to determine which factors were most important in the processes of bioerosion and accretion, a multilinear regression stepwise analysis on log transformed data was undertaken. Factors considered were biomass of algae (epilithic and endolithic), rates of gain or loss of substrate as a result of grazing and or accretion, rates of internal bioerosion (*i.e.* boring) and densities of grazing fish, *Echinometra* and macroborers. Subsequently a cluster analysis using the Ward method (Euclidean distance on standardized data, Saporta, 1978) was carried out. The results of the Ward method were confirmed by centroid clustering (Roux, 1985). As no data for grazing by herbivorous fishes at Tak 2 were available, this site was not included in the analyses. For all the analyses the computer package used was STAT-ITCF (1991).

RESULTS

Estimates of rates of grazing and accretion

The net rates of grazing and accretion varied between sites. At three sites, grazing processes dominated (Tab. 1): at Faaa, grazing rates were estimated at 10.38 ± 8.73 (mean ± standard deviation) kg.m^{-2}.yr^{-1}; at Atimaono,

Table 1

Net rates of grazing, accretion and macroboring together with total net rates of erosion/accretion for each site (mean ± standard deviation given).

	Net rates of grazing kg. m^{-2}. yr^{-1}	**Net rates of accretion kg. m^{-2}. yr^{-1}**	**Net rates of internal bioerosion by macroborers kg. m^{-2}. yr^{-1}**	**Total net rates of erosion by grazing and macroborer/ accretion kg. m^{-2}. yr^{-1}**
Moorea		0.14 ± 0.38	0.18 ± 0.13	− 0.04
Faaa	10.38 ± 8.73		0.07 ± 0.02	− 10.45
Atimaono	1.20 ± 1.36		0.02 ± 0.02	− 1.22
Tikehau 1		0.55 ± 0.76	0.03 ± 0.04	0.52
Tikehau 2		0.06 ± 1.25	0.26 ± 0.51	− 0.20
Takapoto 1		0.94 ± 0.29	0.13 ± 0.24	0.81
Takapoto 2	0.30 ± 0.73		0.08 ± 0.14	− 0.38

Table 2

A one-way analysis of variance (fixed model) of the variation between sites in net changes in weight (as a result of net accretion and grazing) of the blocks together with Gupta test results (α = 0.05). The mean value at the Faaa site is higher than at other sites.

Source of variation	Sum of square	Degrees of freedom	Mean square	Obs F	P
Sites	6 643. 18	6	110. 72	33. 79	< 0. 001
Residual	458. 65	14	32. 76		

	(Tak 1)	(Tik 1)	(Tik 2)	(Moor)	(Tak 2)	(Ati)	(Faaa)
Mean value	– 4. 15	– 3. 89	0. 16	0. 88	1. 43	9. 17	49. 7

1.2 ± 1.36 kg.m^{-2}.yr^{-1}; and at Tak 2, 0.3 ± 0.73 kg.m^{-2}.yr^{-1}. At the other sites, accretional processes dominated. The net rates of accretion were estimated at 0.14 ± 0.38 kg.m^{-2}.yr^{-1} for Moorea; 0.55 ± 0.76 and 0.06 ± 1.25 kg.m^{-2}.yr^{-1} for the two sites at Tikehau; and 0.94 ± 0.29 kg.m^{-2}.yr^{-1} for Tak 1.

A one-way analysis of variance revealed a significant difference ($P < 0.001$) between the net rates of grazing and accretion on the experimental substrates at the various sites after six months of exposure. Application of the Gupta test (Tab. 2) to these results showed the values at the Faaa site to be significantly higher than at other sites: this was caused by extensive erosion (*i.e.* grazing) and about 17 % of the original weight of the block was lost. The greatest amount of net accretion occurred at Tak 1, where the blocks gained about 2.42 % of their original weight during these first six months of exposure.

Estimates of rates of boring by macrofauna

Estimated rates of loss of $CaCO_3$ by the boring activities of macrofaunal animals were highest at Moorea and lowest at Tik 1 and Atimaono (Tab. 3).

In order to investigate the potential variation in the amounts of macroboring in different sections of the same block, the rates of internal bioerosion estimated from slices of each block were subjected to the Kruskal-Wallis test and were found to be not significantly different ($P > 0.05$). An estimate of the potential variation within sections of replicate blocks at a given site was determined using the Friedman test on the percentages of borings; and no significant differences ($P > 0.05$) were found to occur between sections of blocks at the same site.

Composition of the infaunal macroborer communities

The macroborer community (Tab. 4) was dominated by polychaetes. A one-way analysis of variance revealed a significant difference ($P < 0.001$) in the densities of macroborers present at the different sites (Tab. 5). The Gupta test indicated that the density of the macroborer community at Moorea was greater (403.05 individuals.dm^{-3}) than at the other six sites (Tab. 4 and 5). The community at Moorea also differs in composition from the other sites and was dominated by representatives of the subfamily Fabricinae (family Sabellidae) and *Dodecaceria* sp. (family Cirratulidae) together with sipunculans. The site with the lowest density of macroborers was Tak 2 with a density of 17.53 ind.dm^{-3}. Sipunculans and vermetids were poorly represented at all sites after six months of exposure. The sipunculans present in the samples were all located around the bolt and washer. No evidence of boring sponges was found, either in the dissolved substrate or in the sections point-counted for estimating the amount of boring.

Table 3

Parameters analysed at each site (mean ± standard deviation) (NA= not available).

	Total algal biomass mg.cm^{-2}	Net rates of grazing / accretion kg. m^{-2}. yr^{-1}	Net rates of internal bioerosion by macroborers kg. m^{-2}. yr^{-1}	Average density of herbiv. fishes per 100 m^2	Average density of Echinometra mathaei per m^2
Moorea	6. 7 ± 1. 29	0. 14 ± 0. 38	0. 18 ± 0. 13	61	2. 5 ± 1. 5
Faaa	3. 4 ± 1. 24	– 10. 38 ± 8. 73	0. 07 ± 0. 02	177	30. 5 ± 17. 0
Atimaono	5. 7 ± 2. 63	– 1. 20 ± 1. 36	0. 02 ± 0. 02	53	2. 5 ± 3. 2
Tikehau 1	6. 7 ± 1. 58	0. 55 ± 0. 76	0. 03 ± 0. 04	29	0
Tikehau 2	7. 0 ± 3. 35	0. 06 ± 1. 25	0. 26 ± 0. 51	37	0
Takapoto 1	3. 4 ± 1. 23	0. 94 ± 0. 29	0. 13 ± 0. 24	18	0
Takapoto 2	5. 4 ± 3. 04	– 0. 30 ± 0. 73	0. 08 ± 0. 14	NA	0

Table 4

Mean density and standard deviation of macroborers at each site.

	Moorea	Faaa	Atimaono	Tikehau 1	Tikehau 2	Takapoto 1	Takapoto 2
Dodecaceria sp.	20.80 ± 9.80	2.0 ± 1.73	1.75 ± 3.50	2.20 ± 3.83		0.60 ± 0.55	0.20 ± 0.45
Eunice spp.	0.40 ± 0.540			0.60 ± 1.34		0.80 ± 0.83	0.60 ± 0.89
Fabricinae	55.80 ± 25.32	5.00 ± 5.57	16.0 ± 19.89	5.40 ± 3.20	2.80 ± 2.94	14.40 ± 16.43	0.80 ± 0.83
Hypsicomus spp			0.50 ± 1.0		0.40 ± 0.55	0.20 ± 0.45	0.20 ± 0.45
Nematonereis spp	0.80 ± 1.09		1.0 ± 0.81	0.20 ± 0.45		0.80 ± 1.30	0.60 ± 0.55
Polydora spp	2.20 ± 3.83	0.33 ± 0.58	0.75 ± 1.50	0.40 ± 0.55	0.60 ± 1.34		0.40 ± 0.55
Schistomeringos sp	0.20 ± 0.45		0.75 ± 0.96		0.40 ± 0.55	1.80 ± 2.05	0.60 ± 1.34
Total polychaetes	80.40 ± 31.02	7.33 ± 6.03	20.75 ± 16.29	8.80 ± 7.79	4.20 ± 3.11	18.80 ± 16.30	3.40 ± 2.40
Sipunculans	2.80 ± 2.59		2.0 ± 2.70	0.20 ± 0.45	0.40 ± 0.55	0.80 ± 1.30	
Vermetids	0.20 ± 0.45		0.75 ± 0.96	0.20 ± 0.45	0.60 ± 0.89	0.80 ± 0.45	0.20 ± 0.45
Mean numbers of borers per block	83.40 ± 31.05	7.33 ± 6.03	23.5 ± 17.01	9.20 ± 8.04	5.20 ± 3.34	20.40 ± 16.16	3.60 ± 2.70
Mean density of borers per dm^3	403.0 ± 152.50	48.73 ± 39.74	119.52 ± 91.10	44.98 ± 36.55	27.98 ± 16.35	106.41 ± 85.80	17.53 ± 13.44

Microborer communities and algal turf

Composition of the microborer communities

The surfaces of the blocks were covered by algal communities frequently referred to as algal turf. A preliminary study revealed a difference in the composition of algal turf between sites. At Faaa, where the highest losses attributable to grazing occurred, endolithic cyanobacteria (*Mastigocoleus testarum, Plectonema terebrans)* characterized the site. Epilithic algae (non crustose taxa) were sparse and the total algal biomass was estimated at 3.4 mg.cm^{-2} at this site. At Tak 1, the algal communities were dominated by epilithic communities and this was the site of maximum accretion. The maximum biomass of algae occurred at Tik 2 and was dominated by coralline and epilithic algae. At all the other sites, epilithic algae were abundant and the microborer community was dominated by cyanobacteria.

The amounts of algal biomass present at each site (Tab. 6) were compared involving a two-way analysis of variance, involving a nested mixed model, on log-transformed data. This showed that the mean levels of algal biomass present at the various sites were significantly different (Tab. 6, P = 0.012). The Gupta test (Tab. 6) showed that the sites at Faaa and Tak 1 (characterized by lower mean levels of organic material of algae) were significantly different from the other five sites. An SNK test on the same data showed that only the Faaa site was significantly different from the other six sites (Tab. 6).

Agents of grazing

The major agents of grazing of coral substrates occurring in the region are selected fish of the families Acanthuridae and Scaridae, echinoids and some species of gastropods. While no density data of herbivorous fishes were collected during the period of the experiment, some data are available from the literature. The density of herbivorous fishes which are common grazers has been calculated by Harmelin-Vivien at Faaa (published in Ricard *et al.*, 1985), at Tikehau by Harmelin-Vivien (1984, 1990), at Takapoto by Bouchon-Navaro (1977), and by Harmelin-Vivien and Galzin (pers. comm.) at Moorea and Atimaono.

The densities of the echinoid *Echinometra mathaei* have been determined by Bak (1990) at Takapoto and by Peyrot-Clausade (unpubl. data) on the fringing reef of Moorea, Faaa, Atimaono and Tikehau at the commencement of this study in November 1990 (Tab. 3). This urchin species does not wander too far while grazing (Khamala, 1971) so we may assume the algal turf on blocks to be well grazed by surrounding *Echinometra mathaei.*

Table 5

One-way analysis of variance (fixed model) of the variation in the density of macroborers between sites, together with Gupta test results (α = 0.05). (The density of macroborers is calculated as numbers per dm^3.) The mean value at Moorea site is greater than at the other sites.

Source of variation	Sum of square	Degrees of freedom		Mean square	Obs F		P
Sites	23 014.3	6		3 835.72	37.32		< 0.001
Residual	1 438.9	14		102.78			
	(Tak 2)	(Tik 2)	(Tik 1)	(Faaa)	(Tak 1)	(Ati)	(Moor)
Mean value	17.5	28	45	48.7	106.4	119.5	403

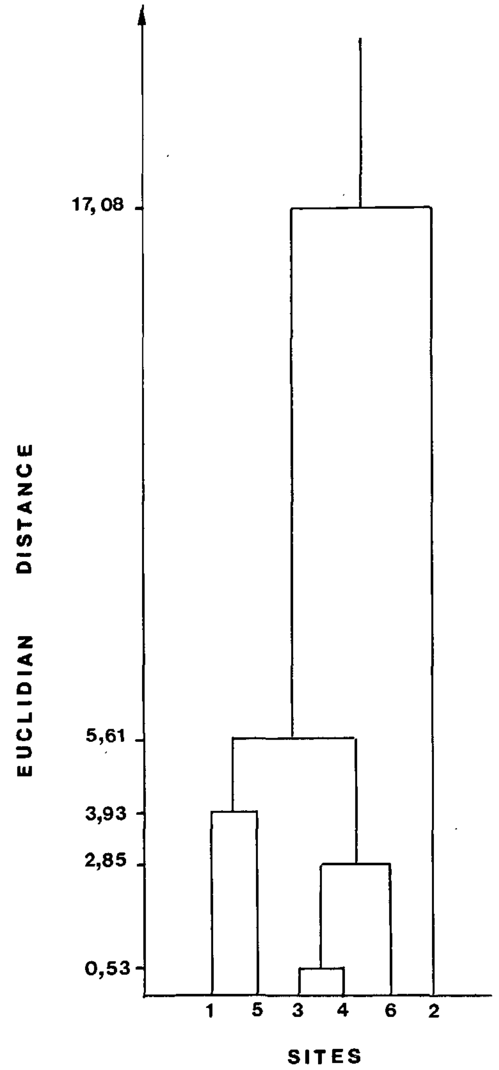

Figure 2

Dendrogram of cluster analysis results using the Ward method. Sites : 1 = Moorea ; 2 = Faaa ; 3 = Atimaona ; 4 = Tikehau 1 ; 5 = Tikehau 2 ; 6 = Takapoto 1.

Densities of herbivorous gastropods have been determined at Moorea and Tikehau in 1988 (Peyrot-Clausade, unpubl. data) and found to vary from eight individuals per 10 dm^3 in the rubble on the fringing reef to 13 on the barrier reef at Moorea. On the inner flat of Tikehau lagoon, densities were much lower, with about two per 10 dm^3 and 15 per 10 dm^3 on the pinnacle at site Tik 2. Assuming that similar densities prevailed during the exposure period, the distribution of herbivorous molluscs appears to be inversely correlated with the levels of net accretion recorded at these particular sites. However, as data on gastropod densities were only available for three sites, they were not included in the following analysis.

Factors which may contribute to the variations in grazing and accretion recorded between sites

Studies by Peyrot-Clausade *et al.* (1992) at Moorea, and Kiene and Hutchings (1994 *a*, *b*) on the Great Barrier Reef have shown the importance of echinoids and herbivorous fishes in grazing of dead coral substrates. In order to assess the importance of the density of echinoids and herbivorous fish as well as other factors listed in Table 3 on the net rates of accretion and grazing on the experimental substrates, a multilinear stepwise regression was carried out. The results indicated that a single variable, the density of *Echinometra mathaei,* accounted for 98.60 % of the net rates of accretion or grazing which occurred on the blocks during the initial six months of exposure. These data were then subjected to a cluster analysis using the Ward method (Euclidean distance on standardized data) (Saporta, 1978), which produced three groups of sites. The three groups comprised: (1) Faaa; (2) Moorea and Tik 2; and (3) Atimaono, Tik 1 and Tak 1 (Fig. 2). The results were confirmed by centroid clustering (Roux, 1985). An analysis of the factors contributing to these groupings revealed that for group 1 (Faaa), the density of grazing organisms was the most important factor. For group 2 (Moorea and Tik 2), similar rates of internal bioerosion, and for group 3 (Atimaono, Tik 1 and Tak 1), low rates of internal bioerosion by macroborers and grazing were the main factors (Tab. 3).

Although one would have expected the number of borers to be related to rates of internal erosion calculated from the point-counts of thin sections, this was not always apparent (Tab. 3). For example, although Moorea had the highest density of macroborers it had only the second highest net rate of internal bioerosion. The highest net rate of internal bioerosion was recorded at Tik 2, which had one of the lowest densities of macroborers. The reasons for this are not entirely clear, but many of the borers present in the dissolved part of the samples were small (1-2 mm in length) and it is possible that their burrows frequently penetrate the pores of the corallites, thus reducing the number of burrows distinguished from pores by point-counting. In addition, some of the microborers may have reproduced during the exposure period and then died but leaving their vacated burrows (Hutchings *et al.*, 1992).

DISCUSSION

The highest net rate of bioerosion (from both grazing and boring) which occurred during the first six months of exposure was a consequence of external bioerosion by grazers. Various organisms are known to graze on dead coral substrates, including echinoids, various species of fish and gastropods (Hutchings, 1986; Harmelin-Vivien *et al.*, 1992; Bruggemann, 1995). The site at Faaa exhibited both the highest density of *Echinometra* (30.5 ± 17.0 m^{-2}) and the largest population of herbivorous fishes (177.100 m^{-2}) present at any of the sites. We suggest that this large number of grazers was responsible for the high rates of $CaCO_3$ m^{-2}.yr^{-1} loss recorded at this site, where, unfortunately, no data are available on the density of herbivorous gastropods. At this stage, we cannot apportion the grazing losses to particular groups of grazing organisms. The other two sites which recorded net losses were Atimaono and Tak 2. At

Table 6

A two-way analysis of variance (nested mixed model) to test the variation in the amount of algal biomass present within and between sites. Sites (factor A) were fixed, blocks (factor B-random) were nested within factor A, n = number of measures per block, p = number of blocks per site, q = number of sites. The data were transformed using $\log_{10}$ to stabilize variances. Cochrans Test value is $P > 0.05$. These results were then subjected to the Gupta test ($\alpha = 0.05$) and showed that the mean values at sites Faaa and Tak 1 were significantly lower than at the other sites. The results were also tested by SNK; in this case the site at Faaa was the lowest ($\alpha = 0.05$).

Source of variations	**Sum of squares**	**Degrees of freedom**	**Mean square**	**Obs F**	**P**	**Expected mean square**
Sites (A)	1.46	6	0.243	4.26	0.012	$\sigma^2 + n\sigma_B^2 + \frac{np}{q \pm 1}\sum^q a$
Blocks (B)	0.80	14	0.057	2.80	0.003	$\sigma^2 + n\sigma_B^2$
Residual	1.28	63	0.020			σ^2
Total	3.54	83				

	(Faaa)	(Tak 1)	(Tak 2)	(Ati)	(Tik 2)	(Tik 1)	(Moor)	
Mean value	0.492	0.505	0.687	0.713	0.814	0.817	0.818	
		—	—	—	—	—	—	**SNK**
			—	—	—	—	—	**GUPTA**

Atimaono, reasonable numbers of herbivorous fish were present as well as some *Echinometra*; at Tak 2 no *Echinometra* (or other echinoids) were present (Bak, 1990); although no data on density of herbivorous fish were available for the latter site, they were certainly present.

Notwithstanding the fact that fish densities may change over time, these findings do provide some indication of levels of populations of fish grazers in the study areas. Ideally, fish censuses should have been taken daily during the six-month experimental period but this was not feasible. However, the data from Moorea are based on counts of herbivorous fishes made twice a year in the vicinity of the study site by Galzin (unpubl. data) since 1979.

Grazing has also been found to be a major erosional force in other reef areas. In Australia, Kiene and Hutchings (1994 *a*, *b*), working at Lizard Island on the Great Barrier Reef, found that different reefal environments on the same reef experienced significantly different levels of grazing. Sites on the reef flat and at depths where the densities of grazers were low experienced low levels of grazing; at sites such as the reef slope where high densities of grazers (primarily scarids) occurred, grazing was the dominant agent of bioerosion. These site differences have been maintained over nine years (Kiene, 1988; Kiene and Hutchings, 1994 *b*). Echinoids were not present in sufficient numbers in these environments on the Great Barrier Reef to have influenced rates of grazing.

Grazers were not only responsible for losses of coral substrate but also induced changes in the composition and abundance of the algal turf. Under intense grazing, such as occurred at Faaa, the endolithic micro-organisms were dominated by cyanobacteria (especially *Mastigocoleus testarum*). At sites experiencing lower net rates of grazing or none at all, the cyanobacteria were replaced by chlorophytes. Chlorophytes are probably better adapted than cyanobacteria for growth in levels of low light under the epilithic algal turf (Le Campion-Alsumard, 1979). We suggest that grazing by echinoids induces a change in the composition and depth of penetration of the endolithic community. Hackney *et al.* (1989) undertook similar experiments on a Caribbean reef in order to investigate the relationship between algal turf composition and herbivory and they also found that the composition of the turf changed with grazing pressures. Hackney *et al.* observed that turf species persisted in zones of intense grazing and commonly displayed adaptations for rapid growth, and that algal crusts (coralline algae) survived greater grazing intensities than turfs and possessed adaptations to resist grazing. Our data would suggest that a similar situation pertains in French Polynesia.

The sites in Tikehau (Tik 1) and Takapoto (Tak 1) lagoons which exhibited the maximum net rates of accretion (Tab. 1) had the lowest densities of grazers, with echinoids completely absent (Bak, 1990) and few herbivorous fishes present. This presumably explains why these sites experienced low net rates of grazing and reasonably high net rates of accretion by coralline algae (Tab. 1). The factors responsible for the low densities of grazers recorded are unknown, but may be a consequence of overfishing and or low nutrient levels which do not encourage extensive turf algal growth.

Of the seven sites in French Polynesia, four experienced net rates of accretion, but these rates of gain were much lower than the net rates of loss attributable to grazing. Accretion was mainly the result of coralline algae, but some encrusting serpulid polychaetes were also present.

Rates of loss attributable to internal bioerosion by macroborers were low, the site at Moorea recording the highest net loss; this site, as would be expected, had the highest density of macroborers. It was also characterized by a net gain by accretionary processes despite a reasonable density of herbivorous fish and the presence of some *Echinometra* (Tab. 3). The Moorea site was also characterized by one of the highest algal biomasses and both epilithic and endolithic algae were common, although coralline algae were absent. We suggest that a well developed algal turf facilitates the recruitment and penetration of the substrate by macroborers. It is thought that the majority of macroborers recruit via pelagic larvae (Hutchings, 1986). During grazing, grazers not only erode the surface of the coral substrate but may well reduce the ability of various macroborers to settle on the substrate and subsequently to bore into it (Kiene and Hutchings, 1994 *b*). Grazing organisms may also prey on, or accidently ingest, the larvae of potential macroborers as they are settling on the substrate.

This inverse relationship between density of macroborers and rates of grazing was also found by Sammarco *et al.* (1987) on the central Great Barrier Reef. Kiene (1988) further suggested that the highest net rates of accretion and boring occur in mature reef environments, and the lowest in young reefal environments where, according to his experimental study on the southern Great Barrier Reef, grazing is the dominant process. Preliminary studies by Brousse (1985) on the age of islands in the Pacific would suggest that the atoll of Tikehau is younger than that of Takapoto. All sites at these atolls experienced similar rates of grazing, suggesting that the model advanced by Kiene (1988) may not be valid for the reefs of French Polynesia.

The macroborer community was dominated by polychaetes at all sites, the most abundant group being the Fabricinae (family Sabellidae). Hutchings *et al.* (1992) have found that the recruitment of fabricinids to sites at Lizard Island, on the northern Great Barrier Reef, increased over the first 12 months of exposure of experimental substrates and then declined. Kiene (1988) reported a similar phenomenon on the southern Great Barrier Reef, during the initial stages of exposure of his experimental substrates. These initial colonizers of newly available substrate, although only 1-2 mm in length and therefore responsible for minimal losses of substrate, may however facilitate subsequent recruitment by other borers (Hutchings *et al.*, 1992). Such a process has been invoked to explain the increase in density of sipunculans with increasing exposure (Hutchings *et al.*, 1992; Chazottes *et al.*, 1995). In this study, recruitment of sipunculans was restricted to areas around the bolt and washer where some shelter was provided during the initial stages of penetration by the larvae.

Kiene and Hutchings (1994 *a*, *b*) have shown that rates of grazing vary between sites on a single reef, and this pattern appears to be present within our data, at least at Tikehau where the two sites within the lagoon were not grouped together by the cluster analysis. As Tak 2 was not included in this analysis, the relationship between the two sites at Takapoto is unknown, although net rates of grazing and accretion were different (Tab. 1). Similarly, our data from the fringing reef of the Tiahura transect at Moorea differ considerably from those obtained by Chazottes *et al.* (1995) on the nearby barrier reef. On the barrier reef, net rates of external erosion (grazing) were estimated to be 0.96 kg.m^{-2}.yr^{-1} after six months of exposure, which was much higher than rates recorded on the fringing reefs during this study. The reason for this high rate of loss by grazing may be the higher densities of herbivorous fishes (Galzin recorded 86. 82 ± 12. 05/100 m^{-2} in 1987, pers. comm.), echinoids: 12.65 ± 7.60 ind.m^{-2}, and gastropods: 13 herbivorous gastropods.10 dm^{-3} of coral substrate (Peyrot-Clausade, unpubl. data) than were present on the nearby fringing reef site of this study (Tab. 3). We suggest that this factor may explain the differences in rates of bioerosion as a result of grazing and boring experienced by the two sites at Moorea (Chazottes *et al.*, 1995, this study). In addition, the density of macroborers was higher in dead *in situ Porites* present on the barrier reef (Hutchings and Peyrot-Clausade, 1988) than in the experimental substrates at the fringing reef site. Extensive borings may have facilitated the loss of substrate by subsequent grazing.

The site at Faaa, which experienced the greatest loss of substrate during the study as a result of grazing, is also the only site close to urban areas and receives significant amounts of domestic sewage and nutrients (Fraizier *et al.*, 1985). At Faaa, dead corals were abundant on the reef flat and were covered with algal turf (Ricard *et al.*, 1985). This algal turf, and the microboring algae which penetrate and erode the substrate, are utilized as food by herbivorous species (Hay, 1981; Hatcher and Larkum, 1983; Bellwood and Choat, 1990). We hypothesize that the high nutrient level from the sewage input recorded by Fraizier *et al.* (1985) and subsequently by the *Délégation à l'Environnement* (unpubl. data) stimulated the production of the algal turf which then encourages the development of large herbivore populations; the latter in turn further increase the rate at which the coral substrate is destroyed by grazing.

Smith *et al.* (1981) in their study in Kaneohe Bay showed a large difference in population of echinoderms and polychaetes according oligotrophic or eutrophic conditions. Quasi-absent in substrate under oligotrophic conditions, these two groups are abundant under eutrophic ones. While these substrates may also be eroded by macroborers, populations of the latter are maintained at low levels because the substrate is continually being eroded and high rates of grazing ensure that the algal turf is kept cropped, which reduces the rate of successful recruitment of the macroborers. None of the other sites receive significant inputs of nutrients and levels of grazing are significantly lower at these sites than at Faaa. Unfortunately, it was not possible to obtain regular nutrient data from the atoll sites.

While the sites at Moorea and Atimaono have similar populations of echinoids and herbivorous fishes, they were not grouped together by the cluster analysis, as one site experienced net losses and the other net gains as a consequence of grazing and accretion respectively. These two sites are both on reefs adjacent to high islands where terrigenous input would be received during the rainy season; on both Tahiti and Moorea some development and clearance of land in the region of the sites is occurring. Similarly, the sites in the lagoons of the atolls were not grouped together (although Tak 2 was not included in the cluster analysis because of the lack of data on herbivorous fish). At this stage, however, we cannot explain the reasons for the differences between sites within the atolls. Our results also indicate the complex relationships between densities of grazing organisms and rates of net accretion and net bioerosion. High densities of grazers do not necessarily signify high net rates of bioerosion on the reef in question. However, high densities of echinoids may perhaps be an early warning sign that some imbalance is occurring on that particular reef and worthy of further investigation.

Apart from the data of Chazottes *et al.* (1995), there are no other comparative data on rates of grazing or accretion over such a short time period, although Kiene (1985) determined rates of grazing of 0.41 $kg.m^{-2}.yr^{-1}$ after three years in similar habitats at Lizard Island. After nine years at Lizard Island, Kiene and Hutchings (1994 *b*) have recorded rates of 2.15 $kg.m^{-2}.yr^{-1}$, which is considerably less than recorded after six months at Faaa. All these studies used *Porites* spp. as the experimental substrate, which should render the results comparable. The greater density of urchins at Faaa than at Lizard may be the factor explaining the difference in external rates of bioerosion.

Finally, we must repeat that our results are preliminary and do not take into account any potential variation in rates of bioerosion occurring on individual reefs; but these studies have highlighted reefs which should be further investigated. Although the rates of grazing occurring at Faaa are so high, observations on nearby coral heads strongly suggest that our experimental rates of grazing are applicable to the reef as a whole in this area, and that urgent action will have to be taken to reduce levels of nutrients and algal cover, and thus populations of grazing echinoids, if this reef is to survive.

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