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REPORT

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The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean)

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Abstract This study investigated the variation of bioerosional processes in relation to disturbances of reefal communities due to eutrophication. La Saline fringing reef (Reunion Island) is subjected to nutrient inputs from the adjacent land. Bioerosion by grazers, microborers, and macroborers was measured using experimental substrata exposed for 1 year in three sites characterized by different levels of nutrient input and benthic community response. The relationship between bioerosion and epilithic algal cover of hard substrata and the interactions between the various agents of bioerosion were analyzed with parametric statistics. Significant variations in bioerosion were found among sites, ranging from 1.63 to 3.52 kg $CaCO_3$ m^{-2} $year^{-1}$ for grazing rates, from 6.73 to 32.25 g m^{-2} $year^{-1}$ for macroboring rates, and from 43.78 to 67.56 g m^{-2} $year^{-1}$ for microboring rates. One of the major factors controlling these variations appeared to be changes in the epilithic algal cover on substrata in response to changes in reefal water chemistry. In low nutrient areas, where dead corals were colonized mainly by algal turfs, erosion by microorganisms was low (43.78 g m^{-2} $year^{-1}$) due to intense grazing (3.52 kg m^{-2} $year^{-1}$). In reef zones receiving high nutrient inputs, the development of encrusting calcareous algae and macroalgae was associated with the lowest grazing (1.63 kg m^{-2} $year^{-1}$) and macroboring (6.73 g m^{-2} $year^{-1}$) rates recorded among sites. In contrast, high microboring rates (57.54 and 67.56 g m^{-2} $year^{-1}$) were found in enriched areas in association with high macroalgal cover.

Keywords Coral reefs · Eutrophication · Bioerosion · Reunion Island

Introduction

The equilibrium between net accretion and net erosion of a coral reef depends mainly on nutrient availability (Wood 1993; Glynn 1997; Hallock 1997). Eutrophication-related disturbances on coral reefs have often been discussed in terms of their implications for primary productivity (Kinsey and Domm 1974; Kinsey and Davies 1979; Birkeland 1987); the recruitment and growth of corals (Kinsey and Davies 1979; Tomascik 1991; Hoegh-Guldberg and Williamson 1999; Ferrier-Pagès et al. 2000; Ward and Harrison 2000); the development of benthic algal assemblages (Berwick and Faeth 1988; Lapointe et al. 1992; Littler et al. 1992; Larned and Stimson 1996; McCook 1999; Stimson and Larned 2000) and, more generally, benthic communities (Smith et al. 1981; Brock and Smith 1983; Birkeland 1987; Hatcher et al. 1989). These authors suggested that increased nutrient inputs to coral reefs increase rates of primary production, inhibit skeletal growth of corals, and stimulate macroalgal growth, leading to a shift from coral to benthic algal-dominated communities. In general, eutrophication of coral reef ecosystems can lead to a shift in dominance from phototrophic species (corals and coralline algae) to heterotrophic suspension-feeding species (e.g. mollusks, polychaetes, and sponges; Smith et al. 1981; Birkeland 1987).

Nutrient availability may also have influenced carbonate buildups in the past and has been implicated in the demise or the drowning of reefs or carbonate platforms in the geological record (Hallock and Schlager

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1986; Hallock 1988; Wood 1993). In contrast, several authors (McCook 1996, 1999; McClanahan et al. 1999; Cheroske et al. 2000) have suggested that nutrient loading alone is unlikely to lead directly to macroalgal overgrowth of corals. Phase-shifts from abundant coral to abundant macroalgae appear to involve the combined effects of eutrophication, physical disturbances, and reductions in herbivory (Wanders 1977; Steneck 1988; Hackney et al. 1989; McCook 1996; Russ and McCook 1999). Examples of such disturbances include cyclones (Russ and McCook 1999), coral bleaching (McClanahan et al. 1999), and sedimentation due to human land-use (McCook 1999). The spatial pattern of eutrophication depends at least in part on the dispersion of nutrients from source to the various reef habitats, a process controlled mainly by the hydrodynamic regime (Hatcher et al. 1989).

Experimental fertilization studies such as those conducted on the Great Barrier Reef in the 1970s (Kinsey and Domm 1974; Kinsey and Davies 1979), in the 1980s (Hatcher and Larkum 1983), and more recently in the ENCORE program (Larkum and Steven 1994; Koop et al. 2001) have improved our understanding of the effects of elevated nutrient input. Only a few studies (Smith et al. 1981; Tomascik 1991) have been conducted on reefs subjected to non-experimental nutrient enrichment.

La Saline fringing reef in Reunion Island was selected for this study because the structure of the benthic communities and the dispersion of nutrients on the reef have been monitored since the beginning of the 1980s, the time from which the first obvious changes in benthic community structure were noted. In the 1970s, La Saline reef was characterized by coral-dominated benthic communities with rare occurrence of fleshy algae (Bouchon 1981; Faure 1982). The first obvious signs of reef degradation were recorded in 1983 by Guillaume et al. (1983), and Cuet (1989) noted an enrichment of reefal waters in nitrates, ammonium, and phosphates. Submarine groundwater discharge (SGD) is the main source of fresh water affecting the La Saline reef (Join 1991). It enriches lagoonal waters with nutrients derived from anthropogenic sources (Cuet et al. 1988). Groundwater discharge has been noted as a source of anthropogenic nutrients to other coastal reefs (D'Elia et al. 1981; Lewis 1987; Lapointe 1997).

The apparently causal relationship between SGD and degradation of La Saline coral communities is supported by the spatial coherence of the distribution of algal communities and nutrient levels in the water column (Cuet et al. 1988). Subsequent studies on this reef focused on the distribution of benthic cover (Montaggioni et al. 1993; Naim 1993), on fish and sea urchin communities (Chabanet et al. 1997; Conand et al. 1997) and their bioerosion rates determined from gut contents (Conand et al. 1997, 1998), and on net rates of community production and calcification (Conand et al. 1997; Mioche and Cuet 1999) in relationship to nutrient levels. These studies indicate that reef zones receiving little or no nutrient enrichment are characterized by high live coral cover, high rugosity, high fish species diversity, and high density of echinoids (up to 74 ind. m^{-2}, on the reef flat). In contrast, degraded reef zones receiving large SGD are characterized by high algal coverage, low live coral cover, low diversity of coral and fish, and low density of echinoids (few ind. m^{-2}). The community gross primary production is higher and calcification rates are lower in eutrophized zones compared to oligotrophic areas (Mioche and Cuet 1999).

Increased bioerosion has been reported on coral reefs subjected to nutrient pollution (Risk and MacGeachy 1978; Rose and Risk 1985; Pari et al. 1998). In contrast, Smith et al. (1981) and Birkeland (1987) have suggested that herbivorous fishes and echinoids would be less numerous in areas affected by high levels of eutrophication.

The purpose of the research reported here was to compare bioerosional processes in areas subjected to various levels of eutrophication and related alterations of benthic community structure. The sites were chosen on the basis of existing data on nutrient content and benthic cover (Cuet et al. 1988; Cuet 1989; Cuet and Naim 1989). Study areas separated by only a few hundred meters were selected in order to reduce potentially confounding variability of environmental parameters such as exposure to ocean waves, sea temperature, reef morphology, and hydrodynamic conditions.

Our aim was to test the hypothesis that rates of bioerosion would be correlated with spatial differences in the benthic cover of macroalgae and the availability of nutrients. We sought to understand the relationships between nutrient availability and benthic cover of the substratum, between epilithic algal cover and bioerosion rates, and among the various agents of bioerosion.

Material and methods

Study area

Reunion Island is located in the Indian Ocean (21°7′S, 55°32′E), 700 km east of Madagascar. The study area is located on La Saline fringing reef, along the western coast of Reunion Island (Fig. 1). From the open ocean towards land, three geomorphological zones are present (Montaggioni and Faure 1980): the outer reef flat or compact reef flat, the inner reef flat typified by transverse strips of branched corals, and the back-reef zone covered with detritic sediment.

Three transects were selected on this reef that are subjected to three patterns of nutrient enrichment due to submarine groundwater discharge (Cuet et al. 1988; Naim 1993; Naim et al. 2000). Transect 1 receives large SGD; nutrient inputs on transect 2 are mainly restricted to the outer reef flat; and transect 3 receives little or no SGD.

The structure of the benthic communities was described for each transect by Chazottes (1996). At the beginning of the 1990s, transect 1 was characterized by highly degraded coral communities largely colonized by macroalgae, especially crustose corallines and phaeophytes. This transect was representative of a phase-shifted reef in which the abundance of corals was less than 3% of reef substratum and the abundance of coralline and fleshy algae was as high as 80%. Transect 3 was located in an area with flourishing coral communities and algal turfs colonizing dead coral substrata. Coralline algal coverage was less than 16% and fleshy algae were

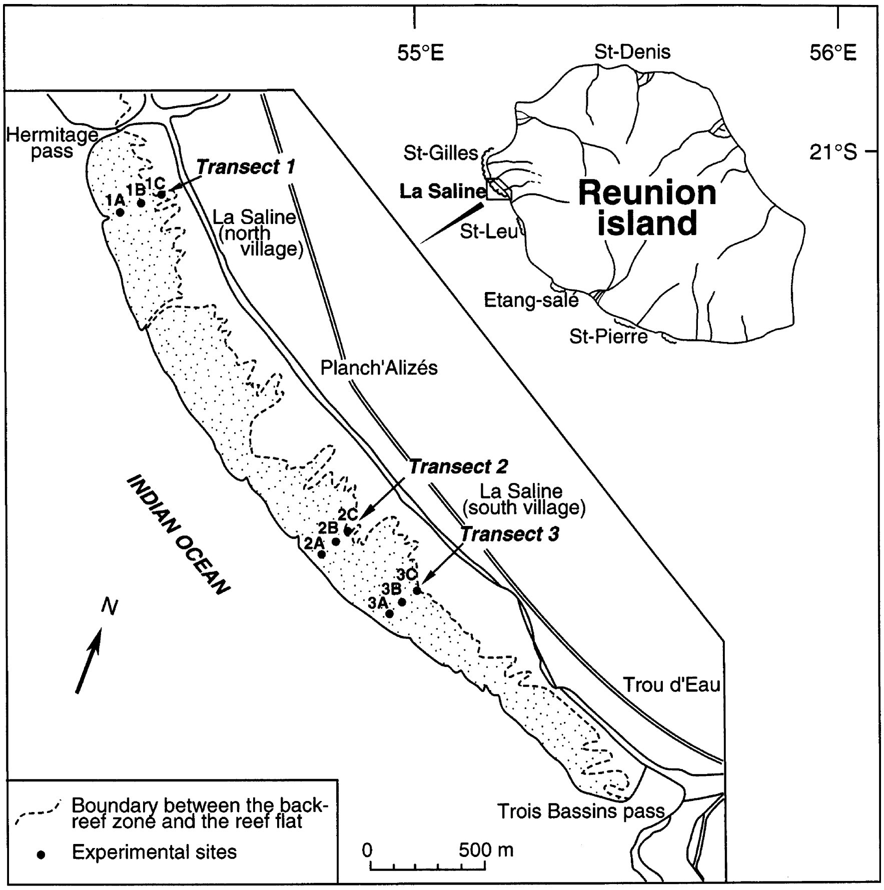

Fig. 1 Location map of Reunion Island and of experimental sites on La Saline fringing reef. Three transects and three stations per transect were selected (*A* outer reef-flat; *B* inner reef-flat; and *C* back-reef zone)

poorly represented on this transect. Transect 2 exhibited an intermediate benthic community structure, with live coral coverage varying between 20 and 30% and macroalgal cover reaching 40% on the reef flat. Similar community structures were observed at these sites in 1998.

One station was selected along each transect in each of three different biotopes: outer reef flat, inner reef flat, and back-reef zone (see Fig. 1).

In situ measurements and experimental substrata

At each station (except the inner reef flat of transect 3 which was very close to the outer reef flat), five water samples were collected hourly between low and high tide, in March, June, and December 1991, and in September 1992. Samples were filtered through 0.45-µm GF/C glass-fiber filters. Ammonium analyses (Koroleff 1969) were performed immediately. Samples were frozen at –20 °C for subsequent analysis of reactive P and nitrate + nitrite on a Bran + Luebbe Autoanalyser II. Salinities were determined with a Grundy Environmental Systems 6230 N salinometer.

Bioerosional processes were studied using standardized substrata. These were regular-shaped blocks (about 9×10×4 cm) cut from large colonies of live *Porites lobata*, soaked in sodium hypochlorite to remove organic material, rinsed, and dried. Blocks showing evidence of boring were discarded. The blocks were then weighed and measured using a Vernier calliper. Initial surface area and volume of each block were estimated from its measured length, width, and thickness. Three blocks per station (four on the inner reef flat of transect 2) were attached to reef substrate, at a water depth of less than 2 m, using aqua cement, in June 1991, and collected after 1 year of exposure. After collection, they were fixed in buffered 5% solution of formaldehyde in seawater.

The blocks (total number = 28) were analyzed to measure the surface areas covered with epilithic organisms, in order to determine the composition of the boring communities (macro- and micro-organisms), and to estimate bioerosion rates (grazing, macroboring and microboring rates). First, photographs were taken of the block surfaces (except the base of blocks cemented on the substrate), and the cover (expressed as percent of exposed surface) of the epilithic communities was estimated using the image analysis software Optilab 2.0.1 (1988–1992). The blocks were then cut in half. One half was used for determining the composition of the boring communities (macro- and micro-organisms) and the microboring rates. The other half was used for estimating the rates of $CaCO_3$ loss by grazing and macroboring.

The first half-block was further subdivided into two parts. One part (60–90 cm^3 in volume) was split into small fragments in order to extract the macroborers. The major groups of macroborers present were expressed as the number per cubic decimeter of substrate. The second part of this half-block was used to determine the composition of the microboring communities and to estimate the rate of $CaCO_3$ loss due to microborers. Resin-embedded sections (at least five per block) and SEM observations were used to study the endoliths from the surface of the substrate down to the limit of endolith penetration (typically less than 1 mm). The surface area occupied by microborers was estimated using image analysis. The values obtained were converted to volumes and then to rates of $CaCO_3$ loss by microborers and expressed in grams per square meter per year. In order to measure the influence of substrate cover on microborers, fragments of the first half-block covered with algal turfs, coralline algae, and phaeophyte macroalgae were examined using light microscopy, and species composition of the microendoliths was determined.

The second half-block was reserved for estimating the erosion rates by grazers and macroborers. It was cut into (typically five) vertical slices, 5 mm in thickness, and photographed after removal of organic matter by chlorax. Grazing rates were determined from scanned photographs of the slices. The final (after exposure) surface area of each slice was measured using image analysis. When crustose coralline algae were present, only the surface area under the encrusting organisms on each slice was measured. The final volume of each slice (final surface area × thickness) was calculated. The initial volume of each slice was estimated from its known initial surface area (measured before exposure) and for a slice thickness of 5 mm. The difference between initial and final volumes represents the volume of the slice lost during exposure to bioerosion. The total volume of each half-block lost by grazing was estimated by adding the lost volumes of its slices. Using a mean coral density of 1.33 ± 0.08 (estimated from the weight and volume measurements of the samples) and by extrapolation from the external surface area of the half-block (the unexposed, cemented base excepted) to a unit surface of 1 m^2, the rate of calcium carbonate loss by grazing was expressed in kilograms per square meter per year. The rates of internal erosion by macroborers were calculated on the basis of carbonate volume removed (see above), which was determined from surface areas of borings visible on scanned slices and measured using image analysis.

For more details on the sample preparation and bioerosion analyses see Chazottes et al. (1995) and Peyrot-Clausade et al. (1995a).

Benthic sampling was carried out at each station between June and August 1992. The number of echinoids present at each station was estimated from counts of individuals in random quadrats of 1 m^2 made at night before collection of blocks. Thirty quadrats were sampled at each station of transects 2 and 3, and 15 at each station of transect 1 where the echinoids were rare. The cover of reef substrata by benthic organisms was measured during the day using quadrats of 1 m^2. Thirty contiguous quadrats were sampled at each station.

Data analyses

Coverage of reef substratum was related to nutrient concentrations of reef waters across sites using simple linear correlation. The proportions of sand and rubble were removed so that only coverage on hard substrata was taken into account in the analysis. The parameters considered were, on the one hand, cover by live corals, algal turfs, coralline algae + macrophytes, dead coral pavement, and clionid sponges, and, on the other hand, mean and maximum concentrations of ammonium, nitrate + nitrite, and reactive P.

The classification of the stations in relation to cover and chemical data was made using Ward's method (Euclidean distance on standardized data; Saporta 1978). For each cluster (class), the squared distance between its center of gravity and the overall center of gravity (here the origin) was broken down for each variable. This allowed an estimation of the contribution of the variables to each cluster. The sign (negative or positive contribution) was that of the average by cluster and by variable.

A series of two-way, nested analysis of variance (ANOVAs) with unequal sample sizes was carried out in order to investigate the variation in rates of bioerosion (grazing, macrobioerosion, and microbioerosion), in densities of macroborers and echinoids, among transects and among stations within a transect (Sokal and Rohlf 1981). When variation among transects was significant, multiple comparisons of means with the Student-Newman-Keuls (SNK) test were used to determine which means were significantly different from each other (significance level $p = 0.05$). Prior to these analyses, the data were tested for the basic assumptions of homogeneity of variance (F_{max} test) and normality (Kolmogorov test).

Linear regressions were used to investigate the relationships between the density of bioeroders and the relevant rates of erosion, and between erosion rates by grazers, macroborers, and microborers. Bioerosion rates were related to the epilithic cover of experimental substrata using simple linear correlation. The parameters considered were rates of grazing (in kilograms of $CaCO_3$ per square meter per year), macroboring (grams of $CaCO_3$ per square meter per year), microboring (grams of $CaCO_3$ per square meter per year), and percentage cover of coralline algae, macrophyte, and algal turfs. The distribution of blocks in relation to bioerosion and cover data was studied using principal component analysis (PCA) performed on standardized variables. The coordinates of each block on the first three axes of the PCA were saved for subsequent hierarchical classification. The classification of blocks was made using Ward's method (Saporta 1978). The isance used was the Euclidean distance computed on the coordinates of blocks in the PCA (Roux 1993, pp 103–104; Lebart et al. 1995). The contribution of the variables to the formation of clusters was estimated according to the method in the references above.

All the analyses were performed using the statistical software ADE-4 (Thioulouse et al. 1997) and SuperANOVA 1.11 (1991).

Results

Grouping of site characteristics

Salinities varied slightly from $35.03 \pm 0.35‰$ in the back-reef zone of transect 2 to $35.16 \pm 0.10‰$ on the outer reef flat of transect 1 (Table 1), but there were no significant differences among stations. The cover of live coral, algal turfs, or clionid sponges was not significantly correlated with any nutrient species (Table 2). Cover by coralline algae and macrophyte was significantly positively correlated with maximum concentration of ammonium ($R = 0.80$, $p = 0.01$, $n = 9$ stations) and with mean nitrate + nitrite content ($R = 0.68$, $p = 0.0455$, $n = 9$). Cover by dead coral pavement was significantly negatively correlated with mean concentration of nitrate + nitrite ($R = -0.73$, $p = 0.0262$, $n = 9$).

The cluster analysis of chemical and cover data revealed four groups of stations (Fig. 2). An analysis of the factors contributing to these groupings (Table 3) revealed that for group 1 (back-reef zones of transects 2 and 3) the most important variables were cover of clionid sponges and dead coral pavement, contributing 27 and 25% (respectively) to the clustering. For group 2 (reef flat sites of transect 3 and inner reef flat of transect 2), 21% was contributed by cover of living corals, with the highest mean value compared to the other groups of sites. Ammonium and nitrate + nitrite contributed significantly to this clustering because of their low concentrations. For group 3 (outer reef flat of transect 2), the most important variables were content of nitrate + nitrite (mean and maximum concentrations contributing 17 and 34%, respectively) and maximum concentration in reactive P (25%). The contributions of cover data to this clustering were not significant. For group 4 (the three sites of transect 1), 24% was contributed by coralline and soft algae, with the highest mean cover recorded, and 24% by living corals, with low mean coverage as shown by the negative contribution. The contributions of ammonium and maximum nitrate + nitrite concentrations to this clustering were significant (between 8 and 10% each).

Table 1 Mean salinity (‰) and nutrient content (μM) ± standard deviation in reef waters along the three transects on La Saline reef, Reunion; $n = 20$ water samples per station. Extreme values (minimum salinity and maximum nutrient concentration) recorded at each station during the sampling period are also given. Stations 3A and 3B, very close to each other, were not separated for chemical analyses. Percentage cover of reef substrata by benthic organisms was measured using 1-m^2 quadrats ($n = 30$ quadrats per station). The proportions of sand and rubble have been removed and only cover on hard substrata (100%) was considered. Experimental stations as in Fig. 1

Sites	Salinity		NH_4^+		NO_3^- + NO_2^-		PO_4^{3-}		Coverage of reef substrata (%)				
	Mean	Min.	Mean	Max.	Mean	Max.	Mean	Max.	Living corals	Algal turfs	Coralline + soft algae	Dead coral pavement	Clionid sponges
1A	35.16 ± 0.10	35.04	0.34 ± 0.24	1.05	0.36 ± 0.14	0.72	0.13 ± 0.03	0.19	0.12	2.68	96.95	0.00	0.00
1B	35.15 ± 0.08	35.06	0.39 ± 0.21	1.01	0.43 ± 0.20	0.98	0.14 ± 0.02	0.18	1.60	21.28	75.86	1.26	0.00
1C	35.08 ± 0.17	34.67	0.37 ± 0.13	0.73	0.38 ± 0.20	0.74	0.10 ± 0.03	0.15	2.58	36.71	59.33	0.79	0.00
2A	35.12 ± 0.14	34.69	0.33 ± 0.21	1.08	0.49 ± 0.54	2.26	0.14 ± 0.07	0.33	28.36	20.06	50.53	0.53	0.52
2B	35.13 ± 0.10	34.88	0.35 ± 0.15	0.77	0.28 ± 0.10	0.59	0.13 ± 0.04	0.27	27.52	14.22	48.29	9.63	0.34
2C	35.03 ± 0.35	33.59	0.40 ± 0.14	0.70	0.25 ± 0.16	0.77	0.11 ± 0.03	0.16	21.81	1.98	11.89	54.05	10.27
3A	35.13 ± 0.12	34.93	0.27 ± 0.08	0.47	0.27 ± 0.11	0.43	0.13 ± 0.02	0.16	18.49	31.32	30.56	18.87	0.57
3B	35.13 ± 0.12	34.93	0.27 ± 0.08	0.47	0.27 ± 0.11	0.43	0.13 ± 0.02	0.16	38.86	19.54	18.75	19.32	3.41
3C	35.14 ± 0.13	34.92	0.32 ± 0.09	0.50	0.24 ± 0.12	0.59	0.12 ± 0.02	0.16	9.27	2.27	8.92	66.43	13.11

In summary, the three sites of transect 1 were grouped together in having the highest cover of dead coral and macroalgae, and high concentrations of ammonium and nitrate + nitrite in reefal waters. In contrast, the reef flat of transect 3 was characterized by high cover of living corals, low algal cover, and the lowest concentrations of ammonium and nitrate + nitrite. The reef flat sites of transect 2 were distinct. The inner reef flat exhibited community structure and water quality comparable to those found on the reef flat of transect 3. The outer reef flat of transect 2 was distinguished from the other sites by the highest mean concentrations of nitrate + nitrite and reactive P, high maximum concentrations of all nutrients, but a low mean concentration of ammonium. Compared to the apparently degraded sites on transect 1 and the relatively healthier sites on transect 3, this site exhibited intermediate cover of dead coral and macroalgae.

The back-reef zones of transects 2 and 3 were characterized by the abundance of clionid sponges, by the predominance of dead coral pavement as hard substratum, and by low nutrient concentrations.

Algal cover on experimental blocks

In situ observations of the experimental substrata during exposure and the identification of epilithic organisms on block surfaces using light microscopy revealed that every experimental substrate was first colonized by cyanobacteria only. After 1 year of exposure, the epilithic algal communities included algal turfs dominated by cyanophyta, the crustose coralline alga *Hydrolithon onkodes*, and the brown macroalga *Lobophora variegata*. The composition of these epilithic communities differed markedly among sites (Fig. 3).

On transect 3, more than 90% of the block surfaces was covered with cyanobacteria and with filamentous algae forming dense turfs. The remaining surfaces were colonized by *Hydrolithon onkodes*. Between 62.7 and 65.3% of the total surface of blocks on transect 2 was colonized by sparse, small filaments of cyanobacteria [referred to as "sparse algal turf" by Hackney et al. (1989)]. The remaining surfaces were covered by *Hydrolithon onkodes* (7.5–23.4%) and by *Lobophora variegata* (13.0–27.2%). *L. variegata* was particularly abundant (35.4 and 45.7%) on two blocks placed on the outer reef flat.

On blocks of transect 1, *L. variegata* was abundant and formed thick encrusting layers, often on top of coralline algae crusts. The highest cover of *L. variegata* was recorded on the outer reef flat, with a mean value of 71.2% of the block surfaces. *H. onkodes* and *L. variegata* exhibited similar mean coverages of blocks on the inner reef flat (24.7 and 28.8%) and in the back-reef zone (25.1 and 23.1%). The remaining block surfaces were covered with sparse algal turfs (22.1% on the outer reef flat, 46.5% on the inner flat, and 51.8% in the back-reef zone).

Table 2 Correlations between mean and maximum nutrient concentrations in reefal waters and cover of reef substrata measured using the quadrat method. Only communities occurring on hard substrata are presented. $n = 9$ experimental stations. * $p \leq 0.05$; ** $p \leq 0.01$

Chemical data	Coverage of reef substratum				
	Live coral	Algal turfs	Coralline algae and macrophyte	Dead coral pavement	Clionid sponges
NH_4^+ mean	–0.47	–0.22	+0.32	–0.02	+0.07
NH_4^+ max.	–0.35	–0.12	+0.80**	–0.61	–0.49
$NO_3^- + NO_2^-$ mean	–0.26	+0.35	+0.68*	–0.73*	–0.61
$NO_3^- + NO_2^-$ max.	+0.11	+0.06	+0.24	–0.33	–0.21
PO_4^{3-} mean	+0.24	–0.06	+0.29	–0.38	–0.39
PO_4^{3-} max.	+0.37	–0.03	+0.23	–0.40	–0.35

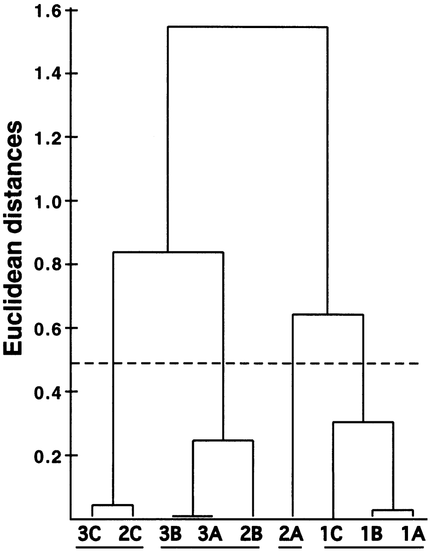

Fig. 2 Dendrogram of cluster analysis results using the Ward method (Euclidean distance on standardized variables). *Dashed line* indicates the cut-off level chosen to separate the classes. Parameters considered were mean and maximum nutrient concentrations of reef waters, and coverage of reef substrata by benthic organisms measured using the quadrat method. Initial non-standardized variables are given in Table 1. Experimental sites as in Fig. 1

Bioerosion of the experimental blocks: grazing, macrobioerosion, and microbioerosion

Grazing

Mean bioerosion rates of grazers greatly exceeded those of internal macro- and microborers (Table 4). A two-way, nested ANOVA (Table 5, Fig. 4) indicated that the grazing rates varied significantly among transects ($p = 0.0001$). The SNK test revealed that all the means were significantly different from each other. The lowest mean rate (1.63 kg $CaCO_3$ m^{-2} $year^{-1}$) was observed on transect 1 and the highest on transect 3 (3.52 kg m^{-2} $year^{-1}$). The grazing rates did not vary significantly among biotopes within each transect ($p = 0.0881$).

The community of grazers effecting this bioerosion was dominated by echinoids, especially *Echinometra mathaei*, representing between 80 and 100% of the total sea urchin density estimated at each station. A two-way nested ANOVA (Table 5) revealed that the density of grazing urchins varied significantly among transects ($p = 0.0001$) and among biotopes within transects ($p = 0.0001$). The SNK test indicated that urchin densities per transect were significantly different from each other. The lowest density was observed on transect 1 (mean density = 0.09 ind. m^{-2}) and the highest on transect 3 (14.02 ind. m^{-2}). The significant differences among biotopes within transects were due to stations from transect 3 (Fig. 5a), with the highest density of 28.2 ± 17.76 ind. m^{-2} recorded on the outer reef flat, and lower densities on the inner flat (6.90 ± 5.71 ind. m^{-2}) and in the back-reef zone (6.97 ± 5.27 ind. m^{-2}).

Scarid fish grazers occurred in low densities (between 0.03 and 0.57 ind. m^{-2}), and were of small mean individual size (length < 8 cm) at every station.

Macroboring

A two-way nested ANOVA (Table 5) revealed that the macroboring rates varied significantly among transects ($p = 0.0002$) and among biotopes within transects

Table 3 Contribution of chemical and cover variables to clustering of the experimental stations. For each cluster, the contribution of each variable to the clustering is expressed in percent and the sign is that of the average by cluster and by variable. A positive contribution indicates that the cluster is characterized by high values of the variable (average of cluster is higher than total average) and a negative contribution indicates that the cluster is defined by low values of the variable (cluster average lower than total average)

Group	Elements	NH_4^+		$NO_3^- + NO_2^-$		PO_4^{3-}		Coverage of reef substratum (%)				
		Mean	Max.	Mean	Max.	Mean	Max.	Living corals	Algal turfs	Coralline + soft algae	Dead coral pavement	Clionid sponges
1:	2C, 3C	2	–4	–8	–1	–6	–3	0	–12	–12	25	27
2:	2B, 3A, 3B	–22	–16	–12	–11	3	0	21	5	–5	0	–3
3:	2A	0	9	17	34	6	25	4	0	0	–3	–1
4:	1A, 1B, 1C	8	10	9	0	–1	–3	–24	2	24	–11	–8

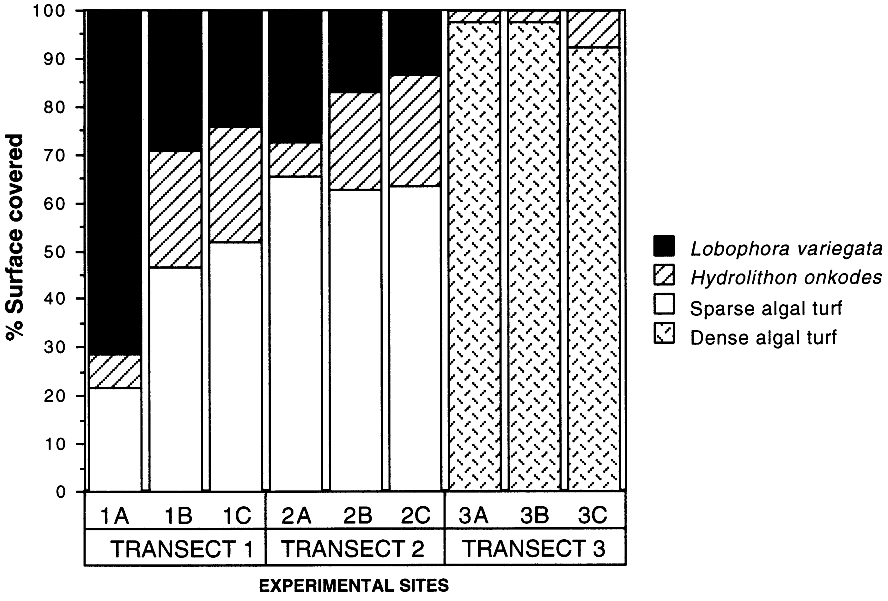

Fig. 3 Coverage of experimental substrata (expressed in percent of total block surface) estimated using image analysis. $n = 3$ blocks per station, except $n = 4$ at station 2B. Experimental sites as in Fig. 1

Table 4 Mean erosion rates (± standard deviation) estimated from experimental blocks using the image analysis method; $n = 3$ blocks per station, except $n = 4$ on station 2B. Original block volumes ranged from 250 to 520 cm^3. Experimental stations as in Fig. 1

Stations	Grazing rates (kg m^{-2} $year^{-1}$)	Macroboring rates (g m^{-2} $year^{-1}$)	Microboring rates (g m^{-2} $year^{-1}$)
1A	1.64 (0.43)	7.60 (4.91)	68.70 (6.88)
1B	1.75 (0.45)	6.84 (4.05)	56.74 (15.07)
1C	1.51 (0.29)	5.73 (1.26)	47.18 (4.58)
2A	2.12 (0.17)	13.33 (7.07)	69.22 (2.97)
2B	2.80 (0.77)	22.54 (2.93)	68.99 (7.39)
2C	2.92 (0.84)	26.99 (7.86)	63.98 (3.19)
3A	4.31 (0.43)	16.52 (13.20)	44.76 (0.32)
3B	2.91 (0.56)	47.30 (21.02)	63.11 (0.19)
3C	3.33 (0.72)	32.92 (13.49)	23.46 (0.39)

($p = 0.0387$). The SNK test showed that the macroboring rates per transect were significantly different from each other. The lowest mean rate was observed on transect 1 (6.73 g $CaCO_3$ m^{-2} $year^{-1}$) and the highest on transect 3 (32.25 g m^{-2} $year^{-1}$). The significant differences among biotopes within transects were mainly due to the low rates recorded in the outer reef flat of transects 2 and 3 (Table 4, Fig. 4).

After 1 year of exposure, the community of boring macro-organisms was still immature. Small polychaetes *Dodecaceria* were the only macroborers found in the majority of the blocks (18 blocks on 28 studied). Other polychaetes, such as Sabellidae, were rarely found (two blocks). The other macroborers including vermetids, sipunculans, and bivalves were separately found in four blocks. Five blocks contained no endolithic macrofauna.

A two-way nested ANOVA (Table 5, Fig. 5b) revealed that the densities of macroborers varied significantly among transects ($p = 0.0210$). The SNK test revealed that the lowest mean density was observed on transect 1 (mean density = 11.9 ind. dm^{-3}) and the highest on transect 2 (85.2 ind. dm^{-3}). Transect 3 had an intermediate value (42.5 ind. dm^{-3}). The densities of macroborers did not vary significantly among biotopes within each transect ($p = 0.9226$).

Microboring

A two-way nested ANOVA (Table 5) revealed that the microboring rates varied significantly among transects ($p = 0.0001$) and among biotopes within transects ($p = 0.0001$). The SNK test showed that the microboring rates per transect were significantly different from each other. The lowest rate was observed on transect 3 (43.78 g $CaCO_3$ m^{-2} $year^{-1}$) and the highest on transect 2 (67.56 g m^{-2} $year^{-1}$). The significant differences among biotopes within transects were mainly due to the stations on transect 3 (Table 4, Fig. 4), with the lowest mean rate estimated at 23.46 ± 0.39 g m^{-2} $year^{-1}$ in the back-reef zone, and the highest at 63.11 ± 0.19 g m^{-2} $year^{-1}$ in the inner reef flat.

The microborers found in the samples included cyanobacteria, chlorophyta, and fungi. The cyanobacteria were represented by two species: *Mastigocoleus testarum* and *Plectonema terebrans*. Filaments of *Mastigocoleus testarum* were typically 5–8 µm in diameter, elongate, often curved, with short branches and pedonculated heterocysts. *Plectonema terebrans* had finer elongate filaments, 1–3 µm in diameter, forming numerous loops. The only chlorophyte found was *Ostreobium quekettii* characterized by branching filaments, varying from 10–60 µm in diameter. Fungi had non-branching tubular filaments ranging in diameter from 1–2 µm with numerous nodes.

The observation of block samples covered with algal turfs, encrusting coralline algae and/or macrophyte

Table 5 Two-way, nested ANOVAs (fixed model) on rates of grazing, macroboring, and microboring and density of macroborers and echinoids for the three transects and three stations (back-reef zone, inner and outer reef-flat) per transect

Source of variation	df	SS	MS	F	*p*
Grazing rates					
Transect	2	15.986	7.993	24.380	0.0001
Station (transect)	6	4.333	0.722	2.203	0.0881
Residual	19	6.229	0.328		
Echinoid density					
Transect	2	7,464.240	3,732.120	69.001	0.0001
Station (transect)	6	9,261.067	1,543.511	28.537	0.0001
Residual	216	11,682.933	54.088		
Macroboring rates					
Transect	2	2,944.675	1,472.337	14.499	0.0002
Station (transect)	6	1,722.322	287.054	2.827	0.0387
Residual	19	1,929.433	101.549		
Macroborer density					
Transect	2	23,825.151	11,912.575	4.766	0.0210
Station (transect)	6	4,684.516	780.753	0.312	0.9226
Residual	19	47,487.957	2,499.366		
Microboring rates					
Transect	2	2,632.666	1,316.333	31.509	0.0001
Station (transect)	6	3,114.587	519.098	12.426	0.0001
Residual	19	793.759	41.777		

allowed us to correlate epilithic colonization with the composition of the microborer community. In block samples covered with epilithic algal turfs (blocks from transect 3 mainly), the community of microendoliths was largely dominated by the cyanobacterium *Mastigocoleus testarum*. The other boring cyanobacterium, *Plectonema terebrans*, appeared in significant proportions only in blocks collected on the outer reef flat. In samples covered with crustose coralline algae and with the phaeophyte *Lobophora variegata* (blocks from transects 1 and 2), the boring cyanobacteria *Plectonema terebrans* and *Mastigocoleus testarum* were commonly found. The chlorophyte *Ostreobium quekettii* was specifically observed under the crusts of coralline algae.

Relationships between the densities of eroding organisms and bioerosion rates

A significant positive correlation was found between mean grazing rates and the mean densities of echinoids estimated at each station ($R = 0.79$, $p = 0.0116$). The relationship is still significant even if only *Echinometra mathaei*, the dominant grazer, is considered ($R = 0.78$, $p = 0.0136$) but not significant if *E. mathaei* is excluded from the analysis ($p = 0.2173$).

No significant correlation was found between the rates of erosion by macro-organisms and the macroborer densities estimated for each experimental block ($p = 0.6075$). Macroboring rates cannot be determined from the number of borers. Such a relationship could not be tested for microboring rates because the microborers constitute a network of filaments and cannot be individually counted.

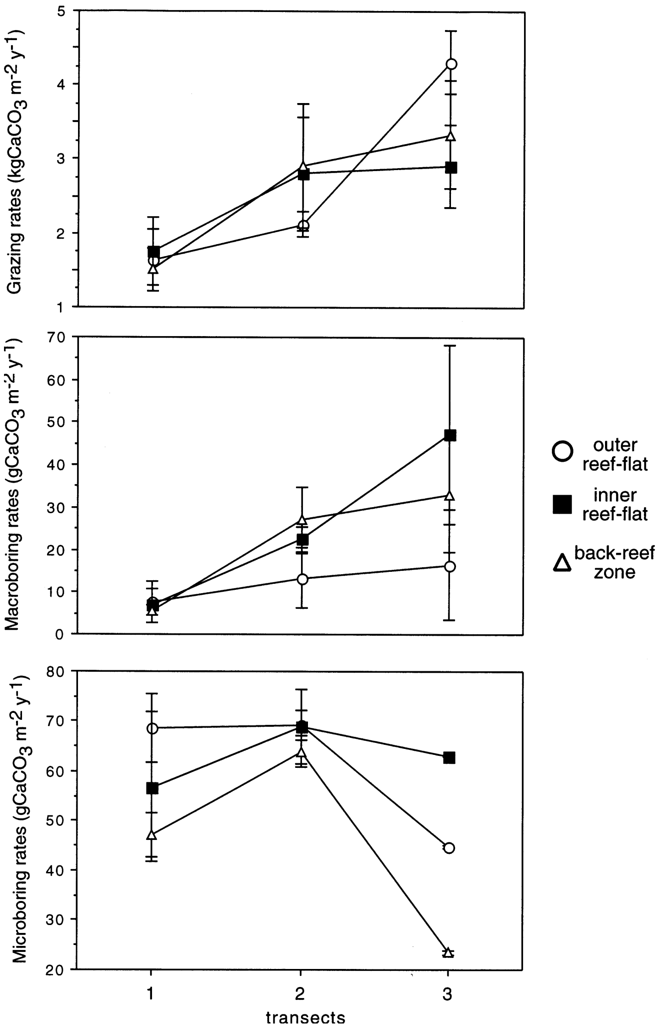

Fig. 4 Spatial pattern of grazing rates (expressed in kg $CaCO_3$ m^{-2} $year^{-1}$) and of macro- and microboring rates (expressed in g $CaCO_3$ m^{-2} $year^{-1}$) along the three transects. Mean rate ± standard deviation is given for each experimental station (site locations in Fig. 1). *n* as in Fig. 3

Relationships between bioerosion intensity and epilithic cover of blocks

Correlations between bioerosion rates and cover of experimental blocks are given in Table 6. Grazing intensity was significantly positively correlated with cover by algal turfs ($R = 0.68$, $p = 0.0001$, $n = 28$ blocks) and significantly negatively correlated with cover of coralline algae ($R = -0.38$, $p = 0.0467$, $n = 28$) and phaeophytes ($R = -0.54$, $p = 0.0031$, $n = 28$). Macroboring intensity was significantly positively correlated with cover by algal turfs ($R = 0.55$, $p = 0.0022$, $n = 28$), significantly negatively correlated with cover by phaeophytes

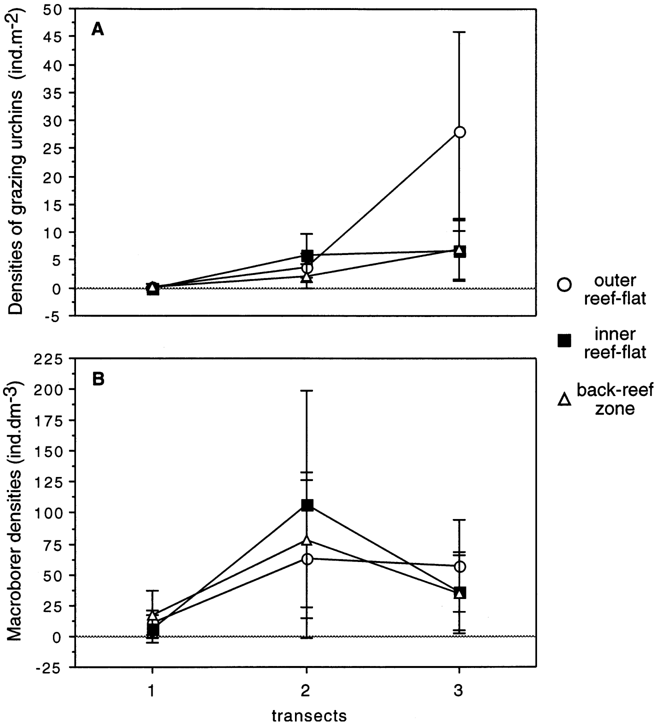

Fig. 5 Mean density (± standard deviation) of bioeroders at each experimental station. **a** Density of grazing urchins (ind. m^{-2}) measured using 1-m^2 quadrats; $n=15$ quadrats (transect 1), 30 quadrats (transects 2, 3). **b** Density of macroborers (ind. dm^{-3}) in experimental blocks; $n=3$ blocks per station, except $n=4$ on the inner reef-flat of transect 2

($R=-0.45$, $p=0.0153$, $n=28$), and weakly negatively correlated with cover by coralline algae ($R=-0.28$, $p=0.1513$, $n=28$). Microboring intensity was significantly negatively correlated with cover by algal turfs ($R=-0.44$, $p=0.0196$, $n=28$) and significantly positively correlated with cover by phaeophytes ($R=0.45$, $p=0.0158$, $n=28$).

The regrouping of blocks in relation to bioerosion and cover data was investigated using a principal component analysis, followed by an hierarchical classification of 28 blocks and six variables (rates of grazing, macroboring, and microboring and percentage cover of block by coralline algae, phaeophyte, and algal turf). The first two axes of the PCA account for more than 71% of the observed variation (Fig. 6). Axis 1, accounting for 51.70% of the variation, displays, on one side, cover by phaeophytes and microboring rates, and, on the other, cover by algal turfs, and grazing and macroboring rates. Axis 2, accounting for 20.21% of the variation, displays, on one side, cover by coralline algae, and, on the other, cover by phaeophytes and microboring rates.

The results of the cluster analysis performed on the first three axes of the PCA revealed three groups of blocks. An analysis of the factors contributing to these groupings (Table 7) revealed that for group 1 (all the blocks from transect 3 and two blocks from transect 2), the most important variables were algal turf cover (25%), grazing (26%), and macroboring rates (16%). Blocks of group 2 (five blocks from transect 1 and three blocks from transect 2) were characterized by the highest cover by phaeophytes and the highest microboring rates, contributing, respectively, 41 and 8% to the clustering, and the lowest cover by algal turfs (29%). For group 3 (five blocks from transect 2 and four blocks from transect 1), the most important variable was coralline algae cover, contributing 68% to the clustering. This group of blocks was also characterized by a low mean grazing rate (–15%).

All the blocks of transect 3 were clustered together. Groups 2 and 3 contained blocks of transects 1 and 2, with blocks of transect 2 located closer to the origin. This indicates that blocks from transect 1 had a higher algal cover and higher microboring rates than blocks from transect 2.

Interactions between the different agents of bioerosion

When considering all the blocks ($n=28$), without referring to the transect on which they were laid, a significant relation of quadratic form (Fig. 7) was found between grazing and macroboring rates ($R=0.57$, $p=0.0066$, $n=28$). From the quadratic model obtained, the macroboring rate was maximum for a grazing rate of 3.30 kg $CaCO_3$ m^{-2} $year^{-1}$. For grazing rates less than 3.30 kg $CaCO_3$ m^{-2} $year^{-1}$, grazing and macroboring rates increased in parallel. As the grazing rate increased beyond 3.30 kg m^{-2} $year^{-1}$, the macroboring rates tended to decrease.

When each transect was considered separately, grazing and macroboring rates were significantly positively correlated on transect 2 ($R=0.77$, $p=0.0087$, $n=10$) and significantly negatively correlated on transect 3 ($R=-0.71$, $p=0.0302$, $n=9$). No significant correlation was found for transect 1 ($R=0.33$, $p=0.3818$). No significant correlation was found between the microboring rates and those of grazing or macroboring.

Discussion

Relationships between nutrients and benthic cover

Submarine groundwater discharge (SGD) fluxes onto coral reefs are well documented (D'Elia et al. 1981;

Table 6 Correlations between bioerosion rates and coverage of experimental blocks estimated using image analyses. $n=28$ blocks. * $p \le 0.05$; ** $p \le 0.01$; *** $p \le 0.001$

Coverage of blocks	Grazing rates	Macroboring rates	Microboring rates
Algal turfs	+0.68***	+0.55**	–0.44*
Coralline algae	–0.38*	–0.28	+0.03
Phaeophyte algae	–0.54**	–0.45*	+0.45*

Johannes and Hearn 1985; Lewis 1987), and some degradation of benthic communities on La Saline reef has been tentatively ascribed to SGD inputs (Cuet et al. 1988; Montaggioni et al. 1993; Naim 1993; Chabanet et al. 1995, 1997; Mioche and Cuet 1999).

Mean concentrations of ammonium, nitrate + nitrite, and reactive P in the reefal waters were not as high (less than 0.5 μM) during our study (Table 1) as the high values (up to 5 μM) found previously (1985–1987) on the same reef (Cuet et al. 1988; Montaggioni et al. 1993). The discrepancy may be explained by different hydrodynamic and climatic conditions. The highest nutrient concentrations were recorded in 1985 during the rainy season (February and December) and in April 1987 during low tide and calm hydrodynamic conditions favoring a large intrusion of the fresh waters (Cuet et al. 1988). In our study, the reef waters were sampled between low and high tide, with three sampling periods during the dry season (March and June 1991, and September 1992), and only one period in the rainy season (December 1991).

Although mean nutrient concentrations were relatively low during our study, maximum values of about 1 μM ammonium and 2.26 μM nitrate + nitrite were recorded locally (Table 1). Because of the rapid uptake and assimilation of dissolved nutrients by algae (Cuet et al. 1988; Naim 1993), nutrient concentrations in reef waters are not indicative of the amounts delivered to the benthic communities, and are poor indicators of reef status (McCook 1999). Our purpose was not to provide an exact measure of eutrophication, but rather to classify the sites from least to most affected by SGD on the basis of chemical and benthic data (Fig. 2, Table 3).

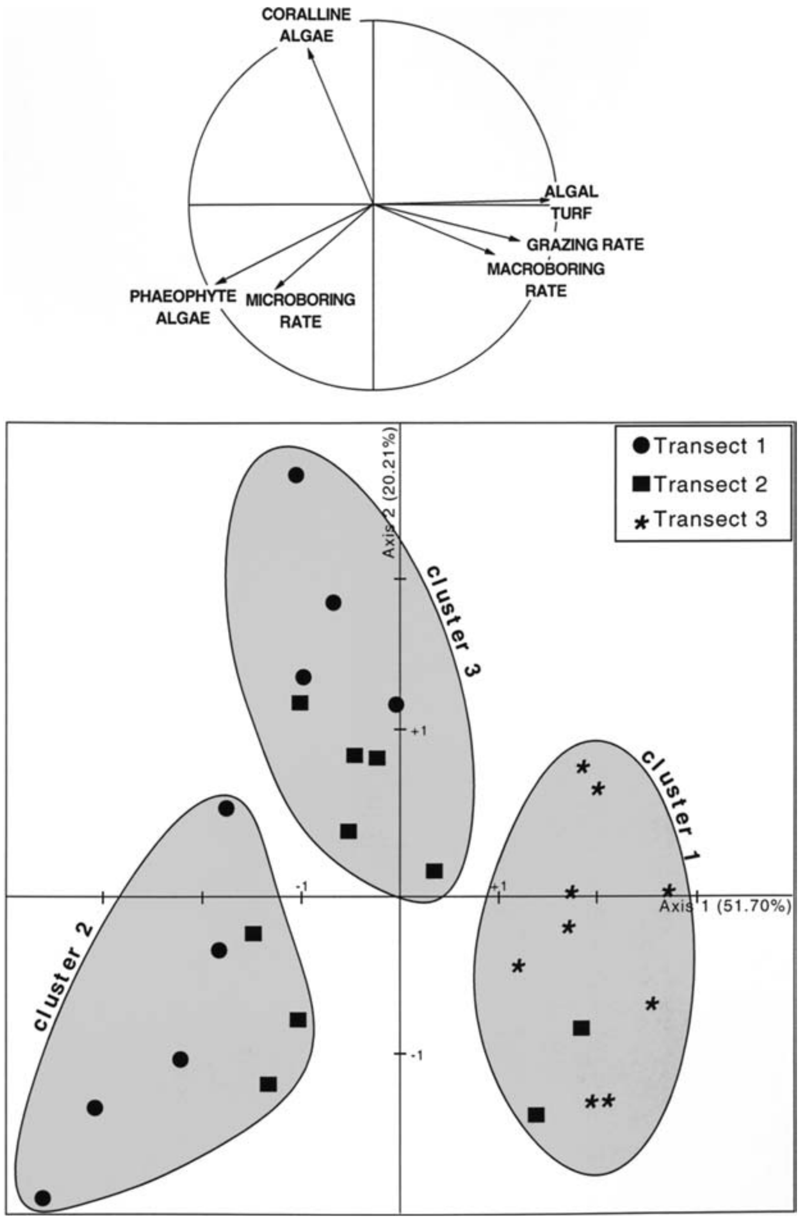

Fig. 6 Principal component analysis (PCA) of 28 experimental substrata using six variables (grazing, macroboring, and microboring rates and coverage of block by algal turf, crustose coralline algae, and phaeophytes). The blocks are represented by *symbols* corresponding to transects. The plane chosen is the one given by the first two axes of the PCA. Classification of blocks into three groups results from the cluster analysis performed, using the Ward method, on the coordinates on the first three axes of the PCA

Table 7 Contribution of bioerosion and cover variables to clustering of the experimental blocks. Contribution of each variable to the clustering is expressed in percent and the sign (negative or positive contribution) is that of the average by group and by variable

Clusters	Coralline algae	Phaeophyte algae	Algal turfs	Grazing	Macroboring	Microboring
1	–13	–13	25	26	16	–7
2	–2	41	–29	–12	–9	8
3	68	–8	–1	–15	–7	0

The reef flat of transect 3, characterized by high cover of living corals, low algal cover, and the lowest concentrations of ammonium and nitrate + nitrite, can be considered as the location least affected by land-based nutrification. In contrast, transect 1 exhibited the highest abundance of dead coral, highest algal cover, and high concentrations of ammonium and nitrate + nitrite. The reef flat sites of transect 2 did not group together (Fig. 2). The inner reef flat exhibited community structure and water quality comparable to those found on the reef flat of transect 3. The outer reef flat of transect 2 was distinguished from the other sites by the highest maximum concentrations of all nutrients, but the apparent degradation of the benthic communities was lower at this site than on transect 1. The reef flat on transect 2 was interrupted by many grooves that favor rapid water exchange and may therefore not experience prolonged residence of nutrient-enriched flows. Cuet et al. (1988) suggested that comparable nutrient inputs may have more severe impact on benthic communities in the northern zone of the reef where the reef flat is almost continuous, than in the southern part drained by a spur-and-groove system. Our study revealed that macroalgae-dominated communities were restricted to transect 1. This area, located in the northern part of the reef, is subjected to the influence of major SGD along the shoreline, and receives nutrient-enriched waters in northerly currents generated by the Hermitage pass (Montaggioni et al. 1993).

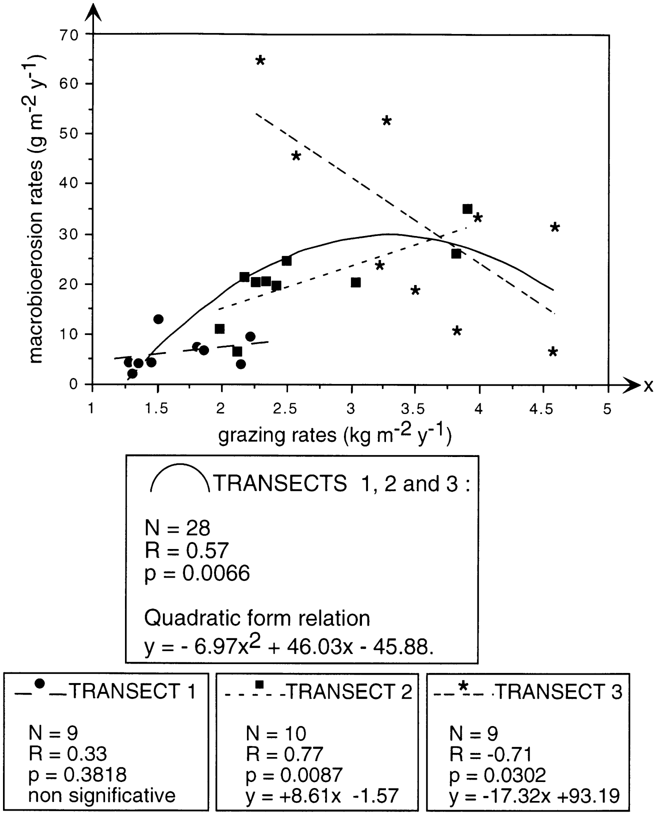

Fig. 7 Graph of quadratic relation between grazing and macroboring rates estimated on each experimental substratum (total number = 28), and linear regressions calculated for blocks on each transect

In our study, algal cover was positively correlated with nutrient concentrations, particularly with ammonium and nitrate + nitrite values (Table 2). The decrease in percent coverage by living corals and the development of macroalgae in areas enriched by nutrients had already been observed throughout the reef between 1985 and 1987 (Cuet et al. 1988; Montaggioni et al. 1993), and more recently on other areas of the Saint-Gilles/La Saline fringing reef (Mioche and Cuet 1999). The convergence of these results provides evidence that a long-term relationship exists between nutrient availability and degradation of La Saline coral communities. Some other communities have not exhibited this relationship. During a fertilization experiment, on the Great Barrier Reef, no significant change of algal and coral cover was observed (Koop et al. 2001). We suggest that the relatively short period of fertilization (2 years) in this experiment explains the lack of response in benthic cover. This hypothesis is supported by the fact that variations in macroalgal and/or coral covers have been reported on reefs subjected to nutrient enrichment for at least 15 years (Smith et al. 1981; Tomascik and Sander 1987a, 1987b). On La Saline reef, the first obvious reduction of coral cover and the expansion of fleshy algae were not reported before 1983, whereas, nutrient inputs have been known to affect reefal waters since the 1970s (Naim 1993). Since the addition of nutrients has been shown to increase coral mortality and to reduce the fertilization and settlement rates of several species of scleractinian corals (Tomascik 1991; Ferrier-Pagès et al. 2000; Ward and Harrison 2000; Koop et al. 2001), a decrease in coral cover is to be expected in the long term.

While the effects of ambient nutrient concentration on benthic cover may require several years to become manifest in natural communities, our study has shown that new dead coral surfaces, represented here by the experimental blocks, exhibit different types of cover after just 1 year of exposure. Widespread cover by the crustose coralline *Hydrolithon onkodes* and by the phaeophyte *Lobophora variegata* developed rapidly in the area that has been most affected by SGD (transect 1), while algal turfs constituted the predominant cover of dead coral substrata in less affected areas (Fig. 3). Before the 1980s, the phaeophytes were extremely scarce on La Saline reef, and high coverage by macroalgae was first recorded at the beginning of the 1980s (Naim 1993). In 1992 (this study), *Lobophora variegata* alone was responsible for covering between 60 and 80% of reef substratum on transect 1, and colonizing up to 71% of the surface of experimental blocks.

The highest cover of macroalgae on this reef is generally recorded during the hot season, and the lowest cover during the cool season (Naim 1993). The cover of *L. variegata* during our study is high even though it was measured during the cool season (June–August). Because this phaeophyte is firmly attached to the substratum, it appears to have remained in place even after death (in situ observations), resulting in year-round biomass.

Abundant macroalgae in areas enriched in nutrients, and algal turfs and calcified algae predominant on unaffected reefs have often been reported (Smith et al. 1981; Littler et al. 1992; Montaggioni et al. 1993; Naim 1993; Delgado and Lapointe 1994; McCook 1999; Russ and McCook 1999). Exceptions can be found in the literature, however. For example, dense algal turfs colonized experimental blocks placed at the polluted site of Faaa (Tahiti, French Polynesia) after exposure periods of 6 months (Peyrot-Clausade et al. 1995b) and 2 years (Pari et al. 1998). The high density of algal turf at Faaa has been correlated with large numbers of sea urchins and extremely high grazing rates (Pari et al. 1998). Reduced herbivory can also lead to macroalgal dominance (McClanahan et al. 1999; McCook 1999).

Bioerosion

The sea urchin *Echinometra mathaei* appears to be the main agent of grazing bioerosion on La Saline reef. The good correlation between the densities of this echinoid and the rates of grazing estimated from experimental blocks supports this hypothesis. The lowest grazing rates and the lowest sea urchin density were recorded in the area of reef receiving the most SGD (transect 1) and having the lowest live, hard coral cover. The highest rates and highest urchin density were found in the least-affected area (transect 3). Birkeland (1987) and Smith et al. (1981) suggested that herbivorous fishes and echinoids would be less numerous in areas exposed to high levels of eutrophication. Our observations on La Saline reef confirmed that echinoids were rare in the most nutrified areas.

In contrast to this pattern, Pari et al. (1998) found high grazing rates (6.87 ± 2.16 kg $CaCO_3$ m^{-2} $year^{-1}$) associated with an extremely high sea urchin density (210 ± 60.4 ind. m^{-2}) at the polluted site of Faaa (Tahiti, French Polynesia). Both reefal waters and sediments at Faaa are polluted by chemicals, and the reef is subjected to large inputs of terrigenous sediments (Fraizier et al. 1985; Pari et al. 1998). Sediment loading is very low on La Saline fringing reef (Naim 1993) and pollutants other than nutrients have never been recorded. Different types of pollution and different algal assemblages (coralline and macroalgae at La Saline and dense algal turfs at Faaa) could explain the differences observed in bioerosion rates between these two sites. Kiene (1997) found nutrients to have no effect on grazing rates during the ENCORE enrichment study at One Tree Reef, Great Barrier Reef, where grazers are all herbivorous fish or gastropods (Kiene 1997). Grazing on Reunion reefs is dominated by sea urchins.

Organically polluted waters are favorable to filter and detritus feeders, which include many macroborers: sponges, sabellid and spionid polychaetes, sipunculans, and bivalves (Risk and MacGeachy 1978; Brock and Smith 1983; Sammarco 1996). High rates of coverage by the sponge *Cliona inconstans* in the back-reef zones of La Saline reef have been related to an increase of organic matter in reefal waters (Cuet et al. 1988). Boring sponges and bivalves were not found in our blocks. Experimental substrata must be exposed for several years before these macroborers can settle (Kiene and Hutchings 1994; Chazottes et al. 1995; Kiene 1997; Pari et al. 1998). The lowest values of macroborer density and macroboring rates were recorded in the area with the greatest nutrient inputs (transect 1). This result should be treated with caution because our experiment was so short. Boring sponges and bivalves are the major agents of internal bioerosion, and previous studies have shown that rates of boring by these organisms are elevated in areas enriched in nutrients and suspended organic matter (Rose and Risk 1985; Risk et al. 1995).

Little is known about the response of microendoliths to nutrient fluctuations. Kiene (1997) found significant differences in microboring rates during the ENCORE enrichment study but suggested that the variations might have been more related to hydrodynamic conditions than to nutrient treatments. In our study, the lowest microboring rate (43.78 g m^{-2} $year^{-1}$) was found on the non-degraded site (transect 3). This value is very close to the highest microboring rate recorded at One Tree Reef by Kiene (43.33 g m^{-2} $year^{-1}$).

Relationships between epilithic communities and bioerosion

Herbivores, including scarids (parrotfishes) and urchins, have a major impact on the distribution of benthic algae. Under intense fish or urchin grazing, reefs are dominated by filamentous algal turfs and few macroalgae (Morrison 1988; Steneck 1988). Turfs are consumed by grazers, but they recover from herbivory due to rapid growth and regeneration (Steneck 1988). Our results demonstrated that the proportion of epilithic surface covered by algal turfs increased with increasing grazing pressure (Table 6). Dense turfs and high grazing rates were found to be characteristic of the area least affected by SGD (Fig. 6, Table 7). In their study, Pari et al. (1998) found the same type of relationship at a polluted site in French Polynesia. This suggests that the cover of algal turfs is controlled more by grazing than by nutrient availability.

Several experimental studies have revealed that exclusion from or reduction in grazing can lead to increases in macroalgal abundance (Scott and Russ 1987; Hackney et al. 1989). Some benthic algae are known to develop strategies for surviving herbivory and therefore they may limit grazer activity. For example, crustose corallines have calcified thalli and morphology that are less attractive to grazers, and some fleshy algae possess chemical defenses that deter herbivores (Morrison 1988; Steneck 1988; Hay 1996).

Such relationships could explain the paucity of grazing echinoids that we observed on the reef flat of transect 1, where crustose corallines and *Lobophora variegata* covered between 60 and 80% of reef substratum in 1992 (Chazottes 1996). The absence of *Echinometra mathaei* has been noted in other disturbed areas of Saint-Gilles/La Saline reef (Conand et al. 1998; Mioche and Cuet 1999). Our results from experimental blocks showed a significant decrease of grazing intensity with increasing cover by corallines and phaeophytes (Table 6). All but two of the blocks from transects 1 and 2 revealed low rates of grazing and high algal cover, with the most extreme values generally found on transect 1 (Fig. 6). For unknown reasons, sea urchins are now very uncommon on degraded sites all over the La Saline reef (Conand et al. 1998; Mioche and Cuet 1999), but during the 1970s, they were abundant at our study sites (Naim 1993). If some areas of La Saline reef are undergrazed now, it was not the case when increases in algal cover began to occur at the beginning of the 1980s.

Comparable densities of sea urchins occurred at sites 2B and 3B (5.9 and 6.9 ind. m^{-2}, respectively), as did grazing rates (2.8 and 2.9 kg m^{-2} $year^{-1}$, respectively). However, no fleshy alga colonized the blocks located at 3B, while cover by phaeophytes averaged 16.4% at 2B and reached 45% on one block. From these results, we conclude that the cover of *Lobophora variegata* is controlled more by nutrient availability than by grazing.

Macroboring rates were found to be positively correlated with algal turf cover and negatively correlated with cover of *Lobophora variegata*. A negative relationship with coralline cover was not statistically significant (Table 6). As suggested by MacGeachy (1977) and by Bromley (1978), encrusting organisms may protect the underlying substrate from borers. In addition, the dense growth forms of coralline algae generally found in exposed environments, such as La Saline fringing reef, are especially detrimental to boring sponges, polychaetes, and sipunculans (Gherardi and Bosence 2001). Our results indicate that algal cover affects the rate of boring by macro-organisms. High macroboring rates characterize the less disturbed areas of La Saline Reef, which have dense algal turfs and few macroalgae (Fig. 6).

The composition of the microborer community was found to differ in relation to the nature of the epilithic colonization. In samples of blocks covered with algal turfs, the endolithic community was largely dominated by the cyanobacterium *Mastigocoleus testarum*. In block samples covered with encrusting algae (corallines and *Lobophora variegata*), the boring cyanobacteria *M. testarum* and *Plectonema terebrans* were found in association with the chlorophyte *Ostreobium quekettii*. *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). In addition, the diameters of *Ostreobium* filaments range between 10 and 60 μm, while filaments of cyanobacteria are much thinner (maximum diameters of 8 and 3 μm for *Mastigocoleus* and *Plectonema*, respectively). These characteristics of *Ostreobium quekettii* (large filaments and deep penetration depth) may explain why the highest microboring rates were found on transects 1 and 2, where the experimental blocks were largely covered with encrusting corallines and phaeophytes. The low microboring rates found on transect 3 may be explained in part by the rarity of the chlorophyte in the experimental substrata, but also by the constant removal of the superficial layers of the substratum due to grazing, especially intense on this transect.

Interaction between bioerosion agents

Interactions between the various agents of bioerosion have been described by several authors. Grazers and microborers are known to act in synergy (Le Campion-Alsumard 1979; Chazottes et al. 1995). Phototrophic microborers penetrate the substrate to their compensation depth and provide a renewable food source for excavating grazers. On the one hand, the phototrophic microborers make the substrata attractive for grazers, and by weakening the superficial substrate layers they facilitate the process of grazing. On the other hand, the constant removal of substrate by grazers extends the depth to which the light can penetrate in the substrate and therefore the depth to which the algae can bore. In conditions of intense grazing, however, the extension of the microborers is not rapid enough to compensate for the rapid removal of the substratum by grazers, such that low microboring rates prevail. Such interactions may explain why the lowest microboring rates were found on blocks from transect 3, which were heavily grazed. In contrast, high microboring rates were found on transects 1 and 2, where grazing pressure was low.

The unpalatable or inedible algae (corallines and *Lobophora variegata*) abundant on these blocks could act as protection for microendoliths by deterring grazers.

Several studies of the interactions between grazers and endolithic macrofauna demonstrate that grazing modifies the development of endolithic communities, and that mature boring communities will be rare where bioerosion by grazers is intense (Risk and Sammarco 1982; Sammarco et al. 1987; Kiene and Hutchings 1994; Risk et al. 1995). On La Saline fringing reef, the relationship found between macroboring and grazing rates is presented under three scenarios of grazing intensity: non-significant on transect 1, significantly positive on transect 2, and negative on transect 3.

Transect 3 on La Saline fringing reef is subjected to intense grazing pressure. Under such conditions, substrata are dominated by filamentous algal turfs and, because of the constant removal by grazers, they provide no protection from predators to boring organisms. This model is supported by the negative correlation between grazing and macroboring rates found on transect 3.

Under moderate grazing levels, some crustose corallines and macroalgae can settle. In such conditions, grazing and epilithic algae both provide, by creating new refuges, protection for the recruitment of macroborers. This model is supported by the positive correlation between grazing and macroboring rates found on transect 2.

In conditions of low grazing rates, as on transect 1, allowing the development of encrusting forms of macroalgae (e.g. *Lobophora variegata* and crustose corallines), no relationship exists between grazing and macroboring intensity. Other factors such as eutrophication exert primary control.

Conclusions

1. Our results suggest that the impact of reef water quality on bioerosion operates through the modification of the epilithic cover on reef substrata.
2. In Reunion Island, increased supply of nutrient in SGD favors the development of macroalgae, while algal turfs remain the main colonizer of dead corals in non-disturbed areas.
3. The extension of macroalgae is favored by low grazing rates encountered now in most of the degraded areas of La Saline reef. However, this reef was heavily grazed when the first depletion of coral communities and extensions of fleshy algae were reported.
4. Grazing rates decrease with increasing cover of crustose coralline algae and of the phaeophyte *Lobophora variegata*.
5. Variations in grazing pressure and in epilithic cover appear to be responsible, in turn, for changes in the composition of microborer communities, and control in part the intensity of internal bioerosion (micro- and macroboring).
6. In healthy reef areas, dead coral substrata are colonized mainly by algal turfs; grazing and macroboring rates are high. In nutrient-enriched areas, cover by macroalgae and crustose corallines is high; grazing and macroboring are reduced, while microborers are protected from removal by grazers.

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