Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northen Great Barrier Reef, Australia

Aline Tribollet, Stjepko Golubic

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Abstract Patterns of bioerosion of dead corals and rubbles on the northern Great Barrier Reef were studied by using blocks of the massive coral *Porites* experimentally exposed at six sites, located on an inshore–offshore profile, for 1 year and 3 years. Rates of microbioerosion by microborers, grazing by fish, and macrobioerosion by filter-feeding organisms were simultaneously evaluated using image analysis. Microbioerosion, grazing, and total bioerosion were lower at reefs near the Queensland coast than at the edge of the continental shelf (1.81 kg m^{-2} and 6.07 kg m^{-2} after 3 years of exposure respectively, for total bioerosion). The opposite pattern was observed for macrobioerosion. Bioaccretion was negligible. These patterns were evident after 1 year of exposure, and became enhanced after 3 years. Microborers were established and were the main agent of bioerosion after 1 year of exposure, and as the principal support for grazing, continued to be the main cause of carbonate loss after 3 years. Full grazing activity and establishment of a mature community of macroborers required more than 1 year of exposure. After 1 year, macroborers and grazers were the second most important agents of bioerosion on both inshore and offshore reefs. However, after 3 years, grazers became the main agents at all sites except at the inshore sites, where macroborers were the principal agents. Because the contribution of microborers, grazers, and macroborers to bioerosion varies in space and time, we suggest that the estimation of reef carbonate budgets need to take in account the activities of all bioerosion agents.

Keywords Total bioerosion · Microbioerosion · Cross-shelf patterns · Great Barrier Reef · Carbonate budget

A. Tribollet (✉)
Centre d'Océanologie de Marseille,
UMR CNRS 6540, Université de la Méditerranée,
Station Marine d'Endoume, rue de la batterie des Lions,
13007, Marseille, France
E-mail: aline@hawaii.edu

A. Tribollet
58 rue Victor Hugo, 37540, St Cyr/Loire, France

S. Golubic
Department of Biology, Boston University,
5 Cummington Street, Boston, MA 02215, USA

Introduction

Coral reefs are among the most complex and dynamic marine ecosystems. Healthy coral reefs are maintained by a balance between forces contributing to reef construction, primarily growth of corals and coralline algae, and reef destruction, essentially due to the agents of bioerosion (Scoffin et al. 1980; Hutchings 1986; Glynn 1997). The existence of barrier reefs and atolls demonstrate the capacity of healthy coral reefs to maintain a positive net growth, which was historically able to keep up with rising sea levels. There is increased evidence that some coral reefs are presently loosing their integrity, and that the balance is shifting in favor of destructive forces (Kiene 1988; Glynn 1997; Pari et al. 1998; Edinger et al. 2000). Factors such as eutrophication (Tomascik and Sander 1987; Szmant 2002), terrestrial runoff (Rogers 1990; Edinger et al. 2000), overfishing (Szmant 2002), rising pCO_2 (Langdon et al. 2000), and rising sea surface temperature (Mumby et al. 2001) are currently contributing to a rise of coral mortality and an accelerated degradation of coral reef structures (Wilkinson 2000). These conditions threaten the very survival of the reef ecosystem, as well as the coastal and insular human communities protected by the coral reefs (see Wilkinson 2000).

A large body of research concerned with the health and functioning of coral reef ecosystems concentrates on coral growth rates (Barnes and Lough 1992; Lough and Barnes 1997) and factors affecting coral growth including detrimental affects such as bleaching (Mumby et al.

2001), coral diseases (Antonius and Lipscomb 2001; Cervino et al. 2001) and coelenterate predation (Pratchett 2001). Some of these effects are reversible, others are detrimental to corals and often measured in terms of coral mortality index (Gomez et al. 1994). As a consequence, large areas of coral reefs become degraded with growing areas of dead coral rock and rubbles, leaving a reduced coverage of live corals (Edinger et al. 2000). Recently, Edinger et al. (2000) argued that coral growth rates (vertical extension) alone are poor indicators of coral reef health, especially for reefs threatened by eutrophication and sedimentation simultaneously. They suggested that reef health is best considered at the scale of whole reef growth and its carbonate budget (bioaccretion−bioerosion).

Research on bioerosion and other destructive forces affecting coral reefs is equally important but has received less attention. Bioerosion is the main destructive force (Scoffin et al. 1980) that modifies reef growth (Stearn and Scoffin 1977), contributes to local sediment production (Hutchings 1986; Conand et al. 1997), and thereby enhances biodiversity of the reef (Hutchings 1986; Moran and Reaka-Kudla 1988). Bioerosion takes place in substrates under live coral (Le Campion-Alsumard et al. 1995; Risk et al. 1995) and under live coralline algal crusts (Tribollet and Payri 2001), but it becomes intensified on dead substrates, that is, substrates not protected from biofouling by live tissues (Hutchings 1986; Tribollet et al. 2002). As the rate of coral mortality increases, so does the area exposed to intensified bioerosion.

Bioerosion on coral reefs consists of the following interacting components: (1) microbioerosion by euendolithic (Golubic et al. 1981) cyanobacteria, algae, and fungi, (2) grazing by gastropods, echinoids, and fish, and (3) macrobioerosion by sponges, worms, and bivalves. Each of these components of bioerosion is the subject of numerous studies that assessed the conditions in natural settings or by measuring bioerosion rates on experimentally exposed substrates, but only a few focussed on interrelations among all the three components simultaneously. For example, microboring rates were studied in sediment grains by Tudhope and Risk (1985), in oyster shells by Mao Che et al. (1996), and in live and dead coralline algae by Tribollet and Payri (2001). Grazing rates were assessed by Bak (1990) and Peyrot-Clausade et al. (2000). Macroboring rates under live corals were studied by Sammarco and Risk (1990), Risk et al. (1995), Edinger et al. (2000), and Holmes et al. (2000) in relation to eutrophication. The interaction between microbioerosion and grazing was studied by Schneider and Torunski (1983), between micro- and macrobioerosion by Zubia and Peyrot-Clausade (2001), and between macrobioerosion and grazing by Kiene and Hutchings (1992, 1994), Reaka-Kudla et al. (1996), and Pari et al. (1998).

Simultaneous assessment of all the three components of bioerosion was carried out at a local scale and for 1 year or 2 years exposure time, using *Porites* blocks by Chazottes et al. (1995) in Moorea Island, French Polynesia (1995) and Reunion Island, Indian Ocean (2002). Tribollet et al. (2002) analyzed microbioerosion, grazing, and macrobioerosion for a year in the large-scale setting of this study on the continental shelf of the northern Great Barrier Reef (GBR), Australia. These studies demonstrated the importance of the integration of all components of bioerosion in the quantification of total bioerosion rates. The present contribution evaluates the temporal progression in bioerosion rates and patterns at the same GBR sites over 3 years of exposure and provides data that will be useful for the estimation of whole reef carbonate budgets.

Materials and methods

Area of study

Six sites were selected near either end of a 200-km-long inshore–offshore profile of the northern Great Barrier Reef (GBR; Fig. 1). These sites include two inshore reefs: Snapper Island and Low Isles, and four reefs located near the edge of the continental shelf: Lizard Island, Harrier Reef, Ribbon Reef N°3, and Osprey Reef, which are considered here as offshore reefs (described in Tribollet et al. 2002). The inshore reefs on the GBR, such as at Snapper Island and Low Isles, are surrounded by nutrient-enriched turbid waters (Johnson and Carter 1987; Bell 1991; Furnas 1996). The waters at Lizard Island are much less influenced by the land (Ikeda et al. 1980; Wolanski 1994, Furnas 1996). Harrier Reef and Ribbon Reef N°3 on the barrier reef and Osprey Reef in the Coral Sea, are surrounded by clear and oligotrophic waters (Bell 1991).

Sampling design and sample treatment

Forty-eight experimental blocks (8 cm×8 cm×5 cm) were cut from the interior of live heads of the massive coral *Porites* sp. using a band saw. The live heads were collected at Snapper Island and Lizard Island in shallow waters. Massive *Porites* was used because the genus is abundant on the GBR, and skeleton of dead *Porites* is a natural habitat for microbial endoliths. Extrapolations from rates of erosion measured for one specific substrate such as massive *Porites* to coral reefs as a whole have limitations as it has been shown that rates vary largely between substrates (Risk et al. 1995; Mao Che et al. 1996; Holmes et al. 2000; Tribollet and Payri 2001; Schönberg 2002). However, *Porites* skeletons have been used in other bioerosion studies (Kiene and Hutchings 1992, 1994; Chazottes et al. 1995, 2002), thus allowing for comparison of the results. The blocks showing evidence of previous bioerosion were discarded. Each block was soaked in fresh water and then dried and its initial dimensions were measured. The density of *Porites* heads from which blocks were cut was also measured (see Tribollet et al. 2002). Eight randomly chosen experimental

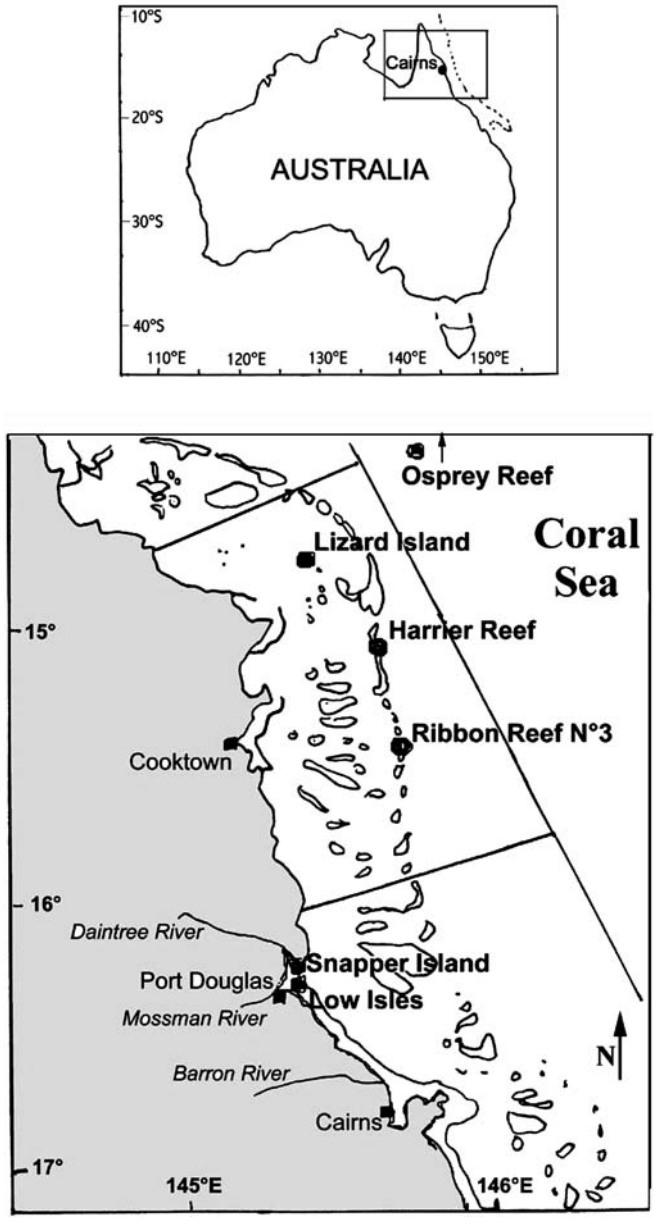

Fig. 1 Study sites in the northern GBR (Australia). From the northern coast of Queensland to the Coral Sea: inshore sites—Snapper Island and Low Isles; mid-shelf site—Lizard Island; outer barrier sites—Harrier Reef and Ribbon Reef N°3; oceanic site—Osprey Reef. The last four sites were considered in this study as offshore reefs as opposed to the inshore reefs

blocks were attached to 1-m×1-m steel grid. Two such grids were mounted on dead coral substrates in September 1996 at each of the selected sites (habitats described in Tribollet et al. 2002), at a distance of 3–5 m to each other and at a depth of 7–10 m. Two blocks per grid were randomly collected in September 1997 and 1999, thus after 1 year and 3 years of exposure.

The collected blocks were preserved in a buffered 7% solution of formaldehyde in seawater and later cut in half with a band saw. One half was used to determine macroboring organisms, while the other half was cut in four 7-mm-thick slices (see Tribollet et al. 2002). Three slices per block were used for quantification of the rates of bioerosion and bioaccretion; each slice allowing one measure of bioerosion and bioaccretion (the slice with anchoring bolt was discarded). No attempt was made to separate biological erosion processes from associated but negligible physical loss of weakened structures (ex: saltation).

The quantification of microbioerosion was approached in two ways. SEM images of the exposed surface of the block were evaluated by Visilog 5.1 (Noesis Co.) to obtain the surface removed by microborers. The depth of microboring penetration was measured from petrographic thin section cut perpendicular to the exposed block surface to obtain the volume of carbonate removed by microborers (see Tribollet et al. 2002). Grazing, macroboring, and bioaccretion rates were measured using NIH-image software (http://rsb.info.nih.gov/nih-image/) and Adobe Photoshop 5.0. These methods were introduced in the present paper and the earlier published data were recalculated according to improved imagery. Micro- and macroboring rates were quantified here as ''residual'' on the basis of the block volume that remained after grazing (for definition, see Chazottes et al. 1995). The participating macroboring organisms were identified by groups on the basis of shapes and sizes of their excavations (Fig. 2). The relative proportion of each group (sponges, worms, and bivalves) was evaluated separately on the basis of the projected surface area of their boreholes and expressed as percent values. The projected bioeroded surface area (or the projected surface area covered by encrusting calcareous algae) on each vertical slice was measured by NIH image analysis and the volume of eroded (or added) carbonate was calculated from the measured thickness of each slice.

The amounts of carbonate removal were calculated from the initially obtained density values for each block. Bioaccretion values were obtained using a density of 1.26 g cm^{-3} for calcareous algae (Laubier 1962). Microboring, grazing, macroboring, and bioerosion rates were expressed in percent of $CaCO_3$ removed per block. All values were extrapolated from the experimental blocks and expressed as kg of removed or added $CaCO_3$ per m^2 of total exposed surface area of block (exposed surface of the six sides) and per year (kg m^{-2} $year^{-1}$). The cumulative rates were also quantified (kg per m^2 of exposed surface area of block after 1 year and 3 years of exposure). Bioerosion or total bioerosion rates were calculated for each block as the sum of microbioerosion, grazing, and macrobioerosion. The role played by each agent in bioerosion was also expressed in percentage. Net bioerosion rates were determined from bioerosion minus bioaccretion.

Statistical analyses

Data sets were tested for normality and homoscedasticity using frequency histograms and Cochran's test

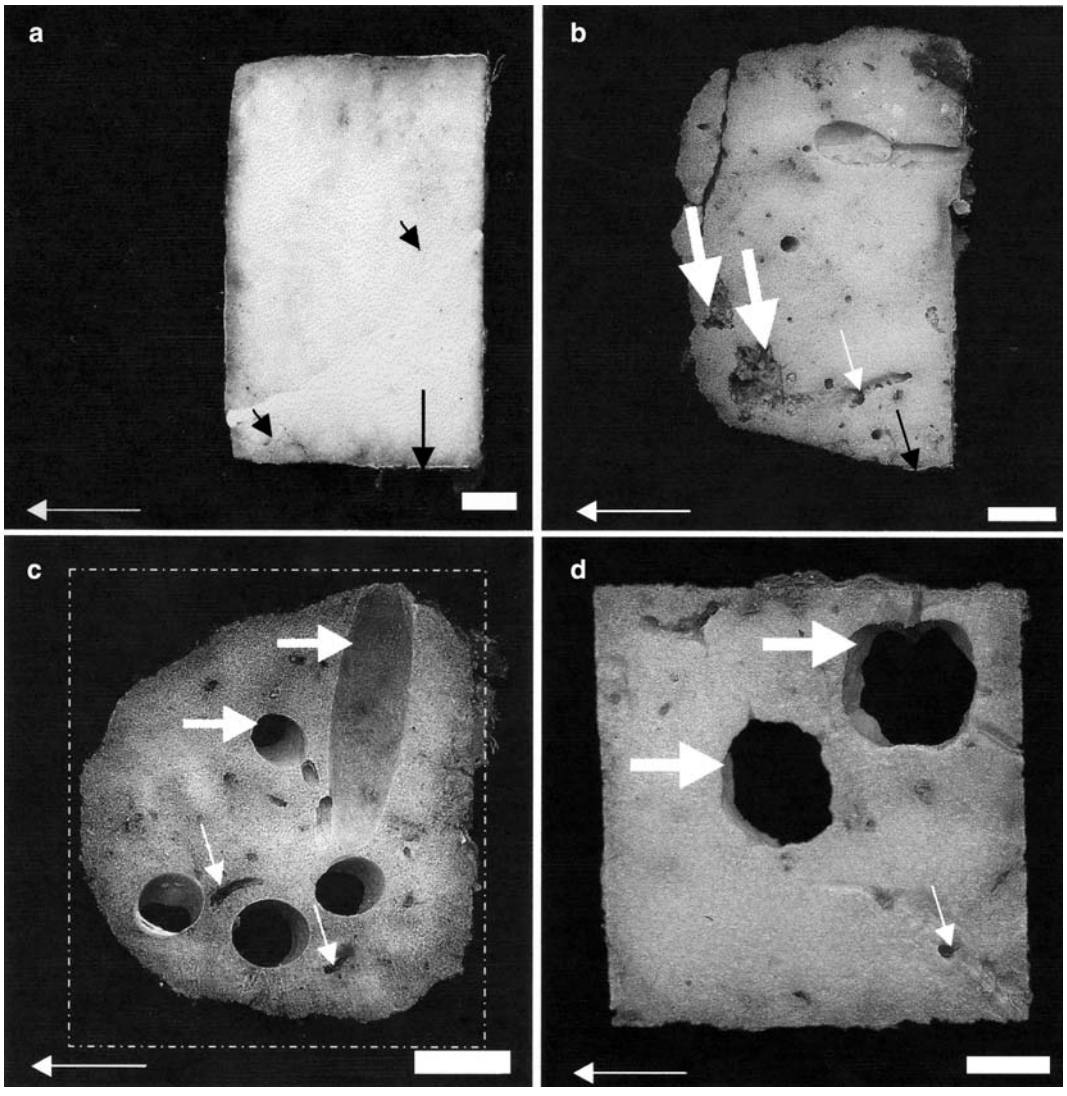

Fig. 2 Scanned slices of dead coral blocks exposed for 1 year (**a**) and 3 years (**b, c, d**) to colonization. The *arrow* at the bottom in the left corner of each picture indicates the block orientation to the water surface. **a**. Block from Ribbon Reef N°3 exhibiting worm boreholes (*short arrow*) and encrusting calcareous algae (*long arrow*). **b**. Block from Harrier Reef (outer barrier reef) showing traces of boring worm (*narrow white arrows*) and sponges (*large white arrow*). Sponge traces were attributed to *Cliona* sp.. The *black arrow* indicates an encrusting calcareous alga. **c**. Block from Ribbon Reef N°3 (outer barrier reef) exhibiting traces of boring worms (*narrow arrow*) and bivalves (*wide arrows*). The *dotted lines* show the initial dimensions of the block. **d**. Block from Low Isles (inshore reef) exhibiting traces of boring worm (*narrow arrow*) and sponges (*wide arrows*). Sponge traces were attributed to *Aka* sp.. The scale bar is 1 cm

(Sachs 1984). All bioerosion and bioaccretion analyses were transformed by $\log(x + 0.01)$ prior to analysis for purposes of normalization (Dagnelie 1970). A series of three-way nested analyses of variance (ANOVA) with equal or unequal sample size was carried out to investigate the variation of microbioerosion, grazing, macrobioerosion, bioaccretion, and net bioerosion data: among blocks of a grid, among grids within a site, and among sites (Sokal and Rohlf 1969). A series of two-way ANOVA tests (cross-classification) was employed to investigate the effects of site and length of exposure on the different rates of bioerosion. After each ANOVA, multiple comparisons of means according to the SNK test (Sokal and Rohlf 1969) were used to identify which sites were significantly different from each other. In both sets of ANOVA tests, the mean and standard error of rates of microboring ($n = 40$), grazing ($n = 3$), macroboring ($n = 3$), bioaccretion ($n = 3$), and net bioerosion ($n = 3$) were used for each block. A series of Spearman's tests ($\alpha = 0.05$ Scherrer 1984) was also conducted to correlate all measured variables after 1 year and 3 years of exposure. The statistics were carried out using the software packages Super Anova 1.11(1991) and Statview 5.0 (1998).

Results

The rates of bioerosion of exposed blocks were measured separately for the main biological agents: micro-

borers (euendolithic cyanobacteria, algae, and fungi), grazers (mainly scarid fish), and macroborers (sponges, polychaete and sipunculid worms, and bivalves). Rates of bioaccretion were measured only for encrusting coralline algae. Data are presented for 1 year and 3 years of exposure, comparing six sites on a coast-to-offshore profile across the GBR, Australia. The three-way nested ANOVAs followed by SNK tests revealed that microbioerosion, grazing, and total bioerosion varied significantly among sites. This distinction was not expressed for macrobioerosion during the first year of exposure, but became established after 3 years. No significant differences within sites were shown for any of the measured bioerosion rates, although differences among blocks within a grid were significant, indicating a patchy distribution of the erosional impacts at the block level (Table 1).

Microboring rates

Microbial endolith community became fully established after 1 year of exposure and did not change qualitatively after 3 years. The dominant microborers, responsible for carbonate removal from the exposed surfaces of the block were the chlorophyte *Ostreobium quekettii* and the cyanobacteria *Plectonema terebrans* and *Mastigocoleus testarum*. Euendolithic fungi were also abundant. A SNK test showed that microbioerosion was lower at the inshore sites than at the offshore sites. At Snapper Island, $0.58 \pm 0.02\%$ of $CaCO_3$ was removed from the experimental blocks by microborers. Extrapolated from the block surfaces, this was equivalent to about 0.13 ± 0.005 kg $CaCO_3$ m^{-2} $year^{-1}$. The highest rate of microboring was found at the oceanic site, Osprey Reef, with $5.26 \pm 0.19\%$ of carbonate

Table 1 Three-way nested ANOVA of $\log(x + 0.01)$ transformed rates of microboring, macroboring, grazing, total bioerosion, and bioaccretion after 1 and 3 years of exposure at six sites from the northern coast of Queensland to the Coral Sea

Source of variation	df	*MS*	*F*	*P*
Microbioerosion after 1 year of exposure				
Site	5	25.69	13.13	0.004**
Grid (site)	6	1.96	1.56	0.24NS
Block (site, grid)	12	1.26	64.02	0.0001***
Residual	976	0.02		
Microbioerosion after 3 years of exposure				
Site	5	11	4.70	0.043*
Grid (site)	6	2.44	1.05	0.44NS
Block (site, grid)	12	2.32	225	0.0001***
Residual	936	0.01		
Macrobioerosion after 1 year of exposure				
Site	5	0.83	2.97	0.11NS
Grid (site)	6	0.28	1.20	0.37NS
Block (site, grid)	12	0.23	8.70	0.0001***
Residual	42	0.03		
Macrobioerosion after 3 years of exposure				
Site	5	1.32	5.07	0.04*
Grid (site)	6	0.26	0.54	0.77NS
Block (site, grid)	12	0.49	7.32	0.0001***
Residual	48	0.07		
Grazing after 1 year of exposure				
Site	5	5.42	38.50	0.0002**
Grid (site)	6	0.14	0.87	0.54NS
Block (site, grid)	12	0.16	2.36	0.02*
Residual	42	0.07		
Grazing after 3 years of exposure				
Site	5	0.91	9.38	0.01**
Grid (site)	6	0.10	1.59	0.23NS
Block (site, grid)	12	0.06	6.22	0.0001***
Residual	48	0.01		
Total bioerosion after 1 year of exposure				
Site	5	30	23.46	0.0007***
Grid (site)	6	1.27	0.68	0.67NS
Block (site, grid)	12	1.86	172.1	0.0001***
Residual	42	0.01		
Total bioerosion after 3 years of exposure				
Site	5	2.93	6.43	0.02*
Grid (site)	6	0.46	0.54	0.77NS
Block (site, grid)	12	0.83	2.96	0.004**
Residual	48	0.28		

df degree of freedom, *MS* mean square, *F* Fisher's index, *P* Greenhouse-Geisser corrected probability, *NS* = $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

removed, that is, 1.35 ± 0.05 kg $CaCO_3$ m^{-2} $year^{-1}$. Intermediate rates were found at Low Isles (0.16 ± 0.013), Ribbon Reef N°3 (0.36 ± 0.014), Lizard Island (0.70 ± 0.055), and Harrier Reef (0.75 ± 0.032; Table 2). The SNK test pooled data from Lizard Island and Harrier Reef (see Table 2).

The general increase of microboring rates from the coast toward the Coral sea remained expressed after 3 years of exposure (Fig. 3), with the lowest values for Snapper Island, with 0.23 ± 0.006 kg $CaCO_3$ m^{-2} removed after 3 years (corresponding to a rate of 0.08 kg $CaCO_3$ m^{-2} $year^{-1}$) and the highest values for Harrier Reef (1.42 ± 0.065 or 0.47 kg m^{-2} $year^{-1}$) and Osprey Reef (1.29 ± 0.059 or 0.43 kg m^{-2} $year^{-1}$). The latter two sites were pooled by the SNK test, as were data for Lizard Island and Ribbon Reef N°3 (see Table 2).

Grazing rates

Only teeth marks of scarid fish were observed on the outer surface of blocks, indicating that they were probably the primary grazers of exposed blocks. The SNK test showed two groups of sites and an increase of grazing from the coast to the ocean (Fig. 3). Snapper Island and Low Isles, the two inshore sites, exhibited the lowest mean grazing rate of 0.007 ± 0.001 kg m^{-2} $year^{-1}$. The four offshore sites showed higher rates ranging between 0.32 ± 0.04 at Lizard Island and 0.77 ± 0.22 kg m^{-2} $year^{-1}$ at Ribbon Reef N°3 (Table 2). The mean grazing rate for the offshore group was 0.53 ± 0.13 kg m^{-2} $year^{-1}$ (2.9 ± 0.72% of $CaCO_3$ removed per block).

After 3 years of exposure, the trend of increasing grazing pressure from the inshore to the offshore sites was enhanced. The SNK test now grouped the data into three groups of sites (Fig. 3). The lowest rates still characterized the inshore sites, Snapper Island and Low Isles, averaging 0.25 ± 0.064 kg m^{-2} for the 3 years or 0.08 kg $CaCO_3$ m^{-2} $year^{-1}$ (1.38 ± 0.36% of $CaCO_3$ removed per block in 3 years), whereas the highest rates were recorded for Ribbon Reef N°3 and Osprey Reef of 4.80 ± 0.89 kg m^{-2} on the average or 1.6 kg m^{-2} $year^{-1}$ (27.10 ± 5.03% of $CaCO_3$ removed per block in 3 years). Lizard Island and Harrier Reef formed an intermediate group with an average rate of 1.30 ± 0.16 kg m^{-2} or 0.43 kg m^{-2} $year^{-1}$ (Fig. 3, Table 2).

Macroboring rates

After 1 year of exposure, macrobioerosion was mainly due to worms (sipunculids and polychaetes) and a few juvenile bivalve molluscs. Only at Snapper Island, macrobioerosion resulted from worms, bivalves, and sponges (Table 3). The three-way nested ANOVA showed no significant differences among sites (Table 1). Rates of macroboring varied between 0.01 ± 0.003 kg m^{-2} $year^{-1}$ at Low Isles and 0.13 ± 0.014 kg m^{-2} $year^{-1}$ at Snapper Island (Fig. 3; Table 2). The mean macroboring rate for the six sites was 0.05 ± 0.023 kg m^{-2} $year^{-1}$, derived from 0.26 ± 0.11% of $CaCO_3$ removed per block.

After 3 years of exposure, the same groups of macroboring organisms were present. The boring sponges increased in frequency and in area of occupancy. The contribution of boring bivalves increased, because of their abundance and individual size increase (Fig. 2, Table 3). Significant differences among sites were highlighted by the three-way nested ANOVA (Table 1). The SNK test showed two groups of sites (Fig. 3). One group of sites comprised of Snapper Island, Low Isles, and Harrier Reef which exhibited the highest mean rate of macroboring of 0.83 ± 0.214 kg m^{-2} after 3 years of exposure or 0.28 kg $CaCO_3$ m^{-2} $year^{-1}$ (4.87 ± 1.26% of $CaCO_3$ removed per block after 3 years) with the participation of all groups of macroborers (Table 3).

Table 2 Amount of calcium carbonate removed by the boring micro-flora, grazers, macroborers, and all agents, from exposed surfaces of coral blocks (kg m^{-2}) after 1 year and 3 years of exposure at six sites from the northern coast of Queensland to the Coral Sea

Sites	Microbioerosion		Grazing		Macrobioerosion		Total bioerosion	
	1 year	3 years	1 year	3 years	1 year	3 years	1 year	3 years
Snapper Island	0.15 ± 0.006 (0.56 ± 0.020)	0.23 ± 0.006 (0.94 ± 0.023)	0.004 ± 0.001 (0.02 ± 0.003)	0.31 ± 0.061 (1.70 ± 0.318)	0.13 ± 0.014 (0.53 ± 0.078)	0.74 ± 0.147 (4.67 ± 1.152)	0.27 ± 0.04 (1.06 ± 0.15)	1.30 ± 0.13 (7.37 ± 1.05)
Low Isles	0.16 ± 0.006 (0.61 ± 0.022)	0.54 ± 0.017 (2.22 ± 0.074)	0.01 ± 0.003 (0)	0.19 ± 0.066 (1.07 ± 0.378)	0.01 ± 0.003 (0.06 ± 0.023)	1.16 ± 0.318 (6.40 ± 1.721)	0.18 ± 0.02 (0.74 ± 0.10)	1.89 ± 0.32 (9.72 ± 1.69)
Lizard Island	0.71 ± 0.055 (2.77 ± 0.115)	0.89 ± 0.023 (3.54 ± 0.100)	0.32 ± 0.040 (0.02 ± 0.003)	0.97 ± 0.081 (5.41 ± 0.482)	0.11 ± 0.003 (0.57 ± 0.217)	0.37 ± 0.162 (2.03 ± 0.883)	1.09 ± 0.13 (4.72 ± 0.47)	2.26 ± 0.26 (11 ± 1.34)
Harrier Reef	0.76 ± 0.032 (2.68 ± 0.097)	1.42 ± 0.065 (5.34 ± 0.266)	0.36 ± 0.075 (0.02 ± 0.006)	1.64 ± 0.156 (8.58 ± 0.987)	0.02 ± 0.003 (0.11 ± 0.017)	0.59 ± 0.084 (3.11 ± 0.462)	1.22 ± 0.14 (4.70 ± 0.35)	3.60 ± 0.28 (17.58 ± 1.82)
Ribbon Reef-3	0.38 ± 0.014 (1.49 ± 0.057)	0.96 ± 0.040 (3.81 ± 0.155)	0.77 ± 0.222 (0.05 ± 0.014)	5.39 ± 1.085 (30.65 ± 6.155)	0.04 ± 0.009 (0.23 ± 0.046)	0.12 ± 0.029 (0.69 ± 0.170)	1.23 ± 0.29 (5.80 ± 1.12)	6.40 ± 0.99 (34.90 ± 5.90)
Osprey Reef	1.40 ± 0.049 (5.26 ± 0.186)	1.29 ± 0.059 (5.12 ± 0.243)	0.68 ± 0.087 (0.05 ± 0.006)	4.23 ± 0.638 (23.50 ± 3.580)	0.03 ± 0.009 (0.18 ± 0.061)	0.21 ± 0.052 (1.16 ± 0.292)	2.19 ± 0.21 (8.23 ± 0.94)	5.74 ± 0.80 (29.66 ± 3.98)

The percentage of the bioeroded volume of block is presented in parenthesis. Means and standard errors are presented for each site ($n = 160$ for microbioerosion, and $n = 12$ for grazing, macrobioerosion and total bioerosion)

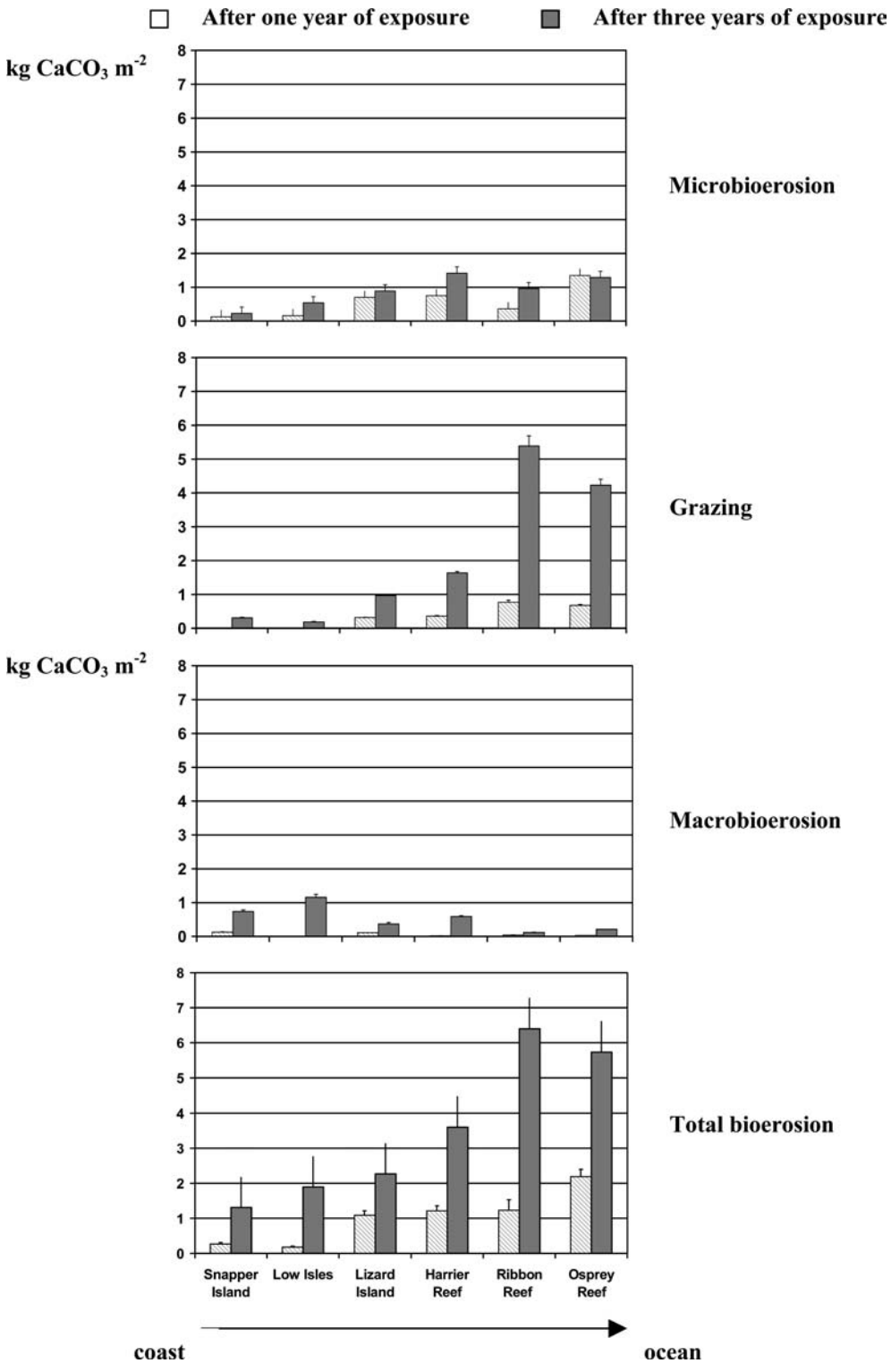

Fig. 3 Histogram presenting spatial and temporal variability of cumulative rates of microboring, grazing, macroboring, and total bioerosion of dead coral blocks exposed for 1 year and 3 years at six sites from the northern coast of Queensland to the Coral Sea. Mean rates are expressed in kg of $CaCO_3$ removed per m^2 of exposed surface area of block after one (*clear grey*) and 3 years of exposure (*dark grey*). The *whisker* represents the standard error

The other group included Lizard Island, Ribbon Reef N°3, and Osprey Reef with a mean rate of macroboring of 0.23 ± 0.101 kg m^{-2} or 0.08 kg m^{-2} $year^{-1}$ ($1.56 \pm 0.61\%$ of $CaCO_3$ removed per block after 3 years). In the latter group of sites, worms played a major role in macrobioerosion process (Table 3).

Bioaccretion rates

In this study, bioaccretion was due entirely to encrusting coralline algae, which showed low rates of colonization and accretion on the experimental blocks. The three-way nested ANOVA did not reveal any significant differences

Table 3 Proportional contribution (%) of the different groups of boring macro-organisms (sponges, worms, mollusc bivalves) to macrobioerosion at six sites from the northern coast of Queensland to the Coral Sea and after 1 year and 3 years of exposure

Sites	Sponges		Worms		Bivalves	
	1 year	3 years	1 year	3 years	1 year	3 years
Snapper Island	22.24 ± 11.64	22.09 ± 10.02	34.52 ± 9.90	33.20 ± 9.32	43.56 ± 10.64	44.71 ± 9.15
Low Isles	0	49.20 ± 13.11	81.60 ± 9.24	30.80 ± 11.15	18.43 ± 9.24	20.02 ± 9.83
Lizard Island	0	20.07 ± 9.51	100	74.80 ± 10.10	0	5.10 ± 3.06
Harrier Reef	0	2.28 ± 2.28	94.50 ± 5.48	87.68 ± 7.11	5.48 ± 5.49	10.04 ± 7.04
Ribbon Reef-3	0	29.40 ± 0.08	100	28.70 ± 9.09	0	41.85 ± 9.06
Osprey Reef	0	18 ± 9.88	92.04 ± 5.83	69.06 ± 11.50	8 ± 5.83	12.90 ± 8.77

Means and standard errors are presented for each site ($n = 12$)

of rates of bioaccretion among sites ($P > 0.2$). After 1 year of exposure, rates were close to zero in all sites, averaging 0.03 kg m^{-2} $year^{-1}$. The rates averaged 0.14 ± 0.04 kg m^{-2} after 3 years.

Bioerosion rates (microbioerosion + grazing + macrobioerosion)

After 1 year of exposure, total bioerosion was mainly due to microborers (their contribution ranging between 61% and 91%, Fig. 4a), except at Snapper Island and at Ribbon Reef N°3. At the inshore site, Snapper Island, macroborers eroded as much material as did microborers. At Ribbon Reef N°3, grazers were the dominant agents (67%) followed by microborers (31%). The SNK test revealed three groups of sites. The two inshore sites exhibited the lowest rates of bioerosion averaging 0.21 ± 0.021 kg m^{-2} $year^{-1}$ or 0.87 ± 0.09% of $CaCO_3$ removed per block (Fig. 3, Table 2). The highest rate was found at the oceanic site Osprey Reef (2.17 ± 0.21 kg m^{-2} $year^{-1}$ or 8.23 ± 0.94% of $CaCO_3$ removed per block). The remaining group (Lizard Island, Harrier Reef, and Ribbon Reef N°3) showed intermediate rates (Table 2).

After 3 years of exposure, the main agents of bioerosion were macroborers (> 57%) at the two inshore sites. At the four offshore sites, grazers were the principal agents of erosion (43–84%) in synergy with microborers (15–39%; Fig. 4b). The SNK test regrouped the sites as follows: Lizard Island was pooled with the two inshore sites, averaging 1.81 ± 0.16 kg m^{-2} after 3 years of exposure or 0.60 kg $CaCO_3$ m^{-2} $year^{-1}$ (9.36 ± 0.81% of $CaCO_3$ removed per block after 3 years, Table 2). Osprey Reef and Ribbon Reef N°3 were pooled and showed the highest rates (average 6.07 ± 0.62 kg m^{-2} or 2.02 kg m^{-2} $year^{-1}$ or 32.28 ± 3.52% of $CaCO_3$ removed per block). The remaining Harrier Reef presented an intermediate rate (3.60 ± 0.28 kg m^{-2} or 1.30 kg m^{-2} $year^{-1}$).

Tests of the duration of exposure versus sites (two-way ANOVAs) showed significant differences between bioerosion rates measured after 1 year and 3 years of exposure, significant differences among the sites (as shown above) and significant interaction between those factors (Table 4). The SNK tests showed that the various annual rates of bioerosion (microboring, grazing, macroboring, and total bioerosion) increased over time at all sites except for microbioerosion at Osprey Reef, where it remained practically constant. The increase for total bioerosion rates was not proportional, but varied from site to site by factors from 2 to 11.

The rates of microboring and grazing were positively correlated over time, whereas the rates of microboring and macroboring were independent (Table 5). The rates of macroboring and grazing appeared to be independent after 1 year, but were negatively correlated after 3 years (Table 5). After 1 year, bioaccretion was positively correlated with grazing and microbioerosion, but no

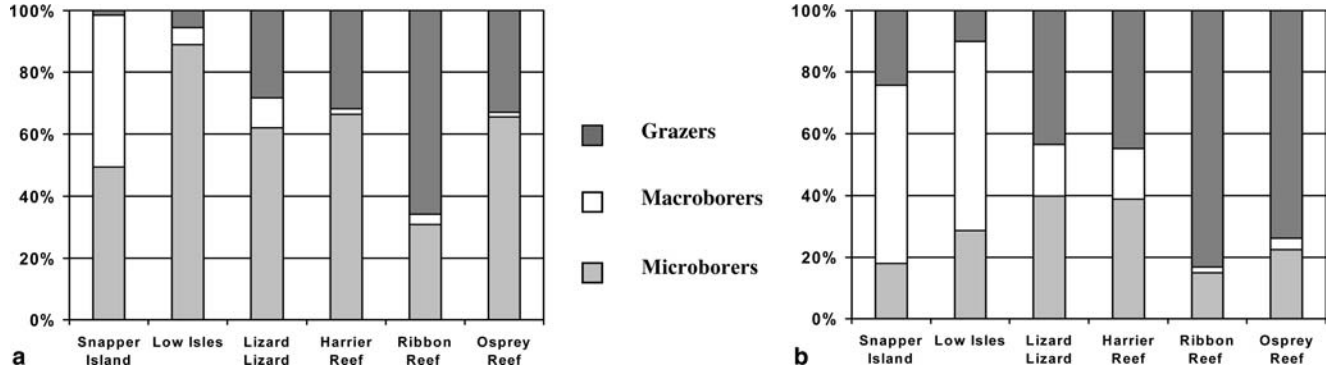

Fig. 4 Relative contribution (%) of microborers, grazers, and macroborers to bioerosion of dead coral blocks at six sites from the northern coast of Queensland to the Coral Sea, after 1 year (**a**) and 3 years (**b**) of exposure

Table 4 Two-way ANOVA of $\log(x + 0.01)$ transformed rates of microboring, grazing, macroboring, and total bioerosion of coral blocks after 1 year and 3 years of exposure at six sites from the northern coast of Queensland to the Coral Sea

Source of variation	df	*MS*	*F*	*P*
Microboring rates				
Time of exposure	1	29.88	597	0.0001**
Sites	5	33.33	666	0.0001**
Time of exposure × site	5	3.28	65.62	0.0001**
Residual	1948	0.05		
Grazing rates				
Time of exposure	1	33.83	226.97	0.0001**
Sites	5	14.7	98.65	0.0001**
Time of exposure × site	5	1.03	6.93	0.0001**
Residual	127	0.15		
Macroboring rates				
Time of exposure	1	24.63	191.73	0.0001**
Sites	5	1.04	8.08	0.0001**
Time of exposure × site	5	1.15	8.95	0.0001**
Residual	125	0.13		
Bioerosion rates				
Time of exposure	1	3.45	196.54	0.0001**
Sites	5	0.64	36.34	0.0001**
Time of exposure × site	5	0.06	3.65	0.004*
Residual	125	0.02		

df degree of freedom, *MS* Mean Square, *F* Fisher's index, *P* Greenhouse-Geisser corrected probability, $*P < 0.01$, $**P < 0.001$

Table 5 Spearman's tests (*R*) of all paired sets bioerosion measures of coral blocks at six sites (pooled) from the northern coast of Queensland to the Coral Sea after 1 year and 3 years of exposure

Sets of variable in pairs	1 year	3 years
Microbioerosion – grazing	0.72 ($P = 0.0005$)S	0.61 ($P = 0.004$)S
Microbioerosion – macrobioerosion	− 0.25 ($P = 0.23$)	−0.12 ($P = 0.57$)
Macrobioerosion – grazing	−0.10 ($P = 0.45$)	−0.41 ($P = 0.05$)S
Microbioerosion – bioaccretion	0.58 ($P = 0.006$)S	−0.03 ($P = 0.89$)
Grazing – bioaccretion	0.63 ($P = 0.002$)S	−0.32 ($P = 0.13$)
Macrobioerosion – bioaccretion	−0.15 ($P = 0.10$)	0.17 ($P = 0.08$)
Microbioerosion – coral skeleton density	−0.23 ($P = 0.26$)	−0.02 ($P = 0.91$)
Grazing – coral skeleton density	−0.68 ($P = 0.004$)S	−0.51 ($P = 0.014$)S
Macrobioerosion – coral skeleton density	0.10 ($P = 0.64$)	0.33 ($P = 0.11$)

R coefficient of correlation, *P* Greenhouse–Geisser corrected probability, *s* means that the test was significant

correlation was expressed after 3 years. There was no correlation between bioaccretion and macrobioerosion. Grazing loss was negatively correlated with the skeletal density of experimental substrates. There was no correlation between skeletal density and micro- or macrobioerosion, although the initial density of the exposed *Porites* coral skeleton varied significantly between coral heads (between 1.15 g cm^{-3} and 1.73 g cm^{-3}; $P = 0.0002$; Tribollet et al. 2002); but not between sites ($P > 0.05$).

Discussion

Record of bioerosion rates over time

Bioerosion under live and growing corals and crustose algae is quantitatively and often qualitatively different from bioerosion on dead carbonate substrates (Le Campion-Alsumard et al. 1995; Risk et al. 1995; Tribollet and Payri 2001). Quantification of rates and progression of bioerosion on experimentally exposed blocks of cleaned coral skeletons is designed to provide a close approximation of processes occurring on dead corals and coral rubbles. The significance of these processes increases as the areas covered by healthy growing corals decreases on degrading reefs. The measured annual rates of bioerosion calculated after 3 years of exposure were significantly and disproportionally higher than those recorded after the first year. The reasons may vary for different organisms and organism groups involved in bioerosion.

Cleaned and newly exposed substrates appear to require an initial time of conditioning, including surface coating by microbial biofilms followed by a succession of epilithic and endolithic microorganisms (Hutchings 1986). The time required for stabilization of the microbioeroding community is probably shorter than that for

grazers and macroborers, which is evident from the comparison of microbioerosion data after 1 year and 3 years of exposure. Grazing patterns show a positive correlation with microbioerosion, because grazing is largely dependent on epilithic and endolithic algal biomass and their growth rates for food (Bruggemann et al. 1994). Conversely, development of microborers depends on grazers as those reduce: (a) the settlement and growth of epilithic organisms, which compete with endoliths for space (Golubic and Schneider 1979) and (b) the shading of endoliths habitat, thus enhancing the growth of phototrophic microborers (Scheinder and Torunski 1983).

The assemblage of macroborers within the block showed a delay in development over a 3-year period. After 1 year of exposure, macroborers were represented mostly by worms at all sites, and the macrobioerosion rates were too low to show any significant trends. After 3 years of exposure, macroborers included larger organisms with longer developmental cycles (e.g. boring sponges and bivalves), indicating that the settlement started with small propagules and the surviving individuals increased multifold in size, enlarging their boreholes in the process. The requirement for several years of exposure before the evaluation of macroborer's contribution to bioerosion has been discussed by several authors (Kiene and Hutchings 1992, 1994; Pari et al. 1998; Chazottes et al. 2002). In our study, larger macroborers were particularly numerous at inshore sites where the grazing pressure was the lowest. The same pattern was repeated at Harrier Reef among the offshore sites, where the higher frequency of endolithic bivalves was coincident with lower grazing pressure. Intense grazing pressure at the offshore sites corresponded generally with a dominance of worms. The inverse relation between grazing pressure and diversification of macrobioeroding community has been documented at a local scale by Sammarco et al. (1987) and Kiene and Hutchings (1994). Kiene (1988), in his study of the GBR, described a similar situation as ''immature reef'', as opposed to a ''mature'' reef where sponges and bivalves were the principal agents of macrobioerosion, grazing pressure was limited and encrustation well developed. Thus, the community of macroborers requires the longest time to become established on experimental blocks.

Bioerosion patterns across the northern Great Barrier Reef

The rates of bioerosion in the present contribution were compared along a 200-km-long inshore–offshore profile on the northern GBR. Microbioerosion rates increase significantly with the distance from the coast. Grazing rates followed the same pattern as a dependent parameter (Fig. 3). In contrast, the macrobioerosion showed the opposite trend of a significant decrease in rates with increased distance from the shore. Total bioerosion followed the trend of microbioerosion and grazing, showing that microborers and grazers were the main agents of bioerosion on the studied profile.

Lower rates of settlement by microbial euendoliths and microbioerosion at the inshore sites, may have been caused by the observed sediment entrapment in the epilithic algal turf and by the resulting light limitation. On the offshore sites, microboring communities were established more rapidly (e.g. the rates at Osprey did not change between the first and the third year of exposure). The inshore–offshore distinction becomes evident after 1 year, and this trend is enhanced after 3 years of exposure. Our rates were 3- to 25-fold higher than those found by Chazottes et al. (2002) at La Reunion after 1 year of exposure (0.04 to 0.07 kg m^{-2} $year^{-1}$). In fact, the data on microbioerosion are difficult to compare without considering grazing pressure. In Chazottes et al. (2002) study, the grazers were mostly echinoids, while they were fish at our sites. Echinoids are the most efficient grazers (Bak 1990; Reaka-Kudla et al. 1996) and thus the measurable microboring activity, that is, the ''residual'' microbioerosion is lower in experimental blocks grazed by echinoids (Chazottes et al. 2002) than in blocks grazed by fish (the present study).

Low rates of grazing on inshore sites may have been caused by food preferences of grazers, as well as by the smaller average size of fish prevalent in coastal waters. Russ (1984) and Bellwood and Choat (1990) showed that scarid fishes are smaller and less abundant at the inshore sites than on the outer barrier reef and in the Coral Sea. After 3 years of exposure, grazing rates were still lower at inshore sites than at offshore sites, following the pattern of microbioerosion. Pari et al. (1998) and Peyrot-Clausade et al. (1999) found important rates of grazing on near-shore sites affected by eutrophication on Tahiti barrier reef, due to the abundance of echinoid grazers. However, the number of echinoids at our sites was negligible (personal observation). Sammarco (1985) showed that the density of echinoids on the GBR is very low (1 m^{-2}) and that their erosive activity can be neglected. This explains why our grazing rates were generally 2- to more than 30-fold lower than those attributable to echinoids as found by Chazottes et al. (1995) at la Reunion Island (1.63–3.52 kg m^{-2} $year^{-1}$), Reaka-Kudla et al. (1996) in Galapagos (22.8 kg m^{-2} $year^{-1}$) and Peyrot-Clausade et al. (1999) at Moorea, French Polynesia (1.74 kg m^{-2} $year^{-1}$). On our profile, intermediate grazing rates found at Lizard Island were probably due to the presence of damselfish (personal observation). Sammarco et al. (1987) demonstrated that grazing pressure by scarid fish is reduced in the presence of territorial damselfish, which protect their turf. In the case of the Ribbon Reef N°3, the microbioerosion appears to become limited by intensive grazing pressure as shown by an inverse relation between the values for microbioerosion and grazing (Fig. 3). Fish grazing was negatively correlated with the initial coral skeleton density of each block but no correlation was shown between skeletal density and micro- or macroboring rates. It is possible that differences in block

density accounted for inter-block variability of grazing. Moreover, the differences between results from the offshore sites, especially the Ribbon and Harrier reefs (both outer barrier reefs), indicate that other factors may be at work in controlling grazing rates.

Macroboring activity showed significant differences among sites only after 3 years. The trend along the studied GBR transect is opposite from microboring and grazing rates. Macrobioerosion showed significantly higher rates at the inshore sites and decreased toward the ocean sites. This trend is consistent with the trend observed at the central GBR by Sammarco and Risk (1990) and Risk et al. (1995). These authors suggested that macrobioerosion increases with rising eutrophication. This is consistent with macrobioerosion values at our inshore sites, which were surrounded by nutrient-enriched waters. In both studies, sponges and bivalves were dominant at inshore sites, consistent with the presence of high terrigenous inputs and low grazing pressure. In general, turbid and nutrient-enriched coastal waters provide important food supply for macroboring suspension-feeding organisms (Rose and Risk 1985; Hallock 1988; Edinger et al. 2000; Holmes et al. 2000). Rates obtained in this study were similar to those found in similar experimental substrates by Chazottes et al. (1995) and Pari et al. (1998) in French Polynesia. They are also comparable with rates found by Reaka-Kudla et al. (1996) on Galapagos reefs, when expressed as percent of $CaCO_3$ removed per block. The rates of macroboring erosion measured after 3 years of exposure were similar to those measured after more than 4 years of exposure recorded by Kiene and Hutchings (1992, 1994) at Lizard Island. This suggests that rates of macrobioerosion reach a stabilized level after more than 3 years of exposure.

In calculating total bioerosion, we have identified three major components: microbioerosion, grazing, and macrobioerosion. These activities on coral reefs are balanced by the processes of bioaccretion. At the level of exposed experimental blocks, the accretionary process was mainly the result of the growth of crustose rhodophytes. The development of rhodophyte crusts modified the rates of microbioerosion by providing local protection from grazing, but also shading. However, this had no effect on macrobioerosion. The same result was found at la Réunion by Chazottes et al. (2002). The total carbonate added by the crust was negligible when compared with the total rate of bioerosion, so that net bioerosion can be considered roughly equivalent to total bioerosion as recorded. The total bioerosion at the block scale increased with the distance from the coast, mainly due to the fact that microbioerosion and grazing were the major processes of bioerosion at the four offshore sites. Macrobioerosion was the principal process only at the two inshore sites. In this study, the 3 years of exposure showed disproportional increase in rates of microbioerosion and especially of grazing and macrobioerosion. This provided an image more closely corresponding to conditions on degraded parts of the reefs, and stresses the importance of long-term settings. Nevertheless, the general inshore–offshore trends were evident after both 1 year (Tribollet et al. 2002, present study) and 3 years of exposure.

Thus, bioerosion in total appeared more important in "pristine reefs" as represented by offshore reefs (especially Osprey Reef) than in nutrient- enriched turbid reefs as represented by inshore reefs. We cannot conclude, however, that offshore reefs were more degraded than the inshore reefs, as we only quantified bioerosion at the scale of experimental blocks of massive *Porites*. Our results showed also that the pattern of macrobioerosion does not necessarily coincide with the pattern of bioerosion in total. From these results, we can extrapolate as to the bioerosion rates on previously degraded portions of the reef, devoid of actively growing and accreting corals. These results complement the studies of the accreting coral-covered portions of the reef.

Edinger et al. (2000) claimed the usefulness of coral growth rates as a measure of health of coral reefs. They studied reefal net carbonate production in polluted versus unpolluted reefs in south Sulawesi and Indonesia, estimating simultaneously live coral cover, coral growth and calcification, skeleton density, as well as macrobioerosion in live corals. Their study revealed that coral growth rates on polluted reefs were not different from those on unpolluted reefs. They also noted that net reef erosion occurred in polluted reefs when live coral cover was low and macrobioerosion intensity high. However, their study did not include microbioerosion and grazing, and did not extend beyond actively growing coral cover. The contrast between constructive and destructive activities in coral reefs would have been more obvious if (1) total bioerosion rather than macrobioerosion alone was considered, and (2) bioerosion in both live and dead corals was quantified. Thus, the model of net carbonate production in polluted versus unpolluted reefs proposed by Edinger et al. (2000), does not include a complete picture of processes in the reef and therefore has to be considered with caution. We suggest, therefore, that the estimates of the state of health of coral reefs and models of reef carbonate cycles, include an evaluation of healthy and growing, as well as damaged, portions of the reef and consider total bioerosion that includes microborers, grazers, and macroborers.

Comparative evaluation of three different components of bioerosion over a large-scale setting connecting different environmental conditions illustrated several salient and distinctive features of each. Microbial bioerosion when acting alone (at the initial stage of bioerosion) is a light-limited and thus, self-stabilizing process which becomes progressive only in the presence of grazing (Schneider and Torunski 1983; Chazottes et al. 1995). The interdependence between microbioerosion and grazing explains the close correlation between the measured values and their patterns across the northern GBR shelf: grazing mitigates the shading effect of epilithic layers, permitting microbial penetration deeper into the rock. With continuing grazing, the zone of microbial endoliths and the amount of carbonate they

remove, moves like a front through the substrate. Thus their activity measured at any time during the exposure experiment represents a net or "residual" microbioerosion, whereas the gross microbial bioerosion includes the part that has been turned over through the grazers. Such interdependence or synergy does not exist between micro- and macroborers, the latter being mostly filter-feeders, which respond more directly to the trophic state of the waters surrounding the reef. Intensive grazing does however, have a selective impact on macroboring organisms by limiting their settlement and early development. Grazers may inflict significant damage on populations of endolithic worms, but affect insignificantly adult endolithic sponges and bivalves. An interesting observation refers to the role of crustose rhodophytes. As they expand over new surfaces, as observed on the oceanic sites of the transect, rhodophyte crusts cover but do not displace the established microbial endoliths. They do, however, introduce additional shading and an added protection from grazing, which also limits the progression of microbial boring and further destruction of the substrate. All these complex interactions highlight the importance of studying simultaneously the different agents of bioerosion to estimate carbonate loss rates under various environmental conditions and through time. This is essential in order to understand the impact of the increasing rate of coral mortality on the reef as a whole, and to better evaluate reefs' health and carbonate cycles.

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