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Distribution patterns of macroboring organisms on Tuléar reef flats (SW Madagascar)

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ABSTRACT: Macroboring organisms that were associated with 3 genera of corals (*Acropora*, *Favia* and *Porites*) principally in 3 different degrees of degradation and occurring at 13 different sites on a cross-reef transect in the Tuléar reefs were studied. Thirty-one species were identified; the most abundant zoological group was sipunculids. Correspondence analysis was used to highlight successively the relationships between species and (1) sites, (2) genera and (3) degree of degradation. The distributional patterns of the macroborers were essentially associated with the physical factors of level of tide and flow energy. Calcareous algal coverage is followed by a decrease in abundance of individuals and species.

INTRODUCTION

Biological destruction of coral reefs is a complex phenomenon and several studies have been undertaken during the past 15 yr to quantify the role of borers and grazers in carbonate budgets of coral reefs. Hutchings (1986) gave an excellent review of these studies.

Samples for this study on macroboring organisms were collected in 1971 by J.-F. Brunel on the reef flats of Tuléar (SW coast of Madagascar). A considerable amount of knowledge has been acquired on the structure of coral reef fauna assemblages of reefs in the western part of the Indian Ocean (Picard 1967, Peyrot-Clausade 1977, Montaggioni 1978, Pichon 1978, Thomassin 1978, Harmelin-Vivien 1979, Vasseur 1981, Faure 1982, Harmelin-Vivien et al. 1982).

In order to further our understanding of the functioning of these communities, it is necessary to consider bioerosion. This study attempts to define the different borer assemblages on the reef flats of Tuléar and the principal factors determining their distribution.

METHODS

Corals, primarily *Porites*, *Acropora* species and Favidae, were collected from the intertidal zone across different reef flats in the vicinity of Tuléar. Three cross-reef flats transects were surveyed: one in the north of Grand Récif near the small pools, a second in the south at Antseteke and a third on Songoritelo Reef (Fig. 1).

The different zones surveyed in each transect are illustrated in Fig. 2. A total of 323 dead corals were chiselled off and for each coral head the following data were recorded: locality, degree of degradation (1 – undamaged head unbored in cross section, 2 – with traces of skeletal degradation, 3 – degradation throughout the skeleton).

In each zone, a minimum of 10 heads (each about 2 dm^3) of *Porites*, *Acropora* and Favidae were collected in each of the 3 degrees of skeletal degradation. The coral heads were then broken up into small pieces to remove the boring organisms. All invertebrates were studied except polychaetes (Clausade 1971) and sponges, which will be discussed elsewhere.

A correspondence analysis (Benzecri et al. 1973, Hill 1974, Naïm 1988) was performed, using an initial matrix including numerical averages of number of individuals for the 10 sample units (coral heads) of the same character (for example original habitat, species of coral, or degree of degradation) and the corresponding observations on boring organisms.

RESULTS

Boring species

Thirty-one species of macroorganisms were collected, belonging to sipunculans, molluscs, echinoids and cirripeds. Sipunculans, with 12 species, represented 74 % of the total of 4374 boring individuals

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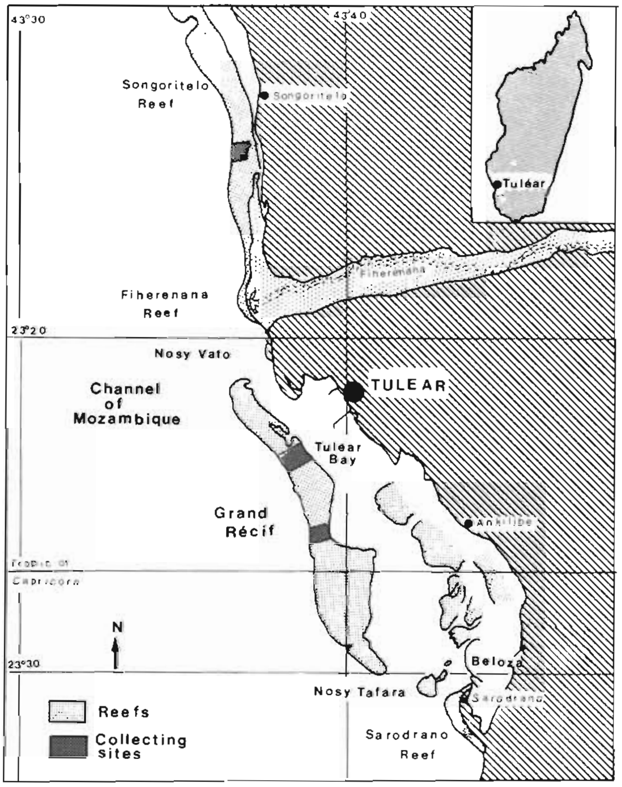

Fig. 1. Tuléar reefs, Madagascar, showing the 3 reef transects sampled

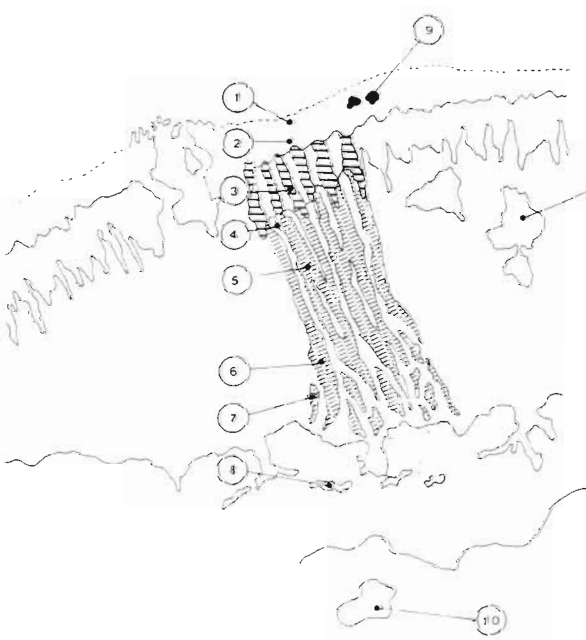

Fig. 2. Collecting sites across a typical reef. 1, outer front; 2, upper reef glacis; 3, boulder tract; 4, residual pools; 5, compact reef flat; 6, reef flat with transverse stripe; 7, reef flat with scattered coral growth; 8, seagrass bed basin; 9, megablocks; 10, pinnacle of inner slope; 11, small pools

identified; molluscs, with 14 species, represented 20 %; echinoids, with 3 species, represented 3.5 %; and cirripeds, with 1 identified species, made up 2.5 % of the total.

Relating total numbers of borers to substrate type (Table 1), it appears that the most bored substrata were those of the megablocks (328 ind./10 samples) (Battistini et al. 1975). Megablocks are blocks reaching sometimes several m^3, torn off outer slopes by cyclones and carried onto outer reef flats. The least bored substratum was the reef platform behind the reef front. The Shannon-Weaver (1963) index indicated that the highest diversity occurred on the outer reef flat. The number of species varied on the reef flat from 12 in the small pool to 24 in the residual pools behind the boulder tract.

There is a relation between the degree of degradation (Table 2) of the coral head and the borer assemblages. The borers were most abundant in the most degraded skeletal substratum with 27 species (of the 31 collected in all) and 189 individuals per 10-sample unit (Fig. 3). Borers were least abundant in substratum covered with crustose calcareous algae (Table 2). In this habitat only 17 species and 45 ind./10 samples were found.

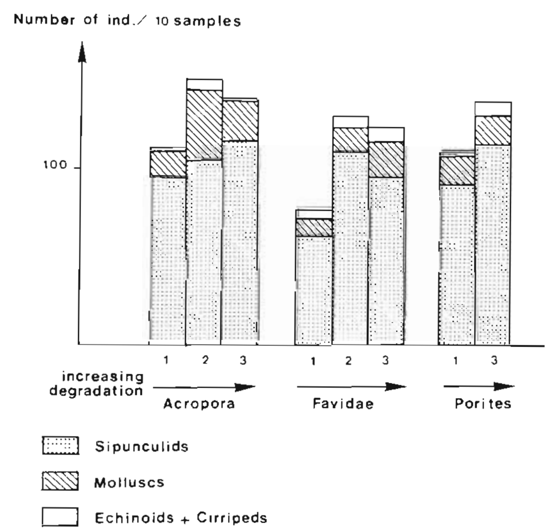

Fig. 3. Importance of the different borer groups as a function of increasing degradation of corals

If we consider the identity of the coral (Table 3), the average number of boring individuals in *Acropora* heads was about 110/10 samples, in Favidae 109/10 samples and in *Porites* 123/10 samples. The highest number of individuals occurred in colonies of *Acropora* with traces of skeletal degradation and the lowest in *Acropora* covered with calcareous algae.

Table 1. Distribution of boring species according to the different structures of the reef for 10 samples. 1, Outer front; 2, upper reef glacis; 3, boulder tract; 4, residual pools; 5, compact reef flat; 6, reef flat with transverse stripes; 7, reef flat with scattered coral growth; 8, seagrass bed basin; 9, megablocks; 10, pinnacle of inner slope; 11, small pools

Species	1	2	3	4	5	6	7	8	9	10	11
Sipunculids											
Aspidosiphon elegans	–	–	–	1.1	–	–	–	–	–	1.0	–
klunzingeri	–	–	–	–	0.8	0.2	0.2	–	–	–	–
ochrus	11.7	0.3	1.7	0.6	3.6	3.8	18.7	0.7	33.5	–	–
steenstrupii	0.5	0.3	0.2	–	0.6	0.5	0.6	–	–	–	–
truncatus	–	–	–	0.8	–	–	–	–	–	–	–
Cloeosiphon aspergillus	22.2	8.8	120.0	61.7	74.0	78.0	73.5	114.8	153.5	39.0	31.0
Phascolosoma nigrescens	0.9	1.6	1.0	0.3	3.0	1.4	0.8	11.0	0.8	–	2.0
pacificum	9.1	2.5	5.7	3.1	2.6	2.9	0.8	0.7	10.4	–	–
perlucens	1.7	3.2	3.6	1.9	6.6	7.1	2.9	22.4	6.2	3.0	–
scoplos	5.3	0.9	6.2	1.4	4.7	0.5	3.3	4.1	4.6	–	6.0
Themiste lageniformis	0.3	0.3	–	–	–	1.9	0.2	0.7	–	–	–
Sipunculid ind.	1.3	–	0.7	1.1	0.2	1.4	0.2	–	3.5	5.0	1.0
Cirripeds											
Lithotrya valentiana	0.7	–	2.1	–	0.8	–	–	1.4	36.9	–	–
Cirriped ind.	–	–	–	–	0.2	–	–	–	–	–	–
Molluscs											
Acanthochiton zelandicus	0.9	–	5.0	2.5	–	–	–	–	16.5	–	–
Cryptoplax striatus	11.6	–	2.1	0.3	0.4	–	–	–	3.5	–	–
Dendropoma sp.	0.2	–	0.5	–	2.8	–	–	0.3	35.8	–	–
Leptochonchus lamarckii	2.1	–	3.1	0.3	1.1	1.4	0.6	0.3	4.2	–	–
Botula cinnamomea	–	0.6	3.2	2.5	0.2	–	0.6	12.4	1.9	1.0	–
Cuspidaria sp.	–	–	1.2	0.3	–	–	–	0.3	1.5	1.0	–
Gastrochaena cuneiformis	0.7	0.3	2.4	2.8	0.2	1.0	5.2	12.4	2.3	4.0	5.0
sp.	0.2	–	0.2	1.4	0.6	–	–	3.8	–	–	–
Gregariella coralliophila	0.3	0.6	1.4	2.2	0.2	0.5	–	–	1.5	1.0	–
Lithophaga hanleyana	2.1	–	6.4	17.0	1.0	1.4	6.0	18.7	1.9	3.0	2.0
lima	–	–	1.7	2.2	–	–	0.6	–	3.1	–	–
malaccana	–	–	–	–	0.2	–	–	2.1	0.4	–	–
nigra	0.5	0.3	16.0	5.6	–	–	0.2	2.4	5.4	11.0	2.0
Petricola divergens	–	–	–	0.6	–	–	–	1.0	–	–	–
Echinoids											
Echinometra mathaei	0.9	2.2	–	9.7	4.5	3.3	5.8	0.3	–	1.0	1.0
Echinostrephus mollaris	0.2	2.5	–	8.9	–	–	0.2	0.3	–	1.0	–
Stomopneustes variolaris	–	–	1.0	1.7	0.2	–	–	–	–	–	1.0
Total	73.4	24.4	185.4	130.0	108.5	106.1	120.0	211.0	327.7	71.0	51.0
No. of species	21	13	22	24	21	15	18	20	20	12	9
Shannon's diversity index	3.12	2.97	2.63	2.95	2.04	1.73	2.06	2.44	2.75	2.45	1.98

Sipunculids

This was the most abundant group of macroboring organisms (Fig. 4). The group represented at least 55 % of the boring organisms of a biotope and at least 70 % in each genus at all stages of degradation. *Cloeosiphon aspergillus* was found in all samples and represented 80 % of the sipunculans collected. This species has previously been collected on the boulder tract of Tuléar Reef (Cutler & Cutler 1979) and throughout western areas of the Indian Ocean. *Aspidosiphon ochrus,* a species described from the Indian Ocean by Cutler & Cutler (1979), was the second most abundant sipunculan. Its preferred habitat was the megablocks on the outer reef flat. *Phascolosoma perlucens, P. scolops* and *P. nigrescens* were present in all the flat biotopes, and on all substrata, but varying in abundance. *P. perlucens* was considered to be rare in the Indian Ocean by Cutler & Cutler (1979). In this survey 175 specimens were collected, most of them from coral heads in depressions in seagrass beds. Rice & MacIntyre (1982) found this species in shallow water on the reef crest and the high relief spur and grooves present on Caribbean reefs. The other 5 species of sipunculans together made up less than 2 % of the total number of sipunculans. *Themiste lageniformis* was most abundant in

Table 2. Distribution of boring species according to degree of degradation of substratum on Tuléar reef flats for 10 samples. 1, Dead head undamaged; 2, traces of skeletal degradation; 3, degradation throughout the skeleton; 4, very altered substrate; 5, heads covered with crustose calcareous algae

Species	1	2	3	4	5
Sipunculids					
Aspidosiphon elegans	0.4	–	–	0.9	0.2
klunzingeri	–	–	0.8	–	–
ochrus	4.0	15.1	2.5	4.1	6.1
steenstrupii	0.5	0.5	0.4	–	–
truncatus	–	0.2	0.6	–	0.5
Cloeosiphon aspergillus	69.6	74.7	87.3	105.3	15.9
Phascolosoma nigrescens	0.6	0.7	3.3	3.8	3.2
pacificum	2.4	6.1	2.5	3.4	3.9
perlucens	3.4	5.3	6.5	7.5	7.7
scoplos	3.1	3.7	5.0	4.8	2.7
Themiste lageniformis	0.3	0.7	0.6	0.3	–
Sipunculid ind.	0.6	1.9	1.5	1.6	–
Cirripeds					
Lithotrya valentiana	0.6	1.4	–	7.2	–
Cirriped ind.	0.1	–	–	–	–
Molluscs					
Acanthochiton zelandicus	0.5	1.9	0.2	2.2	–
Cryptoplax striatus	2.3	–	0.4	2.8	–
Dendropoma sp.	1.6	1.2	–	0.3	–
Leptochonchus lamarckii	0.6	2.3	1.5	0.6	0.2
Botula cinnamomea	0.6	1.6	3.5	5.6	0.7
Cuspidaria sp.	–	0.9	–	0.6	–
Gastrochaena cuneiformis	1.9	5.6	2.3	5.3	0.7
sp.	–	1.2	0.8	1.3	0.5
Gregariella coralliophila	0.4	0.9	1.4	0.3	0.2
Lithophaga hanleyana	4.0	11.2	6.2	9.1	0.7
lima	0.6	1.2	0.9	1.9	1.1
malaccana	–	0.5	0.2	0.3	–
nigra	2.9	3.5	2.3	7.8	0.5
Petricola divergens	–	–	–	1.3	–
Echinoids					
Echinometra mathaei	0.5	2.3	2.9	1.3	0.7
Echinostrephus mollaris	0.9	0.9	–	9.1	–
Stomopneustes variolaris	0.3	0.7	–	–	–
Total	102 7	143.9	130.2	189.3	45.5
No. of species	25	25	23	27	17

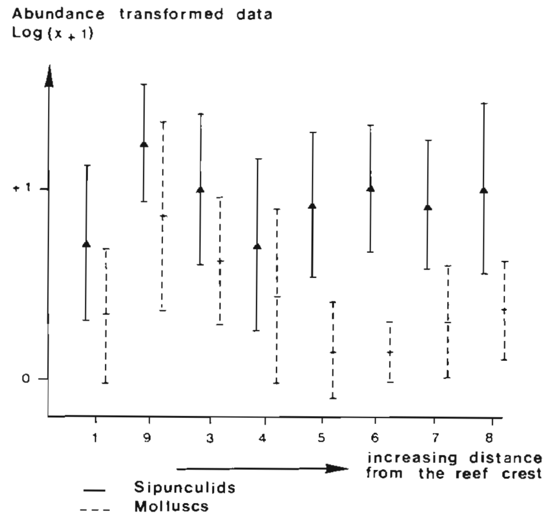

Fig. 4. Means and standard deviations of abundance per 10 samples. Transformed data for sipunculids and molluscs as a function of distance from reef crest. See Fig. 2 for explanation of Sites 1 to 9

Favidae heads collected from the inner reef flat, *Aspidosiphon klunzingeri* occurred in *Acropora* and *Porites* damaged heads, while *Aspidosiphon elegans* and *A. truncatus* were preferentially located in the residual pools present behind the boulder tract. Residual pools are small dips located behind the boulder tract which remain filled with seawater during low tides (Battistini et al. 1975).

The greatest diversity of sipunculans occurred on the inner reef flat with 9 species. The lowest diversity occurred in the megablocks which was also the biotope most inhabited by sipunculans. Sipunculan abundances were similar in the 3 corals with the same degree of degradation, e.g. in *Acropora* with trace of degradation, 107 sipunculans per 10 heads, in Favidae also 107 individuals and in *Porites* 113 individuals.

Cirripeds

The rock boring barnacle *Lithotrya valentiana* was found in hard substrata at the medio-littoral level, i.e. in the boulder tract and principally in the megablocks where they constituted 10 % of the borer assemblage. The preferred habitat was very degraded coral Favidae heads (37 ind./10 samples).

Molluscs

Boring molluscs constituted 20 % of the organisms collected in this survey, and included Amphineura, Bivalvia and Gastropoda. Fig. 4 shows a decrease in mean numbers of this group with increasing distance from the reef crest.

Amphineura. On the reef flat 2 species were present, *Cryptoplax striatus* and *Acanthochiton zelandicus*. *C. striatus* was most abundant in samples from the outer reef flat with fewer individuals present on the boulder tract and the megablocks. *A. zelandicus* occurred in medio-littoral hard substratum formations such as megablocks and boulder tracts, especially in heads of *Acropora* and Favidae.

Gastropoda. An unidentified species of *Dendropoma* was most abundant in the megablocks and this rep-

Table 3. Distribution of boring species according to coral genus and their degradation degree on Tuléar reef flats for 10 samples. 1, Dead coral undamaged; 2, traces of skeletal degradation; 3, degradation throughout the skeleton; 4, *Acropora* covered by concretions; 5, branched *Acropora*

Species	*Acropora*					Favidae			*Porites*	
	1	2	3	4	5	1	2	3	1	3
Sipunculids										
Aspidosiphon elegans	0.9	–	–	–	–	–	–	–	–	–
klunzingeri	–	–	1.4	–	–	–	–	–	–	0.7
ochrus	0.6	15.0	2.4	4.7	0.8	2.0	6.8	2.9	9.6	2.1
steenstrupii	0.3	0.5	–	0.3	0.8	1.0	–	–	0.4	–
truncatus	81.8	–	0.5	–	–	–	–	–	–	–
Cloeosiphon aspergillus	0.9	77.5	98.6	22.7	59.2	47.0	74.3	69.4	71.4	92.1
Phascolosoma nigrescens	3.9	0.5	3.3	0.7	1.7	0.5	1.3	2.3	0.4	4.3
pacificum	2.4	6.5	1.9	5.0	2.5	3.0	8.1	5.3	–	–
perlucens	4.2	5.0	4.3	2.3	5.8	5.5	8.1	10.0	3.0	5.7
scoplos	–	2.5	3.8	3.7	2.5	1.0	6.2	5.3	3.3	6.4
Themistre lageniformis	–	–	–	–	–	0.5	1.8	0.6	0.4	–
Sipunculid ind.		–	1.0	1.0	–	1.0	3.8	1.8	1.1	2.1
Cirripeds										
Lithotrya valentiana	0.6	–	–	0.3	–	1.5	1.3	–	–	–
Cirriped ind.	0.3	–	–	–	–	–	–	–	–	–
Molluscs										
Acanthochiton zelandicus	1.2	4.0	0.5	0.7	–	–	–	–	–	–
Cryptoplax striatus	3.6	–	–	3.3	–	3.0	–	1.8	–	–
Dendropoma sp.	–	–	–	–	–	0.5	0.6	–	3.7	–
Leptochonchus lamarckii	–	1.0	–	–	7.5	2.5	4.8	4.7	–	–
Botula cinnamomea	0.6	2.5	1.4	1.0	0.8	–	–	5.3	1.1	4.3
Cuspidaria sp.	–	0.5	–	–	–	–	1.3	–	–	–
Gastrochaena cuneiformis	1.2	2.0	1.4	1.7	–	0.5	0.6	1.8	3.7	5.0
ind.	–	2.5	–	–	0.8	–	–	1.8	–	0.7
Gregariella coralliophila	0.9	1.5	2.9	–	–	–	0.6	0.6	–	–
Lithophaga hanleyana	3.6	16.0	10.5	3.0	1.7	1.0	4.8	1.7	6.7	4.3
lima	1.2	2.0	1.9	–	–	–	–	–	0.4	0.7
malaccana	–	0.5	–	–	–	–	–	0.6	–	–
nigra	3.6	6.0	3.8	1.3	–	4.5	1.8	2.3	0.7	–
Petricola divergens	–	–	–	–	–	–	–	–	–	0.7
Echinoids										
Echinometra mathaei	0.3	2.5	0.5	–	9.2	0.5	1.8	2.9	1.8	–
Echinostrephus mollaris	0.3	2.0	–	–	0.8	–	–	–	–	1.4
Stomopneustes variolaris	–	1.0	–	–	–	1.0	–	–	0.4	6.4
Total	112.4	151.5	141.1	51.7	94.1	76.5	128.0	121.2	108.1	137.6
No. of species	20	21	18	15	13	18	17	18	16	15

resented about 10 % of their boring population. It was most abundant in *Porites*.

Another species of boring gastropod occurred in this area, *Leptoconchus lamarckii*, which is also known to bore in living corals (Soliman 1969, Scott 1980). It was not abundant but occurred over the whole reef flat, especially in branched *Acropora* and in the Favidae.

Bivalvia. A total of 622 specimens belonging to 10 species were collected. The majority of the bivalves were lithophagines of which 2 species, *Lithophaga nigra* and *L. hanleyana,* represented 50 % of the individuals. *L. nigra,* already reported by Arnaud & Thomassin (1986), occurred preferentially on the boulder tract, small pools, residual pools and megablocks. It was absent only from branched *Acropora* and very damaged *Porites*. *L. hanleyana* occurred in all the biotopes and all 3 corals regardless of extent of degradation. It was the most abundant bivalve species and preferred biotopes almost constantly submerged, such as seagrass bed depressions and residual pools. *Botula cinnamomea* showed a marked degree of specialization: it mostly occurred in very degraded substrata, particularly of the genus *Porites*, in seagrass beds and residual pools. *Gastrochaena cuneiformis* showed no preference for any particular type of biotope. It was present in all the coral genera regardless of degradation, except in branched *Acropora*. It was particularly abundant in *Porites* on the inner reef flat, small pools and pinnacles of the inner slope. *Gregariella coralliophila* was less abundant but had a wide distribution. The remaining 5 species, *Lithophaga malaccana, Petricola divergens, Cuspidaria* sp., *Gastrochaena* sp. and *Lithophaga lima* represented less than 12 % of the bivalve assemblage; *L. lima* is known to be a borer of living corals (Wilson 1979).

Echinoids

Echinoids play an important role in the biological destructions of coral reefs by surface grazing (Bromley 1978, Russo 1980, Bak 1985, Hutchings 1986). This group includes some of the principal grazers of substrates covered by encrusting coralline algae, filamentous algae and blue-green algae.

Three species (about 170 individuals) were recorded in this survey: *Echinometra mathaei, Echinostrephus mollaris* and *Stomopneustes variolaris*. *E. mathaei* was the most abundant, particularly in the residual pools and on the inner reef flat. *E. mollaris* also occurred in residual pools and in small pools. If the nature of substrata is considered, it clearly appears that *E. mathaei*, which was found in all corals was most abundant in branched *Acropora*, and *S. variolaris* in heavily bored *Porites*. *E. mollaris* seemed to prefer bored *Acropora*.

Spatial distribution of borers

Distribution of the 4 groups of boring organisms in relation to reef flat structures is shown in Table 4 and Fig. 5.

Correspondence analysis is used to extract information on the relationship between species and reef structure, and bioeroder species and the different corals, at various stages of degradation.

Macroboring species and reef structures

The first principal component analysis was performed on a matrix data consisting of 31 observations (borer species) and 11 variables (reef structures). All the samples are classified according to their original habitats (outer front, boulder tract, etc.) (Fig. 6).

The first 3 factors of this analysis explain 65.9 % of the total variance. Factor 1, extracting 33.1 % of the variance, is defined by the variable megablocks opposed to residual pools and seagrass bed hollows. Factor 2, extracting 18.3 % of the variance, is defined

Table 4. Importance of the 4 taxonomic boring groups across the Tuléar reef flat for 10 samples. a: abundance (no. ind. per 10 samples); d: dominance (percent of total ind.). 1, Outer front; 2, upper reef glacis; 3, boulder tract; 4, residual pools; 5, compact reef flat; 6, reef flat with transverse stripes; 7, reef flat with scattered coral growth; 8, seagrass bed basin; 9, megablocks; 10, pinnacle of inner slope; 11, small pools

Taxon	1		2		3		4		5		6		7		8		9		10		11	
	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d
Sipunculids	53.0	72.2	17.9	73.4	139.1	75.0	72.0	55.4	96.1	88.5	98.0	92.4	101.0	84.0	154.6	73.0	212.5	64.8	48.0	67.6	40.0	78.4
Crustaceans	0.7	0.1	0	–	2.1	1.1	–	–	1.0	0.1	0	–	–	–	1.4	0.7	36.8	11.3	–	–	–	–
Molluscs	18.6	25.3	1.8	7.4	43.2	23.3	37.7	29.0	6.7	6.1	4.8	4.5	13.2	11.2	54.4	26.0	78.4	23.9	21.0	29.6	9.0	17.6
Echinoids	1.1	1.4	4.7	19.2	1.0	0.5	20.3	15.6	4.7	4.3	3.3	3.1	5.8	4.8	0.6	0.4	–		2.0	2.8	2.0	4.0
	73.4	100.0	24.4	100.0	185.4	99.9	130.0	100.0	108.5	100.0	106.1	100.0	120.0	100.0	211.0	100.0	327.7	100.0	71.0	100.0	51.0	100.0

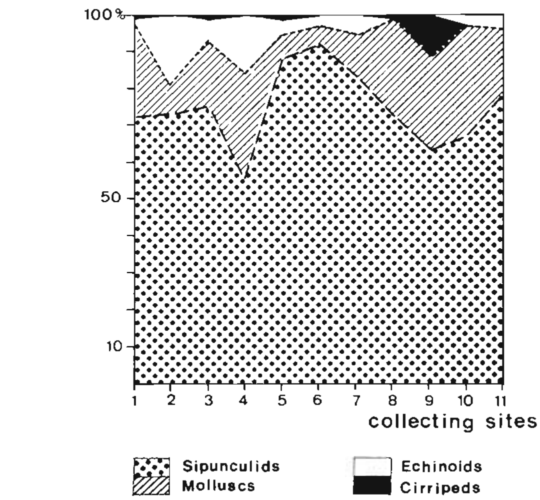

Fig. 5. Distribution of the 4 taxonomic groups of borer organisms on Tuléar reef flats

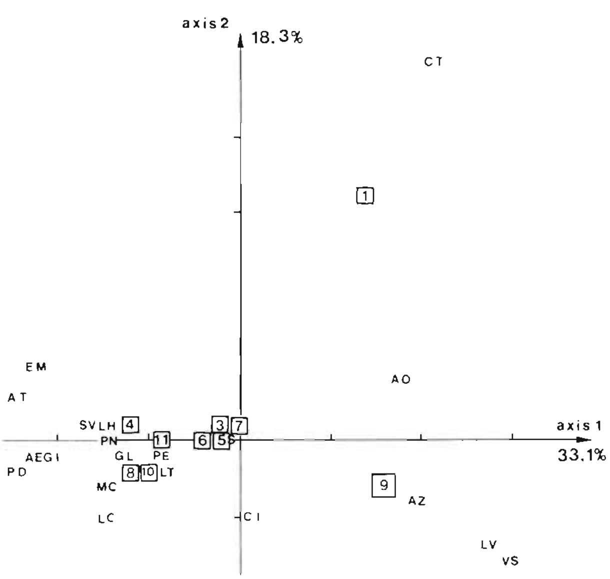

Fig. 6. Correspondence factor analysis. Plot of the 2 first factor axes. Observations are borer species: AO, *Aspidosiphon ochrus*; PE, *Phascolosoma perlucens*; LV, *Lithothrya valentiana*; AZ, *Acanthochiton zelandicus*; CT, *Cryptoplax striatus*; VS, *Dendropoma* sp.; MC, *Botulina cinnamomea*; GL, *Gastrochaenia cuneiformis*; GI, *Gastrochaenia* sp.; LH, *Lithophaga hanleyana*; PD, *Petricola divergens*; SV, *Stomopneustes variolaris*. Variables are the 11 reef habitats (cf. Fig. 2)

by the variable outer front, and Factor 3, extracting 14.5 % of the variance, is controlled by the small pools.

This first analysis allows us to assign Axis 1 to an emersion factor. The megablocks located at the positive extremity of this axis contain the biota which emerge earlier and for longer times, with a high degree of drying up of cavities, and at the opposite extremity residual pools and seagrass bed hollows contain biota nearly always submerged. Axis 2 represents the surf action on the front reef. Axis 3 can be assigned to sedimentation which increases from the front of the reef to the seagrass bed and inner slope (Vasseur 1981). This sedimentation is also very important in the small pools.

Arrangement of the species points within the 3 dimensions forms 3 distinct groups. The first includes species with a high absolute contribution around Stn 9 (megablocks) (Fig. 2). These species are: *Lithotrya valentiana* (barnacle), *Aspidosiphon ochrus*, *Acanthochiton zelandicus* and *Dendropoma* sp.

The second group of species is projected near Stn 8 (seagrass bed) and Stn 4 (residual pools) and is formed by *Gastrochaena* sp., *Botula cinnamomea*, *Petricola divergens*, *Lithophaga hanleyana* and *Phascalosoma perlucens*. The amphineuran *Cryptoplax striatus* is projected near Stn 1 (outer front).

A similar correspondence analysis was performed using the barycentre (center of gravity of a set of vectors) corresponding to the borer assemblage for each habitat and each of the 3 reef sectors studied. The data matrix included 352 observations (22 barycentres were calculated) and 31 variables within the factor space (1.2) and (1.3). Five groups are clearly distinguished (Fig. 7). Group A includes the 2 megablock barycentres and the 3 species *Dendropoma* sp., *Lithotrya valentiana* and *Acanthochiton zelandicus*. Group B comprises the 4 barycentres of the outer reef flat and the species *Cryptoplax striatus*. Group C concerns the residual pools barycentres and the 3 echinoids *Echinometra mathaei*, *Stomopneustes variolaris*, *Echinostephus mollaris* plus the sipunculids *Aspidosiphon elegans* and *A. truncatus*. Group D shows the association between the 3 seagrass bed barycentres and *Petricola divergens* and *Gastrochaena cuneiformis*. Group E is formed by the 3 boulder tract barycentres and *Cloeosiphon aspergillus*.

Macroboring species and corals

The distributions of macroborers in the 3 genera of corals with various degrees of degradation are detailed in Table 3.

Five different categories of *Acropora* were studied: *Acropora* with small branches in 3 different degrees of degradation, *Acropora* covered by algal encrustations, and large branched *Acropora*. This last category contained the least diverse fauna with only 13 species, characterized by *Leptoconchus lamarckii*. *Acropora* heavily encrusted contained 15 species with a density

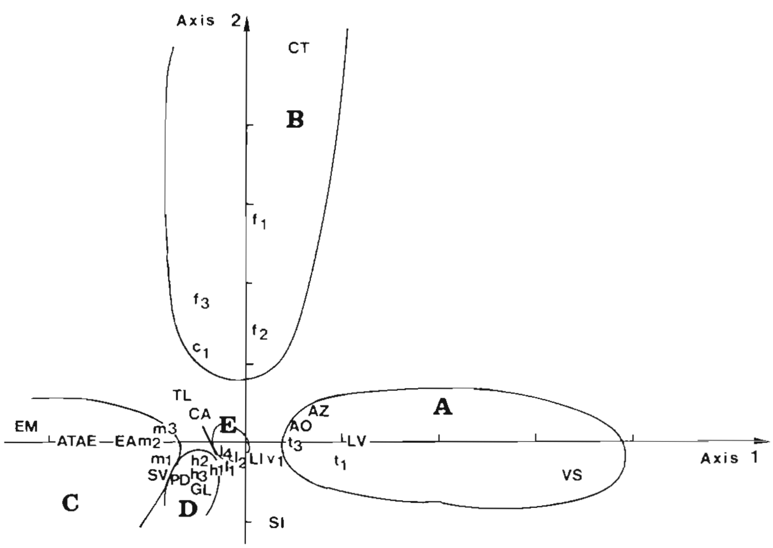

Fig. 7. Correspondence factor analysis. Plot of the 2 factor axes. Projections of barycentres corresponding to borer assemblage for each habitat and each of the 3 reef sectors studied. f_1, f_2, f_3, c_1: barycentres of outer front; m_1, m_2, m_3: barycentres of residual pools; h_1, h_2, h_3: barycentres of seagrass bed basins; i_1, i_2, i_3: barycentres of boulder tracts; t_1, t_3: barycentres of megablocks. Species other than those in Fig. 6: AE, *Aspidosiphon elegans*; AT, *Aspidosiphon truncatus*; CA, *Cloeosiphon aspergillus*; TL, *Themiste lageniformis*; EA, *Echinometra mathaei*; EM, *Echinostrephus mollaris*. Groups A to E are explained in the text

of 51 ind./10 samples. This is the lowest density recorded. In the other 3 categories the number of species varied between 18 and 21 with a maximum number of individuals (15 ind./10 samples) occurring in coral with trace skeletal degradation.

In Favidae, the number of macroborer species was similar regardless of degradation of the skeleton (between 17 and 18 species) but for *Acropora* and *Porites*, the density of macroborers varied according to the level of degradation with the least degraded skeleton having the lowest number of borers.

Porites exhibited the least diversified substrate. Only 2 degrees of degradation were recognized: undamaged heads and degradation throughout the skeleton.

In the correspondence analysis produced from the matrix data including 10 observations (3 corals at different degrees of degradation) and 31 variables (species of macroborer), the first 3 factors extract 59 % of the total variance (Fig. 8). Factor 1 extracting 24.3 % of the variance is largely controlled by the opposition between large branched *Acropora* (absolute contribution, AC = 0.52) and slightly damaged *Acropora* (AC = 0.13). Factor 2 extracting 18.9 % of the variance depends upon damaged *Porites* (AC = 0.53) opposed to encrusted *Acropora* (AC = 0.13). Factor 3 extracting 15.8 % of the variance is defined by undamaged Favidae and *Acropora*. Analysis of proximities between the variables and the observations provides an explanation of the relationships between the corals with their degrees of degradation, and the macroboring species. Samples of large branched *Acropora* are characterized by *Leptoconchus lamarckii* and *Echinometra mathaei*, very damaged *Porites* is characterized by *Stomopneustes variolaris* and encrusted

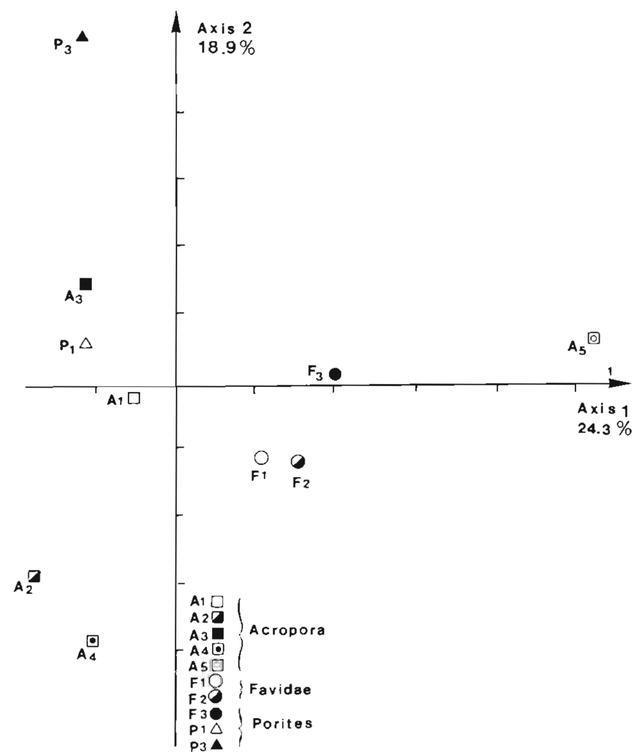

Fig. 8. Correspondence factor analysis. Plot of the 2 first axes. Samples considered according to coral genus or family and their degree of degradation. A_1, *Acropora* undamaged; A_2, *Acropora* with traces of skeletal degradation; A_3, *Acropora* with degradation throughout the skeleton; A_4, *Acropora* covered by concretions; A_5, branched *Acropora*; F_1, Favidae with traces of skeletal degradation; F_2, Favidae with degradation throughout the skeleton; P_1 *Porites* with traces of skeletal degradation; P_3, with degradation throughout the skeleton

Acropora is associated with *Phascolosoma pacificum*. *Cryptoplax striatus* and *Lithotrya valentiana* are projected near the undamaged heads of *Acropora* and Favidae.

A further correspondence analysis was performed utilising the barycentre corresponding to the borer assemblage for each coral and for each degree of degradation according to each original habitat. The results (Fig. 9) show that Axis 1 depends upon barycentres of very damaged *Porites* and slightly damaged *Acropora* of megablocks. Axis 2 is defined by the barycentres of little damaged *Acropora* and undamaged *Acropora* of the outer reef flat. From the spatial ordination of the barycentres of variables and observations within the 2 bidimensional spaces, 4 groups can be distinguished which are the same 4 groups defined in considering only the original structure of the samples, i.e. Group A includes samples of megablocks, Group B those of the outer reef flats, Group C samples of residual pools and Group D those of the seagrass beds. Two barycentres of variables are closely linked to Groups A and C: near A is the barycentre of cirripeds and near C that of echinoids. This analysis shows that the degree of damage is not an important factor for the distribution of macroboring organisms. If we now consider only the barycentres of the 3 corals in terms of their original structures, we obtain (Fig. 10) as before a first axis dependent on *Acropora* and *Porites* of megablocks, a second axis defined by *Acropora* and Favidae of outer reef flats and the same 4 groups of points in the 2 bidimensional spaces. Thus all these different correspondence analyses indicate that on the reef flats of Tuléar, the distribution of the macroborer organisms is associated with 3 major environmental factors: (1) aerial exposure time corresponding to a medio-littoral level, represented by the megablocks with *Lithotrya valentiana*, *Acantochiton zelandicus* and *Dendropoma* sp.; (2) strong wave action which characterizes the habitats in the outer reef flat; *Cryptoplax striatus* is the characteristic species of this zone; (3) very short periods of aerial exposure found in the residual pools and the seagrass bed; these biotopes are the preferred habitat of the urchins and of *Lithophaga hanleyana*.

It appears that the diversity and density of boring communities are correlated with the cover of algae rather than by the coral species, and also that the degree of branching is very important.

The degree of damage does not affect community composition, but the number of individuals is higher in damaged heads.

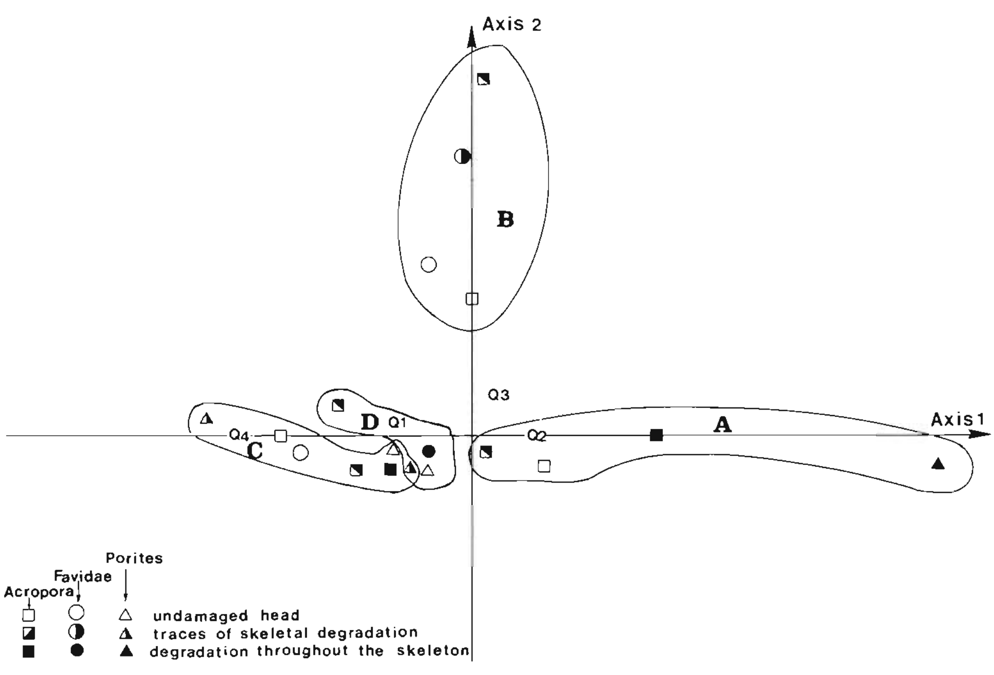

Fig. 9. Correspondence factor analysis. Plot of the 2 first factor axes. Barycentres of variables (taxonomic borer groups) and of observations according to coral genus or family and degree of degradation. A, megablock group; B, outer reef flat group; C, residual pool group; D, seagrass bed group. Q_1, barycentre of sipunculids; Q_2, barycentre of cirripeds; Q_3, barycentre of molluscs; Q_4, barycentre of echinoids

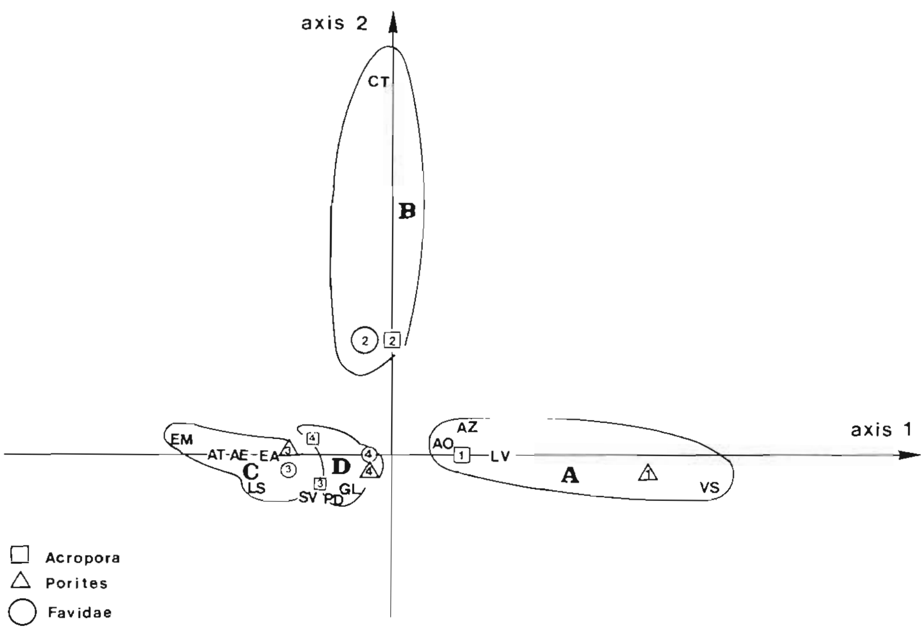

Fig. 10. Correspondence factor analysis. Plot of the 2 first factor axes. Projections of barycentres of observations according to coral genus or family and their original habitats and of variables borer species. A, megablock group; B, outer reef flat group; C, residual pool group; D, seagrass bed group. 1, corals corring from the megablock; 2, from outer reef flat; 3, from residual pool; 4, from seagrass bed

DISCUSSION AND CONCLUSIONS

This survey shows that the boring fauna of *Acropora*, *Porites* and Favidae appears relatively homogeneous across the reef flats of Tuléar.

Sipunculans were the most abundant borers with a maximum number of individuals occuring in the megablock biotope (about 15 ind. dm^{-3}). This maximal density is just lower than that of boring polychaetes found in cavitary blocks: 20 ind. dm^{-3}. The dominant boring polychaete was the eunicid *Lysidice collaris* (Clausade 1971). Eunicidae was considered by Crossland (1903) and by Ebbs (1966) to be the major coral-destroying family among polychaetes. The only detailed study of sipunculan distribution across a reef is that of Rice & MacIntyre (1982) on Carrie Bay off Belize (Caribbean). They found that the greatest concentration and the greatest diversity occurred on the reef crest. They suggested that the distribution of species may be determined more by physical factors associated with locality than by the type of coral skeleton. Our data tend to confirm this view. On Tuléar reefs the distribution of sipunculans relative to the degree of degradation shows that abundance increases with an increase in coral degradation and decreases on substrata covered by sand or by encrustation. Our results also corroborate those of Davies & Hutchings (1983) who showed that sipunculans do not colonize newly available coral substrate. It can be seen in Table 2 that sipunculans are less abundant in new dead heads (undamaged) than in more damaged substrate. Although abundant, sipunculans are not considered very active agents of bioerosion. Highsmith et al. (1983) indicated that only 0.6 % of boring in colonies of *Montastrea annularis* on Belize Barrier Reef was due to sipunculans.

The other very important boring group on Tuléar reef flats is the molluscs. Biotopes in which Bivalvia are very abundant are found on the boulder tract and in residual pools, and the most preferred sites are the blocks within the seagrass beds, which are nearly always immersed. Coral-boring bivalves have been very well studied (Morton 1983). Species found in great abundance are known to bore into dead corals, except for *Lithophaga hanleyana* which is cited by Scott (1980) as boring into living coral species; however, Wilson (1979) and Kleeman (1984) collected it on dead substrata from beach rock, boulder tract and *Porites* of Heron Island (Great Barrier Reef). Morton (1983), in his review of coral-associated bivalves of the Indo-Pacific, discussed the great variability of results concerning the coral host of the different species of *Lithophaga*.

Lithophaga species in Tuléar reef flat did not show a clear preference for a particular genus of coral or degree of degradation. Gastrochaenidae are more abundant in *Porites*. On Hong Kong reefs, Scott (1980) did not find Gastrochaenidae in *Porites*. Carter (1978) mentioned in his study of Atlantic gastrochaenids the specialization of this family for survival in thin and rapidly eroded substrata and also their ability to exclude gastropod predations. The amount of degradation apportioned to boring bivalves varies considerably in the literature. Highsmith et al. (1983) found that 3.3 % of the bored area of *Montastrea cavernosa* on the

Reef Barrier of Belize was due to Bivalvia. Hein & Risk (1975) estimated them to be responsible for 15 % of damage in Florida corals. Trudgill (1976) measured a boring rate of 0.9 cm yr^{-1} for *Lithophaga* in Aldabra (Indian Ocean) limestone.

The 2 chitons *Cryptoplax striatus* and *Acanthochiton zelandicus* are grazing species which are particularly abundant on Tuléar reefs at the mid-littoral level. Taylor & Way (1976) estimated that on Aldabra atoll erosional activities of chitons are responsible for the loss of 40 g m^{-2} of $CaCO_3$ per year.

Other grazers which play an important role in the biological destruction of coral reefs are echinoids. Regis & Thomassin (1982), working on a coral reef at Tuléar, found that the echinoids *Echinometra mathaei* and *Echinostrephus mollaris* are abundant in places with strong currents. These 2 species dominated samples from residual pools where strong tidal movement occurs. Russo (1980) calculated an erosion rate of 0.04 kg $CaCO_3$ yr^{-1} by one specimen of *E. mathaei* at Enewetak (W Pacific). Hughes & Keij (1973), in the Persian Gulf, calculated a rate of 0.18 kg $ind.^{-1}$ yr^{-1} for urchins. Bak (pers. comm.) found 0.1 kg $ind.^{-1}$ yr^{-1} on Moorea Reef (Polynesia).

On Tuléar reefs vermetids *Dendropoma* sp. are particularly abundant on megablocks in undamaged *Porites*.

The cirriped *Lithrotrya valentiana* is also a species occurring at high level on Tuléar reefs. Trudgill (1976) estimated an erosion rate of 0.8 cm ind. yr^{-1} in Aldabra atoll. Arh & Stanton (1973) considered this organism as an indicator of the intertidal or near-intertidal environment and reported an average density of 1 tube cm^{-2} of rock in the beach rock of Cayo Icacos (Puerto Rico).

Unfortunately, it has not been possible to calculate rates of bioerosion for the habitats at Tuléar using published rates obtained elsewhere because of the methods of calculation used: rates of boring activity vary according to habitat and locality. In this work only the environmental factors are correlated with bioerosion patterns. Recently, Sammarco et al. (1987), in their analysis of the effect of grazing and damselfish territoriality on internal bioerosion of dead corals, showed a shift in the taxonomic composition when grazing pressure varies. It is very difficult to give detailed results of macroborer distribution because there are many factors occurring at different levels and different scales which may or may not act in synergy.

The major findings in this study may be summarized as follows:

(1) The borer organism assemblage on Tuléar reef flats is quite homogeneous throughout the infralittoral biotopes.

(2) Local environmental factors affect the abundance of some species: localities with high flow energy are characterized by *Cryptoplax striatus;* in biotopes with long immersion times, boring Mytilidae and particularly *Lithophaga hanleyana*, as well as echinoids, predominate.

(3) The borer assemblages appear not to be correlated with type of coral.

(4) The presence of calcareous algae results in a decrease of the number of boring species and individuals.

(5) In the mid-littoral zone the boring community is characterized by *Lithotrya valentiana, Dendropoma* sp. and *Aspidosiphon ochrus*.

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