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EXPERIMENTAL SHIFT IN BENTHIC COMMUNITY STRUCTURE

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ABSTRACT

In January 1989, hypersedimentation generated by hurricane Firinga was responsible for 99% mortality within the St-Leu reef flat coral community (Reunion Island, S.W. Indian Ocean). In September 1992, one homogeneous zone (400 m^2) of dead *Acropora pharaonis* (60% coverage: cv) was selected on the inner reef flat: corals were almost totally covered by macroalgae and turfs (*Stegastes nigricans* territories). Macroalgae and turfs were removed from half of the zone (zone M, "modified") and the other half was left as control (zone C). In December 1994, despite similar salinity and nutrient concentrations in zones M and C (0.70 ± 0.04 µM DIN, 0.110 ± 0.006 µM DIP on average), macroalgae and turfs had not recovered in zone M (10% and 14% cv respectively) compared to zone C (42% and 35% cv), whereas crustose algal coverage and urchin densities were far higher in zone M than in C (M: 23% cv and 37 ind/m^2; C: 2% cv and 8 ind/m^2). Our experiment suggested that the removal of whole fleshy algae induced the formation of a new algal community controlled by herbivorous organisms, especially sea urchins. A longer monitoring is now necessary to determine whether or not this new state is stable and favourable to living coral recovery.

INTRODUCTION

Shift from coral to algal dominance has important implications for the reef's trophic structure and for reef resource value to human populations (Done 1992). Programmes for remediation of degraded coral reefs are urgently needed, and the factors which govern the structure of coral reef communities have to be recognized (Done 1995). Corals living both in natural conditions and aquaria can support relatively high nutrient water concentrations (Atkinson et al 1995). However, alterations of coral reefs from coral dominance to fleshy algal dominance have been often associated with excessive nutrient increase (Smith and Buddemeier 1992). The balance between algae and corals seems to be mostly controlled by nutrient availability and herbivore activity (Littler and Littler 1985; Steneck 1988). Numerous experimental studies have demonstrated that the removal or exclusion of grazers from coral reefs increases the algal standing crop from 1.5 to 15 in cover (Vadas 1985), although large standing crops of algae often occur on portions of reefs accessible to grazers (Wanders 1976; Veron and Done 1979). An alternative hypothesis is that a change in one or more of the variables which limit primary producers resulted in an increase in the biomass of macroalgae unpalatable for grazers. The role of stochastic events may be considered as preponderant factors in initiating this kind of dominance in reef systems (Doty 1971; Hatcher 1984; Hughes 1994). If some environmental factor reduces the herbivory pressure a long time enough, populations of macroalgae can grow rapidly to reach a critical biomass, after which they get refuge in size, abundance (Birkeland 1977) and unpalatability (Littler et al 1983). At this stage, such macroalgal communities may remain constant over long periods under the same environmental conditions that formerly maintain them as rare components of a completely different community (Littler and Littler 1985).

The Saint-Leu reef flat (Reunion Island, S.W. Indian Ocean), where coral communities were flourishing in 1987 despite some nutrient enrichment due to terrigenous influence, is an illustration of such a phenomenon. In January 1989, hypersedimentation generated by hurricane Firinga was responsible for 99% coral mortality. In 1992, 3 years later, macroalgae and turfs were dominant on the inner reef flat. Coral recovery seemed to be mostly limited by competition with macroalgae, which seemed to have escaped any control. Most experimental studies have focused on the structuring role of herbivory in algal communities, but the role that unpalatable macroalgae and turf overgrowth played in inhibiting herbivory was not really investigated (Vadas 1985). Our study examined the impact of macroalgal and turf removals on an inner reef flat which was subjected to a shift from coral to algal dominance. Indeed, algal manipulations provide another mean of evaluating the influence of grazers. The long-term quantitative monitoring of Saint-Leu reef flat communities, documenting community changes, will allow to propose baselines for management of reefs which have switched from corals to algae.

MATERIALS AND METHODS

Study site

La Réunion (highest point: 3069 m, surface area: 2512 km^2) is a high volcanic island located in the SW Indian ocean (21°70'-19°40' S and 55°13'-61°13' E). Narrow and discontinuous fringing reefs lie along the dry western and southern coasts in exposed conditions (Montaggioni and Faure 1980). Tides are semi-diurnal and the range, highly modified by swells, varies from 0.1 m to 0.95 m. Back reef water temperature ranges from 21°C to 32°C (Mioche unpubl. data).

Experimental design

The Saint-Leu reef is located in front of the town of Saint-Leu. The narrow reef flat (350m wide), exposed to strong waves and currents, is one of the deepest of Réunion Island (max. depth 1.80m). To investigate experimentally the shift within benthic communities, a 400 m^2 area (20 m x 20 m) was selected on the inner reef flat (1m deep) subjected to terrigenous influence (Cuet unpubl. data). This homogeneous severely degraded area was composed of large dead *Acropora pharaonis* colonies and coral rubbles covered with macroalgae. Small, 10 to 20 cm high, and very diverse coral recruits were observed among the dead coral branches (Naim et al 1993).

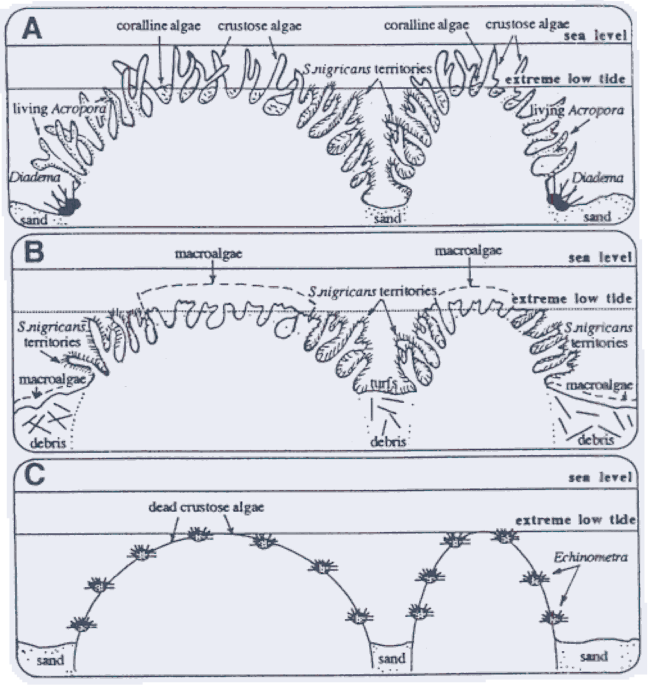

Fig. 1: The *Acropora pharaonis* macrocolonies and their dominant biological environment: A. before Firinga (1987 to 1988), B. and C. 3 years and 1/2 after Firinga (Sept. 92), B. the control zone, C. the modified zone.

This area was divided into 2 zones: a 200 m^2 (20 m x 10 m) control zone (zone C) and a 200 m^2 zone experimentally modified in September 1992 (zone M) as follows :(1) *Acropora* shrubs were "pruned": most of the branches covered with macroalgae and turfs were removed. (2) Surrounding channels were cleared by removing algae and rubble until uniformely sandy (Fig. 1). Due to the heavy calcification of the coral colonies, a hammer and a chisel had to be used for cutting the *Acropora* branches and a pick to break away the consolidated de-

bris. Coral branches were then spread out on the substratum of the back reef zone. During the work, young living coral colonies were removed and then held into the crevices of the modified *Acropora* shrubs. Siltation generated by the manipulation rapidly decreased due to strong currents generated by trade-winds.

Water analyses
A survey of reef water salinity and dissolved inorganic nutrient content was made just after the modification of zone M. From November 1992 to October 1993, 3 to 4 water samples were collected on a monthly basis at low and high tides in zones M and C. Triplicate reef water samples were also collected at high tide near the reef front, and at low tide along the shore.

Water samples were filtered within two hours through 0.45 µm GF/C glass-fiber filters (or HA Millipore for silicate determination). Colorimetric ammonium analyses (Koroleff 1969) were immediately performed. Samples were frozen for dissolved inorganic phosphorus (DIP) and nitrate+nitrite analysis, or stored at 4°C for silicate determination. For ammonium, optical densities were measured on a Perkin-Elmer Lambda 3 spectrophotometer. Other nutrient analyses were conducted on a Bran+Luebbe Autoanalyser II. Salinities were determined with a Grundy Environmental Systems 6230 N salinometer.

Benthic communities
Benthic communities were investigated before (March 1987) and after (March 1989) hurricane Firinga, before and after the modification of zone M in September 1992 and, later, in December 1994. In 1987 and 1989, a survey on relative dominance of organisms (in terms of coverage or density of individuals) was performed. In September 1992, the Line Intercept Transect method (LIT), commonly used in base-line and impact studies (English et al 1994), was applied to establish the relative dominance of benthic communities on the studied area. In December 1994, 30 x 1m² quadrats (i.e. 16% of the bottom) were randomly placed on hard substratum (sandy channels were avoided) in zones C and M to estimate the respective coverage of living corals, fleshy macroalgae and turfs, and determine the densities of sea urchins and gastropods.

Total ichthyofauna and the damselfish *Stegastes nigricans*
Surveys of total ichthyofauna were made during austral summer by visual counts on a permanent transect (50m long x 2m wide), parallel to the shore, running across the study zone. Three replicates were done in each of three years : in February-March 1989 (following hurricane Firinga), January-February 1992 (after the modification of zone M) and January-February 1995. In January 1995, 30 quadrats (1m x 1m each) were randomly determined in zones C and M to quantify the population of *S. nigricans* (number and total length of individual fish).

RESULTS

Water analyses
Salinity and DIP concentrations (Table 1) were similar in zones M and C (Mann-Whitney; three-way ANOVA simultaneously assessing the effects of the factors "zone", "tide" and "date"). Reactive silicate, ammonium, and nitrate+nitrite concentrations were slightly higher in zone M (three-way ANOVA, factor "zone": $p < 0.015$, $p < 0.003$ and $p < 0.008$ respectively).

Salinity decreased from the start of the rainy season (December) on the reef flat, the lowest values being found from February to May, and increased afterwards (Fig. 2). There was a significant increase in salinity between the shore and zones M and C (low tide only; Mann-Whitney; $p = 0.0001$), and a negative linear relationship between silicate and salinity in the samples collected along the shore (Table 2). Such relationships were frequently observed on the reef flat during the rainy season, and until July 1993 (not shown). Besides, silicate was higher in zones M and C than on the reef front (high tide only; Mann-Whitney; $p = 0.0001$).

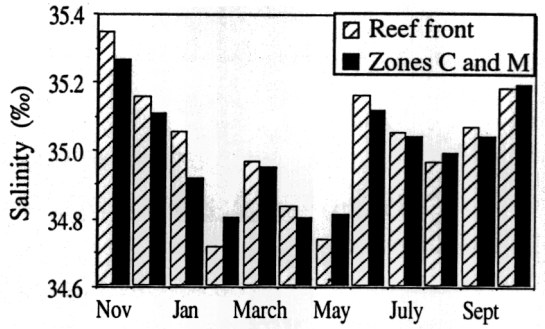

Fig.2 : Mean monthly salinity on the reef flat from November 1992 to October 1993. Reef front: high tide only (3 samples); Zones C and M: average from samples collected at low and high tide (3 to 4 per zone).

Table 2: r (above) and p values (below in brackets) for Spearman rank order correlations between freshwater tracers (salinity and reactive silicate) and dissolved inorganic nutrients in the samples collected along the shore from November 92 to October 93.

	Silicate	$NO_3^- + NO_2^-$	NH_4^+	DIP
Salinity	- 0.88	- 0.78	- 0.55	- 0.37
	(0.0001)	(0.0001)	(0.002)	(< 0.04)
Silicate	-	0.72	0.66	0.49
	-	(0.0001)	(0.0001)	(< 0.004)

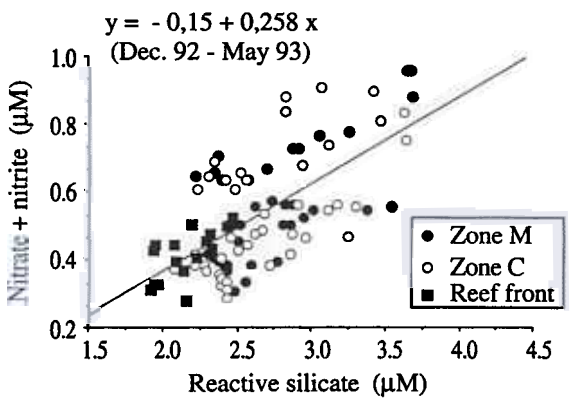

Fig.3: Reactive silicate vs. nitrate+nitrite mixing diagram on the reef flat (reef front, zones C and M) from December 92 to May 93. Spearman rank order correlation: $r = 0.61$, $p = 0.0001$.

Table 1: Salinity and concentrations of inorganic nutrients from Nov. 92 to Oct. 93.
Mean ± 95% confidence interval. Number of samples in brackets.

		Sub-marine beach	Zone M	Zone C	Reef front
Salinity	Low tide	32.741 ± 0.784 (35)	35.027 ± 0.056 (37)	35.012 ± 0.042 (47)	•
(‰)	High tide	•	34.992 ± 0.055 (37)	34.993 ± 0.051 (48)	35.019 ± 0.067 (36)
Reactive silicate	Low tide	33.9 ± 12.2 (36)	2.94 ± 0.16 (38)	2.85 ± 0.15 (47)	•
(µM)	High tide	•	2.84 ± 0.11 (38)	2.80 ± 0.09 (46)	2.42 ± 0.11 (35)
Ammonium	Low tide	0.52 ± 0.15 (34)	0.24 ± 0.04 (38)	0.23 ± 0.03 (48)	•
(µM)	High tide	•	0.24 ± 0.05 (38)	0.20 ± 0.03 (46)	0.17 ± 0.03 (34)
Nitrate + nitrite	Low tide	10.4 ± 4.1 (35)	0.56 ± 0.07 (37)	0.55 ± 0.05 (48)	•
(µM)	High tide	•	0.41 ± 0.04 (38)	0.38 ± 0.03 (48)	0.37 ± 0.04 (34)
DIP	Low tide	0.159 ± 0.027 (36)	0.116 ± 0.013 (38)	0.116 ± 0.011 (48)	•
(µM)	High tide	•	0.106 ± 0.013 (38)	0.101 ± 0.008 (48)	0.106 ± 0.010 (35)

Table 3 : Principal changes generated in the dominant fauna by the impact of the cyclone Firinga (Janv.89) on the inner part of the reef flat (% in coverage)

GROUP	DISPARITION AND/OR DEATH OF…	ABUNDANCE OF…
ALGAE	… crustose calcareous and coralline algae	… *Lobophora variegata* and fleshy macroalgae *(Dictyota sp., Padina sp.)*
CORALS	… 99% of the coral community	…none
WORMS	… common large (l=20cm) wandering Polychaetes	…none, except foraging sipunculids
GASTROPODS	…a diverse fauna of Gastropods and Nudibranchs	…a Prosobranch Trochidae, *Clanculus puniceus* (until 50 ind./m^2 of hard substratum)
CRUSTACEANS	…crabs and particularly shrimps	…Paguridae mostly established into the *Clanculus* shells
ECHINODERMS	…Urchins Diadematidae *(Diadema setosum,* and some *Echinothrix)* that were common (2 or 10 ind./metric *Acropora* bush) and *Echinometra mathaei* within the coral branches … large holothurians *Holothuria leucospilota* (l>30cm) on sand	… *Tripneustes gratilla* (5ind./m^2) on debris covered with fleshy algae
FISH	Diverse community of reef fish, characterised by larger forms than on other reef flats. Presence of *Stegastes nigricans* territories (20% of *Acropora pharaonis* cov.)	Dominance of *Stegastes nigricans* and *Acanthurus triostegus* in number of individuals

There was a highly significant relationship between NO_3^- + NO_2^- and salinity (or reactive silicate) along the shore (Table 2). From December 1992 to May 1993, when the lowest salinities were observed (Fig. 2), NO_3^- + NO_2^- was related to reactive silicate on the reef flat (Fig. 3). Ammonium and DIP concentrations were higher along the shore than in zones M and C (low tide only; Mann-Whitney; $p = 0.0001$ and $p < 0.006$ respectively). Along the shore, the relationships found between ammonium or DIP and the freshwater tracers were weak, although significant (Table 2). From December 1992 to May 1993, r values for Spearman rank order correlations between reactive silicate and ammonium or DIP were low on the reef flat ($r = 0.45$ and $r = 0.41$ respectively). However, both relationships were highly significant ($p = 0.0001$).

Description of benthic communities

1987
The Saint-Leu inner reef flat communities were among the richest of all Réunion reef flats in terms of coral abundance, species richness and biodiversity of associated fauna (Naim 1989). The coral community was dominated by large (plurimetric) and coalescent *Acropora pharaonis* colonies, emerging at very low tides. Algae were crustose, coralline and turfs. The emerging coral branches were entirely covered by crustose coralline algae, and the base totally covered by *Amphiroa fragilissima* thalli. More rarely occurred small *Actinotrichia rigida* cushions. Turfs (*Stegastes nigricans* territories) were restricted to the branches facing the narrowest channels between coral bushes (Fig. 1). Abundant gastropods (particularly Nudibranchs) and shrimps were housed by coral colonies. Nocturnal Diadematidae (2 to 10 ind./m^2), mostly *Diadema setosum* and some *Echinothrix calamaris*, sheltered underneath coral shrubs while numerous *Echinometra mathaei* and rare Cidaridae took shelter among colonies.

March 1989
In January 1989, the impact of hurricane Firinga, mostly characterized by heavy rains and sedimentation, greatly modified the shallow coral reef communities (Table 3). In March 1989, all corals were dead, except some *Porites lutea* and small patches of *Pavona divaricata*, but the structure still intact. The substratum was covered by terrigenous sediments that disappeared 6 months later (Letourneur et al 1993). One year later (summer 1990), the substratum was covered by macroalgae (Cuet, pers.obs.).

September 1992. (1) Before experimental modification
Three and half years after Firinga, the area was characterized by a very low percentage of living corals, while macroalgae and turfs dominated (Table 4). *Lobophora variegata* was the most dominant alga: on emerging branches, an encrusting form had replaced the previously dominant crustose algae, while in crevices and on *Acropora* coral rubble, a foliose form had spread out. Foliose thalli of *Dictyota sp* and *Padina spp* totally covered the remaining hard substratum. The algae formed a mosaic of imbricated thalli. An abundance of gastropods Trochidae *Clanculus puniceus* (Table 3) was preferentially established in shady crevices, on the foliose *Lobophora variegata*, while the sea urchin *Tripneustes gratilla* was preferentially associated with the surrounding macroalgae covering coral rubble. Some *Echinometra mathaei* were hidden among dead coral branches and no *Diadema* was observed.

September 1992. (2) After experimental modification
Following the "pruning" of *Acropora* outer branches, sciaphilous crustose algae which were exposed to light died within 2 days. The "pruned" colonies were then covered with a thin white layer of dead crustose algae, forming a substratum available for colonization. The cryptic *Echinometra mathaei* population was exposed by the branch cutting and did not show any obvious perturbation one month after the cutting. Following the removal of the dead coral debris, *Tripneustes gratilla* first found shelter among the "pruned" colonies and then disappeared within one month, while still abundant in the control zone.

Table 4 : Percents of coverage and densities in benthic communities, in 1987, 1989, in Sept.1992 before (LIT) and after the experiment, in Dec.1994 in the control (C) and modified (M) zones (quadrats)(standard deviation into brackets)

YEAR AND IMPACTS	LIVING CORALS	BARE SUBSTRATUM	CALCAREOUS ALGAE	MACROALGAE	TURFS	SEA URCHIN DENSITY ind./m^2	
before cyclone(1987)	*Acropora pharaonis* dominant		Dominance (see Tab.1)		20%	Abundance of Diadematidae	Healthy internal reef flat
after cyclone (Mar. 89)		0%			*S.nigricans* : dominant in the fish community	No sea urchins	Heavy degradation
before exp. (Sept. 1992)	Coral recolonisation 0.6%			66%	28%	*Tripneustes gratilla* :5. Cryptic *Echinometra mathaei*	State dominated by algae
after exp. (Sept. 1992) Part M	0.6%	100%	0%	0%		*T.gratilla* : 0 *E. mathaei*: 5	
3 years & 1/2 after the exp. (Dec.1994)							
MODIFIED ZONE (part M)	1.9 % (2.8)	50.5 % (36.2)	23.5 % (27.2)	10.0 % (13.4)	14.1 % (15.6)	*E. mathaei* : 36.9 (26.6)	**Evide of a shift**
CONTROL ZONE (part C)	1.3 % (2.0)	19.2 % (29.2)	2.0 % (5.5)	42.1 % (31.6)	35.4 % (32.7)	*E. mathaei* : 7.8 (10.0)	

December 1994. (1) Control zone
Macroalgae and turfs associated to *S. nigricans* territories were still dominant (Table 4), but the macroalgal mat displayed a decrease in coverage and thickness. Since September 1992, living coral coverage increased twofold.

December 1994. (2) Modified zone
Macroalgae and turfs did not entirely recover on the "pruned" *Acropora* bushes (Table 4). The sea urchin *Echinometra mathaei* became abundant. Bare substratum reappeared and photophilous crustose coralline algae settled back on substrates exposed to light. The channels where rubbles were removed, were still clean and sandy. Since September 1992, living coral coverage increased threefold.

Ichthyological communities

Total ichthyofauna
In summer 1989-90, 1993-94, 1994-95, *Stegastes nigricans* represented more than half of the total abundance of fishes (Table 5). The total abundance of fishes did not significantly differ in 1989 (following Firinga) and in 1993-94 and 1994-95. Nevertheless, fishes were more numerous in 1994-95 than in 1993-94 (SNK test, $P<0.001$).
The percentage of macroalgal grazers plus *Stegastes nigricans* did not show any significant change over time, whereas the percentage of all herbivorous fishes combined significantly increased between 1993-94 and 1994-95 (+34.7%, SNK test, $P<0.001$) (Table 5). This pattern was mainly the result of an increase in *Scarus spp* and *Ctenochaetus striatus* populations. Herbivorous fishes were very abundant on the Saint-Leu inner reef flat, reaching 89% of the total fish counts. On other Reunion inner reef flats, percentages of herbivorous fishes, including *Stegastes nigricans*, ranged from 51% to 62% (Letourneur 1996).

Table 5. Total ichthyofauna expressed as mean number of individuals per $100m^2$, and percentages of herbivores, consumers of macroalgae and *Stegastes nigricans* (standard deviation in brackets)

	1989-90	1993-94	1994-95
Total ichthyofauna	395.0 (118.2)	355.7 (41.9)	479.3 (37.6)
% of herbivores	71.2 (16.8)	78.5 (1.5)	89.2 (1.7)
% of consumers of macroalgae	63.5 (15.5)	71.0 (2.7)	70.1 (2.2)
% of *Stegastes nigricans*	55.0 (15.4)	56.9 (4.3)	56.4 (2.7)

Stegastes nigricans in control (C) and modified (M) zones
In December 1994, the number of individuals in zone C was about twice as high as in zone M (Table 6). Although mean sizes were not significantly different between zones (Table 6), the size structures were significantly different ($\chi^2 = 28.03$, $P<0.005$, df = 8). The fish were smaller in the modified zone than in the control zone, as clearly observed when sizes were pooled into three size-classes (Table 6).

Table 6 : Characteristics of *Stegastes nigricans* populations in control and modified zones (standard deviation in brackets)

Stegastes nigricans	Control zone	Modified zone
Total number	89	48
Mean number/m^2	2.97 (2.08)	1.61 (1.59)
Mean size (cm)	8.44 (1.82)	7.43 (1.71)
%< 6cm	13.6	23.0
% 7-8 cm	28.6	52.1
%> 9 cm	57.9	24.9

DISCUSSION

Chronic terrigenous input of nutrients
Seasonal variations in reef water salinity are thought to be mainly due to submarine groundwater discharge (SGD). Evidence of SGD occurring along the shore comes from the increase in salinity found between the shore and zones M and C, and from the relationship found between silicate, naturally high in groundwater, and salinity along the shore. Such relationships are also observed on the reef flat during the rainy season, and, on average, silicate is higher in zones M and C than on the reef front. Groundwater discharging along the beach thus appears to reach zones M and C part of the year.

The relationships found between $NO_3^- + NO_2^-$ and reactive silicate, used as a freshwater tracer, suggest that SGD might produce a significant enrichment of $NO_3^- + NO_2^-$ to the reef. The mean $NO_3^- + NO_2^-$ content of the freshwater, roughly estimated as the ordinal intercept value obtained from the dilution line (linear regression between $NO_3^- + NO_2^-$ and salinity found along the shore), is about 148 µM. Ammonium and DIP concentrations are higher along the shore than in zones M and C. However, the relationships found between ammonium or DIP and the freshwater tracers are weak. Whether the increase in ammonium and DIP observed along the shore is due to SGD or to some nutrient export from the reef flat (or to some export of particulate organic matter undergoing mineralisation in the back reef zone) is thus unclear.

In zones C and M, levels of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in 1992-93 (0.70 ± 0.04 µM DIN; 0.110 ± 0.006 µM DIP) were slightly lower than the eutrophication thresholds suggested by Bell (1992) for coral reef waters. The chronic enrichment of terrigenous nutrients to the reef flat through groundwater inputs, a common phenomenon in Réunion island (Cuet 1994), appears to be moderate, and even not significant for phosphorus.

Switch to algal dominance just after hurricane Firinga
After the hurricane, the mass coral mortality induced by hypersedimentation was followed by a colonization of dead coral skeletons by algae, as observed on other reefs struck by hurricanes (review: Harmelin-Vivien 1994). Increased area for settlement (skeletons of dead corals), increase in availability of nutrients, and mass mortality of sea urchins were presumably among the main factors enhancing algal growth (Hatcher 1984).

Abiotic factors
Some nutrient enhancement may have lasted for some time after the hurricane, resulting in an increased macroalgal production. Relatively high concentrations of N can occur in runoff (Gabric and Bell 1993). Heavy rains may wash some P off the watershed (Marsh 1977). Most of the nutrients in runoff are transported as particles (Gabric and Bell 1993). Terrigenous materials were trapped in the reef framework during the hurricane, and silt-associated nutrients may have been recycled into the dissolved phase at a later time. The increase in availability of phosphorus may have been especially significant, as nitrogen is provided by SGD.

Biotic factors
Reduced herbivory alone may have been sufficient to promote the fleshy algae settlement. Littler and Littler (1985) consider that, on undisturbed reefs, nutrients set only the potential upper limits to algal biomass: grazing is considered the more important direct control of algal growth. Before the hurricane, fishes and Diadematidae were abundant and grazing may have kept algal biomass at a low level.

After the hurricane, the Diadematidae totally disappeared, reminiscent of the well-known example of the Caribbean-wide decline of *Diadema antillarum* which resulted in an increase in algal biomass (Lessios et al 1984, Hughes 1994). Experiments from Carpenter (1986) showed that low *Diadema* grazing resulted in a shift in algal component composition: crustose algae were reduced in abundance in favour of fleshy algae, suggesting that encrusting calcareous Rhodophytes required the removal of faster growing algal species by herbivores to persist (Steneck 1983).

Herbivorous fishes, despite a temporary spatial redistribution, did not show a significant increase in density, suggesting a constant pressure on algal communities (Letourneur et al 1993). Competition between urchins and fishes is usually high, and low densities of urchins may affect both density and foraging behaviour of herbivorous fishes (Hay 1991). Contrasting with the Caribbean example where fish grazing increased by 2- 4-fold (Carpenter 1988, 1990), herbivorous fishes did not respond to the increase in algal cover and reduction of competition linked to *D. setosum* mortality, probably due to limitation in recruitment (Letourneur et al 1993).

Persistence of the algal community in the control zone

Abiotic factors
Most of the factors responsible for nutrient enhancement after the hurricane (silt-associated nutrients, mineralisation of coral tissues,...) were obviously not involved anymore. SGD produced a chronic enrichment of nitrogen to the reef, but phosphorus input was not significant. Further increase in nutrient levels may

have occurred in pulses, such as during wet season runoff. This phenomenon might be responsible for sustaining the algal biomass in Moorea, French Polynesia (Done 1992).

Biotic factors
However, macroalgal dominance may persist in the absence of any continuing nutrient enrichment, due to grazer-resistance of macroalgae, through a perturbation-induced escape in size (Hatcher 1984), or because a deterrent effect making them unpalatable (Ogden and Lobel 1978; Norris and Fenical 1982; Littler et al 1983; Steneck 1988). Numerous chemical deterrents were isolated from algae, and their significant protection against herbivores evidenced. Dictyol compounds, issued from *Dictyota* species, have been extensively tested as defenses against several herbivorous fishes (Hay et al 1987; Hay 1991). Other factors may be involved.

Exclusion of herbivores by Stegastes nigricans. According to Montgomery (1980), *S. nigricans* defends an area larger than its turf territory (35% of the substratum in zone C). Abundance of macroalgae at the periphery of *Stegastes* territories is marked (Naim 1993), as exclusion of both herbivorous fish and urchins results in rapid accumulation of algae (Sammarco et al 1974; Carpenter 1981; Sammarco 1982; Williams 1984; Vadas 1985). Considering its patchy distribution, *S. nigricans* protects much more than 35% of the substratum against any other herbivore intrusion (including sea urchins). Moreover, territorial behaviour against other herbivorous fishes, more pronounced in medium and large individuals (Letourneur 1994), is higher in zone C where *S.nigricans* individuals are larger than in zone M.

Reproductive strategy of algae. Lewis et al (1987) considered the foliose form of *Padina spp* as highly suceptible to grazing. Its abundance in zone C suggests a reduced activity of the herbivores. But at certain times and places, foliose *Padina* exhibits rapid growth, reproductive maturity and high reproductive output, and effectively occupies large areas of reef (Lewis et al 1987). In these circumstances, the magnitude of the resulting algal standing crop is no longer primarily controlled by grazing activity, but rather by species-specific growth characteristics of the dominant macroalgae in response to abiotic and biotic factors (Hatcher and Larkum 1983).

Shift in benthic communities after the experiment: the modified zone

Abiotic factors
Salinity is similar in zones M and C, and reactive silicate only slightly higher in zone M, suggesting that freshwater inputs do not greatly differ between the two zones. The strong currents prevailing on the Saint-Leu reef flat presumably prevent any patchiness in freshwater distribution and nutrient input through SGD. DIP is similar in zones M and C, and DIN only slightly higher in zone M, again suggesting that mixing and diffusion homogenize nutrient levels in the two zones. It is thus unlikely that nutrient availability is limiting macroalgal growth in the modified zone.

Biotic factors
Echinometra mathaei and Stegastes nigricans: competition for space and food. In zone C, the *Echinometra mathaei* population is under *Stegastes nigricans* control. Thus, urchins are confined to cavities, and probably feed on detritus falling into the crevices and sciaphilous crustose algae. In zone M, following the "pruning" of the *Acropora* shrubs, *E. mathaei* ended up in the upper part of the substratum. The sea urchins had to feed outside of the shallow excavations in which they sheltered, because those excavations did not trap the detritus as well as deep ones. Thus, liberated from *Stegastes* territorial influence, the sea urchins adopted a wandering behaviour (Prigent obs.). They might then increase rugosity, favour alteration of the surrounding communities by grazing, and, among with other epilithic organisms, particularly reduce the growth of young and tender algae. In Caribbean, density of 5 ind./m^2 was supposed to be suffisant to limit the recolonisation of the young algae (Lawrence and Sammarco 1982). Three and half years after the experiment (December 1994), *E.mathaei* has excavated the substratum and its density has increased 7fold. Diadematidae were still rare, indicating that the environmental conditions were still unsuitable to this family and/or that no recruitment of larvae had occurred.

Herbivorous fish and Stegastes nigricans: competition for space and food. After the experiment, the surface of *Stegastes* territories was smaller in zone M than in zone C. In agreement with this observation, small *S.nigricans* (zone M) slightly fed on algae and strongly relay on invertebrates whereas medium and large indivuduals (zone C) highly fed on algae (Letourneur et al in press). Thus, besides low densities of *Stegastes nigricans* in zone M, the decrease in territories surface lead to an increase in accessibility to herbivorous fish. There is little evidence that herbivorous fish have capacity to select individual plants or part of plants, such as young stages or parts rich in nitrogen (Robertson and Gaines 1986; Hay 1991). However, on Réunion reefs, fish distribution is mainly determined by geomorphology (Letourneur 1996). Since nutrient availability was favourable to algal growth, herbivorous fish closely linked to the small St-Leu inner reef flat, would feed on zone M, in preference to the rest of substrata which is dominated by unpalatable algae.

Rapid or slow shift
Macroalgal dominance can last indefinitely, either because environmental conditions favour algal growth over coral growth, or because the shift towards algal dominance is difficult to reverse: the latter is referred to a "phase shift" and was suggested to be a universal symptom of coral reef degradation (Done 1992). This was not the case in our study: macroalgae decreased slowly in time in the control zone.

Herbivory reduces algal biomass and induces a shift in community dominance from macroalgae to turfs, and ultimately to encrusting corallines (Steneck 1988). From the experiment, the density of herbivorous fish and sea urchins increased and the relative coverage of fleshy algae, turfs and crusts (Fig. 4) has changed. As Littler and Littler (1985), and Steneck (1988) have shown in their work, figure 4 suggests that nutrients decreased while total herbivory increased in zones M and C. In the modified zone, a rapid shift in the algal community structure, induced by the experiment, ended in a new equilibrium dominated by turfs and crusts. In the control zone, a slower shift (over several years) is occurring. Further investigations will show whether the re-establishment of coral communities will occur by a slow constant process, or by a very rapid recovery, once a threshold is reached.

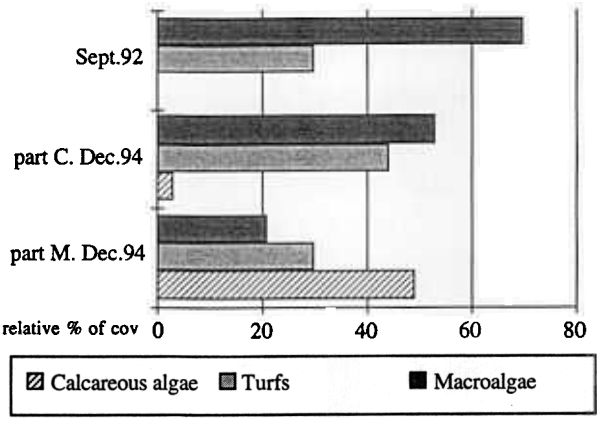

Fig.4 : Relative cover percentages of macroalgae, turfs and calcareous algae in Sept. 92 and Dec. 94 in control (C) and modified (M) zones.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Hatcher (1984) has summarized the problem of the shift from coral to algal dominance in the following terms : "Are the shifts simply a result of natural cycles in the relative abundance of predators and prey? Or are they perturbation-related changes between alternate stable states requiring another perturbation or natural catastrophe to return the community to its original structure?".

Our experiment of algal removal suggested that the occurrence of a macroalgae-dominated state required another perturbation to return rapidly to a strong control of turfs and macroalgae by herbivores. Long-term monitoring of the area will test the apparent trends observed in December 1994. If a faster recovery of hard

corals in the modified zone is confirmed, active rehabilitation, by "cleaning" the substrata, could be considered as a prioritary management action in order to facilitate coral recruitment and accelerate the recovery of coral reefs.

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