Algal growth on two sections of a fringing coral reef subject to different levels of eutrophication in Réunion Island

Coral reef
Macroalgae
Eutrophication
Groundwater discharge
Réunion Island

Récif corallien
Algues molles
Eutrophisation
Percolations d'eaux souterraines
Ile de la Réunion

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ABSTRACT

The temporal variations in macroalgal coverage and biomass of two sectors of a fringing reef complex in Réunion Island, subject to different levels of nutrient enrichment, were compared over eight months. Little difference was detected in the back reef zone, but in the narrow coral strip zone the highly enriched site showed significantly higher coverage, biomass and diversity of macroalgae throughout the whole study period. Differences in the levels of nutrient enrichment of the reef waters of the two sites are implicated as potential reasons for the observed differences. The seasonal variations of macroalgae on the reef, and aspects of several of the dominant algal species encountered are also discussed.

RÉSUMÉ

La croissance des macroalgues dans deux secteurs de récif soumis à un enrichissement différent en sels nutritifs (La Réunion).

Les variations spatio-temporelles de la couverture et de la biomasse des macroalgues molles ont été suivies pendant huit mois sur deux secteurs de récif frangeant de géomorphologies comparables mais soumis à un enrichissement différent en sels nutritifs. De faibles différences sont décelées dans la dépression arrière-récif. En revanche, sur le platier récifal fortement enrichi en sels nutritifs, la couverture algale et sa biomasse est plus grande et sa diversité plus importante tout au long de l'étude. L'écart entre les concentrations en sels nutritifs dans les eaux récifales des deux secteurs peut expliquer ces différences. Les variations saisonnières des algues molles ainsi que la dominance de certaines espèces rencontrées sont également détaillées.

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INTRODUCTION

Although coral reefs are known to be among the most luxuriant and productive ecosystems in the world (Lewis, 1977), it is most often for their fauna that they are noted, with benthic plants often being relatively inconspicuous. Algal dominance of coral reef ecosystems can occur after certain phenomena such as the mass death of herbivores (*e.g.* Carpenter, 1985), but such events are rare. A more common cause of the presence of abundant assemblages of algae is eutrophication, where an increase in nutrients levels in the ecosystem, occurring most often as a result of human activities, leads to the abnormal growth of algae, which eventually replace coral, and an increase in the populations of filter and detrital feeders (Bell, 1992). One of the earliest reported cases of eutrophication was that of

Kaneohe Bay, Hawaii (Banner, 1974) but more recently it has also been recognised in the Red Sea (Mergner, 1981), Barbados (Tomascik, 1990), the Great Barrier Reef (Bell, 1991; Bell and Elmetri, 1995), Martinique (Littler *et al.*, 1992) and Réunion Island (Cuet *et al.*, 1988; Naim, 1993).

The competition processes between algae and coral are very sensitive to disruption (Pastorok and Bilyard, 1985). Under eutrophic conditions algae tend to out compete coral (Littler and Littler, 1985; Naim, 1993), coral growth rates are reduced (Kinsey and Davies, 1979; Tomascik and Sander, 1985), bioerosion of corals is promoted (Hallock, 1988), and the rate of settlement of coral larvae falls (Tomascik, 1991). Eutrophication also appears to affect the reproductive patterns of coral species, and the number of larvae that they produce diminishes (Tomascik and Sander, 1987*a*). On a broader scale, coral species diversity is lower in eutrophic conditions, and the structure of coral communities is altered (Tomascik and Sander, 1987*b*). Ichthyological communities are also affected (Chabanet, 1990; Letourneur, 1992), and thus eutrophication is damaging from an economic as well as from a purely ecological standpoint.

In the 1970s, the fringing reef complex of St Gilles/La Saline of Réunion Island was in good health (Bouchon, 1981; Faure, 1982), with flourishing coral communities and algae present only during the summer season, and then only as a narrow band on the outer reef flat. However, by 1983 this reef was noted to be undergoing serious degradation (Guillaume *et al.*, 1983). Later, Cuet *et al.* (1988) highlighted the presence of high concentrations of nitrate and phosphate in the reef waters and proposed a link between the demise of coral communities associated with macroalgal dominance of the reef complex, and the extension of submarine groundwater discharge (SGD) onto the reef. This discharge is rich in nutrients which seem to originate from human activities, following the growth of the population in the watershed alongside inefficient sewage treatment. Naim (1993) described the seasonal responses of one of the most degraded sectors of the reef to eutrophication stress; in this and other highly enriched sectors of the reef, a nutrient-regulated change (*sensu* Atkinson, 1988) appears to have occurred *i.e.* changes have occurred not merely in a rate process, but actually in the trophic structure of the reef, with macroalgae now dominating over the previously healthy coral communities. The decline of this and other such fringing reefs poses serious problems not only in ecological terms, but also for the economy of the island. By shielding them from wave action, the reefs protect and maintain the island's beaches. In addition, the lagoons act as nurseries for many fish species (Letourneur, 1992), and thus play a vital role in maintaining a traditional fishing industry.

In order to assess the extent of this phenomenon, the cover and biomass of macroalgae were compared at two sectors of the reef, subject to very different levels of nutrient enrichment (Cuet, 1989), over a period of eight months from December 1992 to August 1993.

MATERIALS AND METHODS

Location and Physiography

Réunion Island is located in the south-west Indian Ocean (Fig. 1) and has a surface area of 2512 km^2. Its fringing reefs form a discontinuous belt along the dry western coast. The most developed reef complex is that of St Gilles/La Saline, which extends for approximately 9 km, with a maximum width of just over 500 m (Fig. 2).

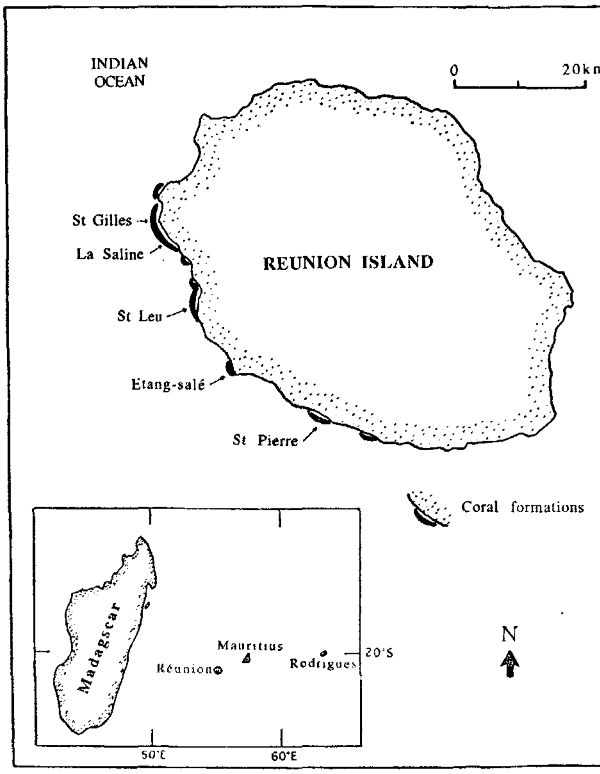

Figure 1

Location of Reunion Island and the studied reef complex.

Essentially, the reef can be divided into three sections, according to Battistini *et al.* (1975) (Fig. 3):

(1) a reef flat, exposed at low tide, which can be further divided into three subzones (a) an outermost compact reef flat, exposed to strong wave action, and consisting of a roughly horizontal pavement, (b) a zone of narrow coral strips, and (c) a zone of large coral strips, separated by narrow, shallow detrital channels,

(2) a zone of scattered coral colonies, principally composed of branching corals, and

(3) a back reef zone, which represents the deepest zone of the reef (1-1.5m) and is largely detrital in nature.

The studied reef is not subject to any input of surface water from the island.

Environmental factors

The climate of Réunion Island alternates between a hot, wet summer season (from November to April), and a cool, dry winter season (from May to October); August is typically the coldest month and January the

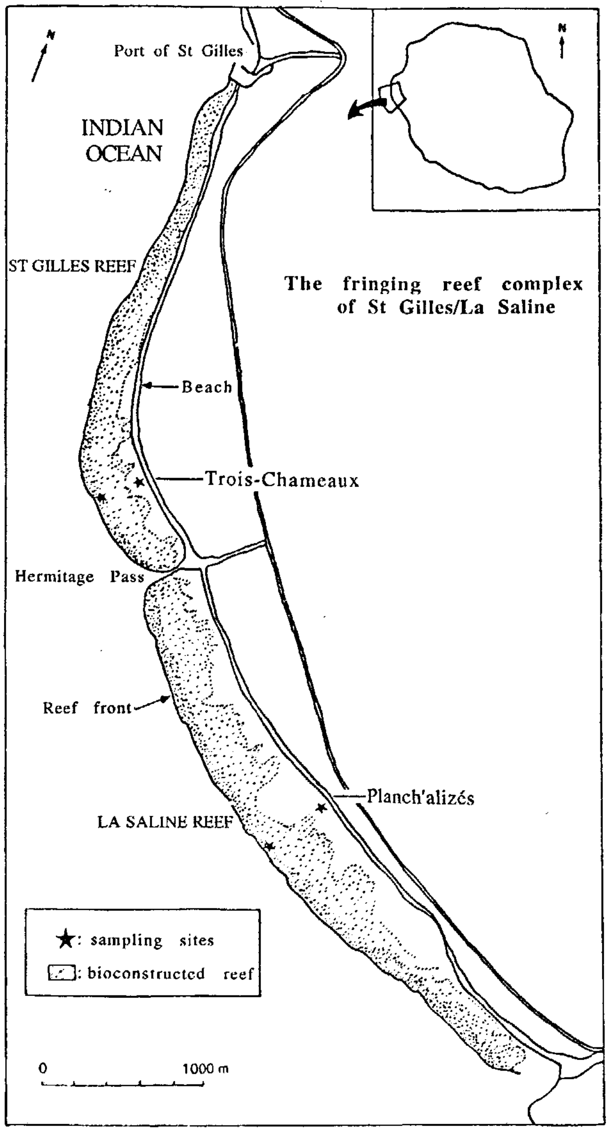

Figure 2

The St Gilles/La Saline reef complex, with the two study sites indicated.

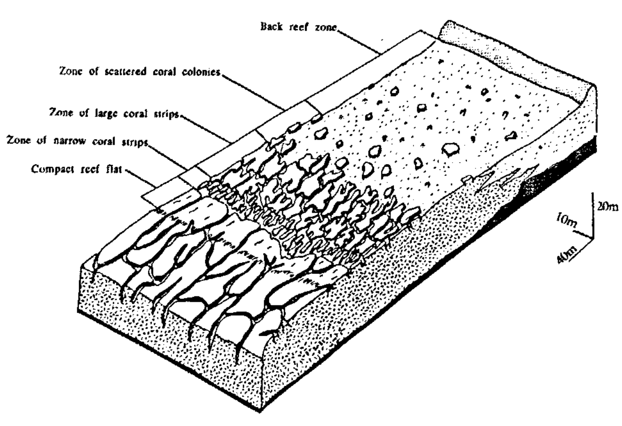

Figure 3

Geomorphology of the St Gilles/La Saline reef.

warmest. Water temperatures on the studied reef vary from 23.8 °C (July/August) to 28.0 °C (January/February) (Cuet, 1989). Ocean tides are semi-diurnal and range from 0.1-0.8 m, although ocean swells can cause more pronounced variations.

Three types of ocean swells contribute to the high hydrodynamism to which the reef complex of St Gilles/La Saline is subject:

(1) the most frequent are those caused by the south-east trade winds which are most common in the fresh season but persist throughout the year; these swells have a maximum amplitude of 0.5 m during the summer season and 2.0 m during the winter season

(2) during the summer season, tropical depressions and cyclones can give rise to violent swells (up to 4.0 m in amplitude) but their occurrence is relatively rare and their duration normally less than 48 h (Montaggioni and Faure, 1980); otherwise, this season is characterised by very small swells

(3) the third type of swell results from polar depressions in the region of Marion Island; these swells are more common during the winter season, but can occur throughout the year. Their amplitude can approach that of cyclonic swells but their duration is usually limited to 24 h.

METHODS

The cover and biomass of macroalgae were measured in the back reef zone and the zone of narrow coral strips of two geomorphologically comparable sectors of the St Gilles/La Saline fringing reef complex. The first, "Trois-Chameaux" is only slightly enriched in nutrients, while the second, "Planch'alizés" is strongly enriched. These two sites are 2 km apart, lying to the north and south side respectively of the Hermitage Pass. The strong enrichment of Planch'alizés is due to the percolation of SGD into the lagoon during low tide.

The back reef zone and the zone of narrow coral strips were chosen for this study, because the former is the zone receiving the highest concentrations of nutrients from SGD (Cuet, 1989), while the latter is the zone in which the greatest proliferation of algae occurs (Naim, 1993). The sampling in each zone of each site was performed by the quadrat method around permanent transect lines of 50 m in length, laid down parallel to the shore. A quadrat of 25 cm × 25 cm, divided internally into squares of 5 cm × 5 cm was thrown thirty times at random in the study area. On each occasion, the coverage of all macroalgal species (to the nearest 25 cm^2) was noted on a marine field board. Each species was then removed from the substrate and placed in an individual plastic bag, along with sea water to prevent desiccation and a label providing all the details of the sampling. Immediately on return to the laboratory, the sea water was replaced by 5 % formaldehyde to preserve the integrity of the samples.

Later, samples were rinsed thoroughly under fresh running water to remove particulate matter and any associated micro-organisms. Excess water was removed by spinning the samples in a salad wringer, and wet weight was then measured. In order to measure their dry weight, samples were placed in a laboratory oven at 100 °C for 24 h. On removal from the oven, all samples were weighed immediately to minimise absorption of atmospheric moisture.

The cover and biomass of macroalgae between the two test sites were compared using the Student test. The Shannon index of diversity was calculated for cover and biomass (dry weight) for each zone of each site during each month and for the total duration of the study.

RESULTS

Species list

A list of the species encountered during this study, and their distribution among the four zones studied is shown in Table 1. At Trois-Chameaux, twelve species of macroalgae were sampled in the back reef zone during the study period, of which two were not seen in any of the other three zones studied. At Planch'alizés ten species were sampled in the back reef zone, one of which was not sampled in the other three zones studied.

In the zone of narrow coral strips at Trois-Chameaux, ten species of macroalgae were sampled, of which two were not seen in any of the other three zones studied. In the corresponding zone at Planch'alizés, the greatest number of algal species was observed, with twenty-two species in total being sampled during the study period, of which nine were not sampled elsewhere.

Table 1

List of species sampled during the present study with their distribution within the four study zones. (c – species not found in the other three zones studied.)

	Trois-Chameaux		Planch'alizés	
	BRZ	NCSZ	BRZ	NCSZ
PHAEOPHYCEAE				
Dictyota divaricata	-	-	-	c
Hydroclathrus clathratus	+	+	-	+
Lobophora variegata	+	-	+	+
Padina sp. 1	-	+	+	+
Padina sp. 2	-	-	-	c
Turbinaria ornata	+	+	+	+
CHLOROPHYCEAE				
Boergesenia forbesii	-	+	+	+
Caulerpa serrulata	-	-	c	-
Cladophoropsis sp.	-	c	-	-
Dictyosphaeria cavernosa	-	+	-	+
Dictyosphaeria setchellii	+	+	+	+
Valonia ventricosa	c	+	-	+
Valoniopsis pachynema	+	-	-	-
RHODOPHYCEAE				
Acanthophora spicifera	-	-	-	c
Actinotrichia fragilis	+	-	-	+
Digenea simplex	-	-	-	c
Galaxaura subverticillata	+	+	-	+
Gelidiella acerosa	+	-	+	-
Gelidiopsis intricata	-	-	-	c
Gelidium sp.	+	-	+	+
Gracilaria crassa	-	-	+	+
Hypnea valentiae	+	-	+	+
Wurdermannia miniata	-	-	-	c
UNIDENTIFIED SPP.				
Species 1	-	c	-	-
Species 2	-	-	-	c
Species 3	-	-	-	c
Species 4	-	-	-	c
Species 5	c	-	-	-
Total Number of Species	**12**	**10**	**10**	**22**

Macroalgal diversity

Cover

The Shannon index of diversity for each zone for each month and for the entire study period, calculated for percentage cover, are shown in Table 2. On considering the back reef zones of the two study sites, there appears to be little difference between them. However, the narrow coral strip zone of Planch'alizés shows a higher diversity of macroalgae than Trois- Chameaux, not only for the study period as a whole but also for every month in which sampling occurred.

Biomass

The Shannon index of diversity for each zone for each month and for the entire study period, calculated for biomass, are shown in Table 3. For the back reef zone, Trois-Chameaux shows a higher diversity for the total study period than does Planch'alizés. In the narrow coral strip zone of Planch'alizés, a higher diversity of macroalgae was found than at Trois- Chameaux for every month in which sampling occurred and for the total study time.

Coverage and biomass

Back reef zone

The cover, wet weight and dry weight of macroalgae in the back reef zones of the two test sites are shown in Figure 4. Overall coverage and biomass in this zone was low, with only one species, *Hypnea valentiae*, being significant. This species showed a maximum for both measures in the month of February (11.3 % cover, 183.7 g/m^2 wet weight and 16.1 g/m^2 dry weight at Trois-Chameaux; 14.5 % cover, 327.9 g/m^2 wet weight and 26.0 g/m^2 dry weight at Planch'alizés), and accounted for almost all of the overall temporal variation (a prominent peak in February) observed during the study in the back reef zone at the two study sites. This alga was more abundant within the sampling zone at Planch'alizés than at Trois-Chameaux, and elsewhere in shallow areas of the back reef zone at the former site showed 100 % coverage over large areas of substrate.

Extrapolating the data from the present study to the total surface area of the back reef zones of the two study sites – 18,750 m^2 at Trois-Chameaux and 31,250 m^2 at Planch'alizés – (Naim, *pers. comm.*), it is calculated that in February the total wet weight of algae present in the back reef zones of Trois-Chameaux and Planch'alizés was approximately 5.8 tons (of which 5.4 tons was accounted

Table 2

Shannon index of diversity of macroalgae (by coverage) in the four zones studied, for each month and for the total study time.

	Back Reef Zone		Narrow Coral Strip Zone	
	Trois-Chameaux	Planch'Alizés	Trois-Chameaux	Planch'Alizés
December	2.15	1.44	0.43	3.27
January	2.17	1.05	0.55	3.02
February	0.33	0.80	1.76	2.93
March	-	-	-	-
April	1.00	0.92	1.68	2.44
May	1.58	0.00	1.53	2.74
June	1.00	0.00	1.93	2.65
July	-	-	-	-
August	0.00	0.00	1.38	1.70
Whole study	**1.58**	**1.29**	**2.23**	**3.21**

Table 3

Shannon index of diversity of macroalgae (by dry weight) in the four zones studied, for each month and for the total study time.

	Back Reef Zone		Narrow Coral Strip Zone	
	Trois-Chameaux	Planch'Alizés	Trois-Chameaux	Planch'Alizés
December	0.76	1.52	0.18	2.71
January	2.32	0.67	0.35	2.12
February	0.18	0.31	1.54	2.50
March	-	-	-	-
April	0.76	1.25	1.44	2.14
May	1.47	0.00	1.36	2.47
June	0.57	0.00	1.62	2.67
July	-	-	-	-
August	0.00	0.00	1.21	1.56
Whole study	**1.69**	**0.83**	**1.85**	**2.82**

Table 4

Nutrient concentrations of reef waters in the study zones 1985-1986 (from Cuet, 1989).

	Back reef zone		Reef flat	
	Trois Chameaux	Planch'alizés	Trois Chameaux	Planch'alizés
Nitrate (mean) (mM/l)	0.73±0.35	3.23±0.99	0.71±0.36	0.96±0.42
Nitrate (max) (mM/l)	2.18(Jun '86)	12.20 (Apr '87)	1.59 (Feb '86)	2.60 (Dec '85)
Phosphate (mean) (mM/l)	0.23±0.06	0.36±0.18	0.39±0.18	0.33±0.09
Phosphate (max) (mM/l)	0.46 (Jan '86)	1.60 (Nov '86)	1.08 (Feb '86)	1.10 (Nov '86)
Ammonia (max) (mM/l)	0.85 (Summer '86)	1.20 (Feb '85)	0.38 (Feb '86)	>2 (March '86)

for by *Hypnea valentiae*) and 11.5 tons (of which 10.2 tons was accounted for by *Hypnea valentiae*) respectively. The biomass calculated in the same manner for the same month was 485 kg (of which 470 kg was accounted for by *Hypnea valentiae*) at Trois-Chameaux and 865 kg (of which 810 kg was accounted for by *Hypnea valentiae*) at Planch'alizés.

Zone of narrow coral strips

The macroalgal cover, wet weight and dry weight in this zone for the two test sites are shown in Figure 5. At Trois-Chameaux, the maximum for all three measures occurred in December (10.8 % cover, 582.4 g/m^2 wet weight and 37.9 g/m^2 dry weight), due to the presence of *Hydroclathrus clathratus*, which had declined by January and was absent in February. The other two species which showed significant cover and biomass during the study are *Turbinaria ornata*, which showed a peak in May (2.4 % cover, 101.8 g/m^2 wet weight and 9.4 g/m^2 dry weight), and *Dictyosphaeria setchellii*, which also showed a peak in May (3.2 % cover, 95.9 g/m^2 wet weight and 5.1 g/m^2 dry weight). At Planch'alizés, algal cover, wet

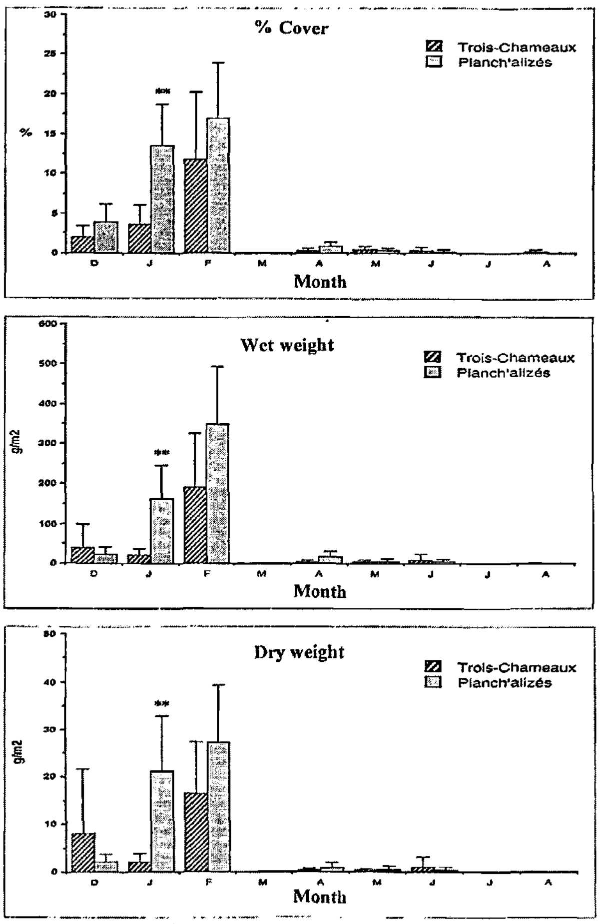

Figure 4

Coverage, wet weight and dry weight of macroalgae in the back reef zone of Trois-Chameaux and Planch'alizés (P < 0.05; ** P < 0.01).*

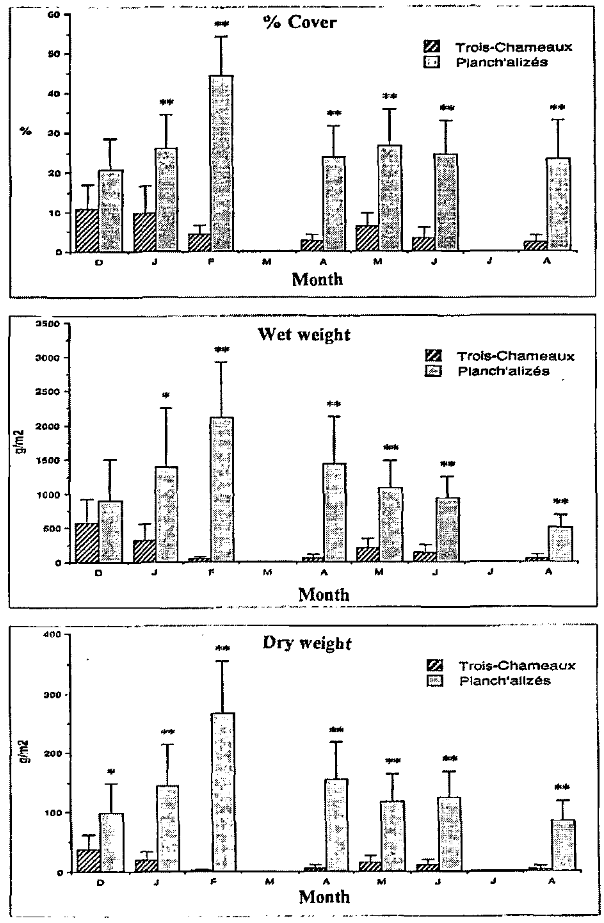

Figure 5

Coverage, wet weight and dry weight of macroalgae in the narrow coral strip zone of Trois-Chameaux and Planch'alizés (P < 0.05; ** P < 0.01).*

weight and dry weight were significantly higher than at Trois-Chameaux. The maximum of these three measures, observed in February (44.4 % cover, 2110.4 g/m^2 wet weight and 266.8 g/m^2 dry weight) was mainly attributable to the abundance of *Gracilaria crassa* (10.1 % cover, 946.7 g/m^2 wet weight and 69.0 g/m^2 biomass), although other species such as *Digenea simplex*, *Gelidiopsis intricata* and *Padina spp.* were also important. The subsequent decline in April (to 23.9 % cover, 1436.8 g/m^2 wet weight and 154.6 g/m^2 dry weight) reflects the reduction particularly of *Gracilaria crassa* and *Digenea simplex*. Throughout the remainder of the study period, these two species continued to decline while the abundance of three other species – *Turbinaria ornata*, *Dictyosphaeria setchellii* and *Dictyosophaeria cavernosa* – increased. Throughout the study, a lawn of *Gelidiopsis intricata* presented a fairly constant coverage (mean 10.57 %) and biomass (mean 58.7 g/m^2) over the whole of this zone.

Extrapolating the data from the present study to the total surface area of the studied narrow coral strip zones - 5000 m^2 at Trois-Chameaux and 7500 m^2 at Planch'alizés – (Naim, *pers. comm.*), it is calculated that in December the total wet weight of algae present in the zone of narrow coral strips at Trois-Chameaux was approximately 2.9 tons

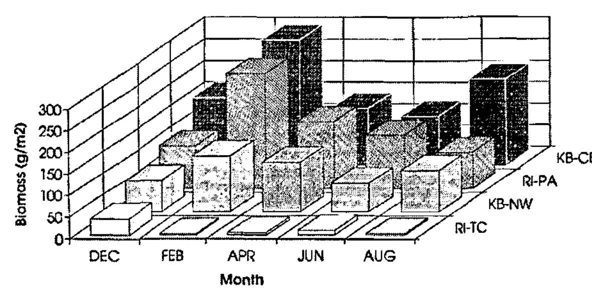

Figure 6

A comparison of the biomass of benthic algae at two sectors (KB-CE and KB-NW) of Kaneohe Bay (before sewage diversion), and the narrow coral strip zone of Trois-Chameaux (RI-TC) and Planch'alizés (RI-PA) from December to August.

(of which 2.8 tons was accounted for by *Hydroclathrus clathratus*). The corresponding result for Planch'alizés for February is 15.8 tons (of which 7.1 tons was accounted for by *Gracilaria crassa*). The biomass calculated in the same manner for the same months was 190 kg (of which 186 kg was accounted for by *Hydroclathrus clathratus*) at Trois-Chameaux and 2000 kg (of which 520 kg was accounted for by *Gracilaria crassa*) at Planch'alizés.

DISCUSSION

Diversity

The back reef zone of Trois-Chameaux appears to show a greater diversity than the corresponding zone at Planch'alizés, especially with respect to biomass; However, very small amounts of macroalgae were present in the back reef zone of the reef from April until the end of the study. Therefore, small differences between the two sites in terms of algal biomass sampled are reflected as large differences in the index of diversity, and thus caution must be exercised in drawing firm conclusions from the comparison.

However, in the zone of narrow coral strips the large number of samples consistently collected throughout the study allows a far clearer comparison to be made. In each month, and for the entire study period, Planch'alizés presents a greater diversity than Trois-Chameaux both in terms of coverage and biomass. This phenomenon may be related to differences in the nature of the herbivorous guild at the two sites; at Planch'alizés, the density of herbivorous fishes is higher than at Trois-Chameaux (Chabanet, 1994), but densities of urchins are very low (Naim, 1993).

Biomass

The most useful manner in which to deal with the results obtained in the present study is to compare them with the results obtained by SMITH *et al.* (1981) for "hard bottom algal biomass" in Kaneohe Bay, Hawaii, *before* sewage diversion occurred. Thus, in Figure 6, the algal biomass found in the narrow coral strip zone at Trois-Chameaux and Planch'alizés is compared with two sectors of Kaneohe Bay, the data having been extrapolated from Figure 37 of Smith *et al.* (1981). It can be seen from this comparison that Trois-Chameaux shows a significantly lower biomass of macroalgae than was found in Kaneohe Bay. At Planch'alizés, however, the values for the mean biomass for the study period (146 g/m^2) and the peak of biomass (267 g/m^2) are comparable with the values found in the worst affected area – sector CE - of Kaneohe Bay (180 g/m^2 and 292 g/m^2, respectively).

These data highlight the gravity of the problem at Planch'alizés, and suggest that restorative measures such as those implemented in Kaneohe Bay should be initiated as soon as possible in Réunion Island.

Seasonal variation

In all of the four zones studied except the narrow coral strip zone at Trois-Chameaux, macroalgae showed a peak in abundance during the summer season. *Hydroclathrus clathratus* was responsible for the high coverage and biomass in the one zone not conforming to this pattern; this one species was sufficiently abundant to mask the trend of the total of all the other species, which was similar to that found in the other three zones studied. At Planch'alizés, the assemblages of macroalgae are known to be correlated to three environmental factors (Naim, 1993). The first, which causes the increase in standing crops during the summer season, is the decrease in hydrodynamism in conjunction with increased water temperatures. This stagnation of the lagoon waters may lead to a more efficient recycling of nutrients within the ecosystem (Lewis, 1977); it is important to note that no increase in the concentrations of nutrients in SGD has been observed in the summer season. Secondly, an increase in water turbulence, linked to the onset of trade winds around March, appears to cause the removal of many macroalgal species from the reef; at this time *Turbinaria ornata, Dictyosphaeria setchellii* and *Dictyosphaeria cavernosa* are the dominant benthic algae on the reef. Thirdly, the establishment of a permanent trade wind regime in winter and a drop in water temperatures cause the removal of nearly all algae from the reef; at this time, only the epilithic *Gelidiopsis intricata* shows a significant cover on the reef flat.

Dominant species

A description of all the species encountered during this study is inappropriate, but four of the more important will be described. *Hydroclathrus clathratus* and *Gracilaria crassa* were the dominant species of the zone of narrow coral strips of Trois-Chameaux and Planch'alizés, respectively. *Hypnea valentiae* was the dominant alga in the back reef zone, while *Turbinaria ornata* was present in all four studied zones and presents an important abundance during the fresh season.

Hydroclathrus clathratus

This phaeophyte was only found in the zone of narrow coral strips, being more abundant at Trois-Chameaux than at Planch'alizés. This species appears to have been at or past its maximum abundance at the start of the study (December), at which time it showed a cover of 10.1 %, a wet weight of 570.7 g/m^2 and a dry weight of 37.1 g/m^2 at Trois-Chameaux. At Planch'alizés, it showed a cover of 1.9 %, a wet weight of 91.4 g/m^2, and a biomass of 8.9 g/m^2. This alga had disappeared from the reef flat by February. This type of seasonal variation is in accord with the observations that this species may be adversely affected by high temperature (Benayahu and Loya, 1977), changes in salinity following heavy rainfall (Tsuda, 1974) or strong wave action (following, for example, Cyclone Colina, which hit Réunion Island in late January 1993). The author proposes that the low abundance of this species at Planch'alizés may be due to competition of its dormant stage with other perennial macroalgae; the epilithic *Gelidiopsis intricata*, which persists throughout the year at this site, may prevent successful colonisation of the substrate by the juvenile stages of *Hydroclathrus clathratus*.

Gracilaria crassa

This alga was only sampled in the narrow coral strip zone of Planch'alizés, but was occasionally observed on the reef flat in far lower quantities at Trois-Chameaux. *Gracilaria* spp. were reported to be present in Kaneohe

Bay, which was subject not only to eutrophication but also chronic sedimentation (Banner, 1974) and eutrophic reefs in Mauritius and the Seychelles (Cuet and Naim, *unpubl. data*). These observations suggest that the greater abundance of *Gracilaria crassa* at Planch'alizés (where it reached a cover of 10.0 %, a wet weight of 1006.9 g/m^2, and a dry weight of 82.8 g/m^2 in January) than at Trois-Chameaux may be linked to the greater enrichment of the reef waters at the former site. Koch and Lawrence (1987) showed that another species in this genus, *Gracilaria verrucosa*, is able to adapt to changes in salinity and if *Gracilaria crassa* demonstrates a similar ability, this would favour it on the studied reef where changes in salinity result from SGD encroachment (Cuet, 1989). *Gracilaria* spp. also demonstrate an ability to take up and store nitrogen, especially when this element is present in the form of ammonia (Ryther *et al.*, 1981). Ammonia also increases the rates of photosynthesis of this species (Nelson, 1985), and therefore NH_4 pollution (Cuet, 1989), and excretion by fish may play a role in maintaining the abundance of this species since the zone of large coral strips of the reef is heavily populated by the territorial damselfish, *Stegastes nigricans* (Letourneur, 1992). Importantly, algae in the genus *Gracilaria* also appear to be rarely consumed by herbivores (Littler *et al.*, 1983); the urchin *Diadema setosum* is known to consume *Gracilaria crassa* (Shunula and Ndibalema, 1986) but the density of this urchin is very low at Planch'alizés (Naim, 1993), possibly contributing to the abundance of this alga.

Hypnea valentiae

Small patches of this alga were noted in the back reef zone along the entire length of the reef complex, from early December. By January, it was abundant at Planch'alizés (10.9 % cover, 141.4 g/m^2 wet weight and 19.2 g/m^2 dry weight), but still sparse at Trois-Chameaux (1.9 % cover, 8.2 g/m^2 wet weight and 0.9 g/m^2 dry weight). Throughout February, it formed a carpet over much of the back reef zone of both sites (14.5 % cover, 327.9 g/m^2 wet weight and 26.0 g/m^2 dry weight at Planch'alizés and 11.3 % cover, 183.7 g/m^2 wet weight and 16.1 g/m^2 dry weight at Trois-Chameaux), but its abundance rapidly diminished. By April, it had completely disappeared from the reef. It therefore seems likely that the growth of this species is linked to increases in water temperature or light levels. Its earlier increase in abundance and greater total cover and biomass at Planch'alizés compared to Trois-Chameaux may reflect the higher levels of nutrients at this site.

Turbinaria ornata

This lithophytic alga was sampled in all four studied zones, showing a maximum abundance during the fresh season (April/May). It was more abundant in the narrow coral strip zone (where in May it showed maxima of 2.4 % cover, 101.8 g/m^2 wet weight and 9.4 g/m^2 dry weight at Trois-Chameaux, and 6.8 % cover, 397.2 g/m^2 wet weight and 40.8 g/m^2 dry weight at Planch'alizés) than in the back reef zone (where in April the corresponding maxima were 0.1 % cover, 2.6 g/m^2 wet weight and 0.2 g/m^2 dry weight at Trois-Chameaux, and 0.3 % cover, 6.2 g/m^2 wet weight and 0.6 g/m^2 dry weight at Planch'alizés). This difference is probably due to a lack of attachment sites in the latter zone (Payri, 1987).

On comparing the two test sites, *Turbinaria ornata* was more abundant at the nutrient enriched site, Planch'alizés. Payri and Naim (1982) suggested a possible link between this alga and nutrient enrichment of reef waters; in addition, at the uplifted atoll of Makatea (French Polynesia), this species was only observed in areas exposed to inputs of naturally occurring phosphate (Montaggioni *et al.*, 1985). The greater abundance of *Turbinaria ornata* at Planch'alizés may also reflect the decline of the coral communities here, which leads to a reduction in spatial competition and an increase in substrate suitable for colonisation; Nishihira and Yamazato (1974) and Tsudaa (1977) noted that this species predominates in areas of coral degradation.

Reasons for differences in macroalgal coverage and biomass between the two test sites

Differences in levels of nutrient enrichment

The fringing reef complex of St Gilles/La Saline is subject to enrichment by nutrients carried in SGD (Table 4) (Cuet *et al.*, 1988; Cuet, 1989); this phenomenon has also been recognised in Guam (Marsh, 1977) and Jamaica (D'Elia *et al.*, 1981). Johannes (1980) first highlighted the ecological significance of such discharges: by affecting levels of salinity, nutrients and pollutants, SGD can lead to changes in the zonation and species composition of the benthic community.

Coral reefs receiving elevated levels of nutrients tend to show increased standing crops of algae (Crossland *et al.*, 1984; Pastorok and Bilyard, 1985; Bell *et al.*, 1989) and even relatively minor increases above background levels can bring about profound changes (Bell, 1991). Therefore, it seems that the observed differences in the standing crops of macroalgae between the two sites are to a great extent attributable to the different degrees of enrichment to which they are exposed. Indeed, a previous study indicated that the extension of SGD onto the reef was closely linked to the decline of the coral communities and the flourishing of populations of macroalgae (Cuet *et al.*, 1988).

Nutrient enrichment promotes algal growth, by alleviating their nutrient limitation; initially, nitrogen was thought to be the limiting element (Odum and Odum, 1955; Ryther and Dunstan, 1971), but more recently, the consensus that it is in fact phosphorus which limits algal growth in coral reefs has emerged (Entsch *et al.*, 1983a; Lapointe, 1985; Lapointe, 1987). Cuet and Naim (1992) have shown that coral reefs subject to high levels of nitrate are not degraded, while serious degradation occurs when phosphate levels are elevated in conjunction with those of the nitrate. Limitation by both nitrogen and phosphorus can occur simultaneously (Lapointe, 1987), and other elements may also be involved (*e.g.* Entsch *et al.*, 1983*b*). In addition, water residence times and biochemical processes may also affect which element is limiting at any one time (Smith, 1984; Bell *et al.*, 1989). Without wishing to delve deeper into the exact nature of the process, it seems clear that nutrient limitation of algal growth has been alleviated on the studied reef, to different degrees in different areas, according to the degree of nutrient enrichment to which they are subject.

Nutrient enrichment also directly inhibits the growth rates of coral communities (Kinsey and Davies, 1979); this phenomenon is thought to be attributable to the inhibition of calcium carbonate formation by phosphate (Simkiss, 1964). Thus, the reduced growth of coral and the promoted growth rates of algae, as well as the occupation of sites suitable for settlement of coral larvae by algae (Birkeland, 1977), lead to a disruption of the equilibrium between these two components of the benthic community and this situation of imbalance is then perpetuated by one or a combination of mechanisms.

The overgrowth of coral heads by macroalgae has been observed at Planch'alizés, with *Gracilaria crassa* overgrowing living coral colonies (Naim, 1993). This phenomenon deprives coral of light and causes their ultimate demise (Banner, 1974). In the shade under algal mats, marine fungi may also proliferate and kill coral colonies by dissolving their carbonate skeletons (Banner, 1974). In Kaneohe Bay, Hawaii, Banner (1974) noted the invasion of living coral colonies by the green alga, *Dictyosphaeria cavernosa*; direct invasion of coral heads by the algae *Dictyosphaeria cavernosa* and *Dictyosphaeria setchellii* was observed in this study. Such invasion is detrimental to coral, not only due to the deprivation of light, but also due to the interference by the algae with the complex processes which occur at the coral surface. Under eutrophic conditions, algae also colonise damaged portions of coral tissue (Walker and Ormond, 1982), thus preventing their normal growth and repair.

Some cyanophytes also directly penetrate coral skeletons (Le Campion-Alsumard, 1988), and this has been seen on the reef of La Saline (Guillaume, 1988), where an alga of the genus *Ostreobium* has been observed penetrating the skeleton of *Porites lutea*. During 1985, the cyanophyte *Lyngbya majuscula* was seen to occupy the cavities in the skeleton of *Montipora circumvallata* and *Porites* spp. at Planch'alizés, but this species was absent from the site of Trois-Chameaux (Naim, 1993). During the present study, *Lyngbya majuscula* was found at Planch'alizés, but not at Trois-Chameaux.

The mechanical sweeping action of the thalli of macroalgae is especially pronounced with two species of algae on the studied reef flat – *Digenea simplex* and *Turbinaria ornata*. The former is abundant at Planch'alizés, but absent from Trois- Chameaux; the latter is present at both sites but more abundant at Planch'alizés. Such sweeping action can inhibit the successful settlement of coral larvae and damage established coral colonies.

On decomposing, algae return nutrients to the ecosystem (Sassi *et al.*, 1988), particularly in the back reef zone (Crossland *et al.*, 1984; Kinsey, 1985) which in turn lead to increased algal growth; thus a type of positive feedback loop is established in areas where high levels of nutrient enrichment occur.

Several species found on the reef flat at Planch'alizés but absent from Trois-Chameaux were observed to be loaded in sediments, particularly *Digenea simplex* and *Gelidiopsis intricata*. This sediment becomes resuspended by wave action during periods of high hydrodynamism, and thus the presence of such species may lead to increased levels of suspended particluate matter, which is negatively correlated with coral growth (Tomascik and Sander, 1985).

Differences in levels of herbivory between the two test sites

The activities of herbivorous fish and urchins play a key role in determining the structure, zonation, species diversity and standing crop of coral reef benthic algal communities (*e.g.* Ogden, 1976; Hay *et al.*, 1983; Hay, 1985; Lewis and Wainwright, 1985; Lewis, 1986), and therefore herbivores can greatly affect the competition between algae and coral. Indeed, Littler and Littler (1985) proposed that herbivory plays a more important role than do nutrient levels in terms of controlling the relative dominance of coral and algae on coral reefs. Moreover, a review by Steneck (1988) showed that low or reduced levels of herbivory are essential for the presence of dominant macroalgal assemblages.

It is possible that the nutrient enriched site of Planch'alizés is under-grazed, and that this effect contributes to the abundant standing crops of macroalgae found there. The density of herbivorous fish is greater at Planch'alizés than at Trois-Chameaux (Chabanet, 1994), as is to be expected considering the higher algal biomass at the former site (Galzin, 1985). However, the density of urchins, particularly that of *Diadematidae*, has fallen dramatically from the numbers found in the mid 1970s (Naim, 1993) and urchin densities are lower at Planchalizes than at Trois Chameaux (Semple, 1993). Exclusion or mass death of urchins of this family is known to cause a shift from a benthic community characterised by turf and microalgae to one dominated by macroalgae (*e.g.* Carpenter, 1981; Sammarco, 1982), and therefore the low density of *Diadematidae* at Planch'alizés undoubtedly compounds the problems of nutrient enrichment there.

Severe natural phenomena

Extremely low tides have in recent years affected the St Gilles/La Saline reef complex, most notably in 1982-83 (Naim, 1993), and such events may have exacerbated the problems of nutrient enrichment found in certain areas, and promoted the shift to an alternate stable state (Hatcher, 1984), dominated by macroalgae.

CONCLUSION

The fringing reef complex of St Gilles/La Saline is subject to an obvious degradation of its coral communities, as a result of enrichment of its waters following extensive SGD encroachment. This enrichment leads to unrestrained algal growth in the worst affected areas. Reduced levels of herbivory and severe natural events may have compounded this effect. Given the ecological and economic importance of this and other reef complexes in reunion Island, it is imperative that efficient conservation and management policies be implemented as soon as possible in order to alleviate the eutrophication of the reefs and to attempt to return them to their former health.

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