

Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution

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Abstract

This work describes the distribution of fish communities, including species richness, abundance of individuals and trophic structures on the four main fringing reefs of Reunion Island. Patterns are quantified on several spatial scales: an intra-reef scale and an inter-reefs scale which includes within-reefs, between-reefs, and between-reefs and zones scales. The total ichthyofauna (217 species) is structured into three main communities – back-reef, inner reef flat and outer reef flat communities – which are influenced by the wave exposure and topographic relief. These communities are organized in a spatial continuum rather than into three totally separate communities. Herbivorous (mainly acanthurids) and omnivorous fishes (mainly pomacentrids) are the most numerous on the inner and outer reef flats. Diurnal carnivorous (mainly mullids) and herbivorous fishes (mainly schooling juveniles) are the dominant fishes in the back-reef zones. The low abundance of carnivorous fishes on the reef flat, irrespective of diet, is most likely due to alterations of benthic communities (e.g. coral damage, increase in algae populations) as a result of anthropogenic activities. The ichthyofauna of each of the four reefs is organized into the same three fish communities. There is a north-south gradient of decreasing distribution of species and abundance of individuals in these communities. However, fish communities are more clearly separated on the northern reefs compared with those of the southern reefs. This pattern is probably due to differences in coral vitality, habitat complexity and width of the reefs. Hydrodynamic conditions, more pronounced in the south of the island, might also lead to a higher flux of recruitment of fish larvae on the northern reefs.

Keywords: Between-reef distribution; Coral reef fish; Fringing reef; Reunion Island; Within-reef distribution

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1. Introduction

Coral reefs are among the world's most complex marine ecosystems, in which fish communities reach their highest degree of diversity (Sale, 1991), although this diversity may vary according to both the geographical area and morphology of the coral reef. Understanding the great heterogeneity of reef substrata over a wide range of spatial scales and the manner in which fishes respond to it, is one of the most fundamental aims of ecological studies on coral reefs. Despite their potential high mobility, most reef fishes inhabit a determined habitat in a precise reef zone (Harmelin-Vivien, 1979; Russ, 1984a; Galzin & Legendre, 1988; Letourneur, 1992). The processes determining the distribution and abundance of coral reef fishes among habitats over a wide range of spatial scales have been reviewed by Williams (1991).

In the 1970s, the Reunion coral reef ecosystems were characterized by flourishing coral communities and the occasional occurrence of algal communities (Bouchon, 1981; Faure, 1982). However, during the two last decades, the Reunion coasts have been affected by a significant increase in urbanization. At the same time, eutrophication phenomena were recorded on the reefs. Their impact on benthic communities has been studied by Cuet et al. (1988), Cuet & Naim (1989) and Naim (1993). Unfortunately, during this time, the ichthyofauna of Reunion coral reefs was not studied, with the exception of a single study (Harmelin-Vivien, 1976). Investigations on Reunion reef fish communities have only recently begun (Letourneur, 1992; Letourneur et al., 1993; Chabanet, 1994; Letourneur & Chabanet, 1994; Chabanet et al., 1995). Moreover, coral reef fish communities from the southwestern Indian Ocean have been only poorly described. Most studies of reef fishes are performed either over small spatial scales, e.g. patch reefs, or large spatial scales, e.g. similar zones (mainly outer slopes) from different and distant reefs. In contrast, data on fish communities from both different zones of a reef and similar zones from several reefs are scarce (Russ, 1984a,b).

As part of an on-going study of the ichthyofauna of coral reef flats of Reunion Island (Letourneur, 1992), 13 coast-to-ocean transects were studied on the four principal reefs to determine the spatial and temporal scales on which their fish communities are organized and fluctuate. The aim of this paper is to provide qualitative and quantitative data on the organization of the fish communities on different spatial scales: (1) an intra-reef study (small spatial scale) and an inter-reefs study (large spatial scale) which includes (2) a within-reef study, (3) a between-reef study and (4) a between-reef and zone study. Items (2), (3) and (4) are not separate studies, but different comparisons that are made using the same data set of the large spatial scale study. This study will allow patterns in species composition and abundance to be quantified over a range of spatial scales.

2. Material and methods

2.1. Study areas

Reunion Island is located in the southwestern Indian Ocean (21°70'S and

55°32'E), about 800 km east of Madagascar (Fig. 1) and, along with Mauritius and Rodrigues Islands, constitutes the Mascarene archipelago. The mountainous and rugged topography of the island (3069 m) leads to abrupt coastlines and a very narrow insular shelf (< 5 km width). These conditions are mainly responsible for the poor development of Reunion coral reefs: 12 km² compared with about 200 km² for Rodrigues and 300 km² for Mauritius (Montaggioni & Faure, 1980). All are fringing reefs (Montaggioni & Faure, 1980) and are located along the dry western coast of the island, where they form a discontinuous reef belt (Fig. 1). Two seasons can be distinguished on Reunion Island: a warm wet season from November to April (summer), and a cooler dry season from May to October (winter). Located on the leeward coast of the island, the reefs are protected from

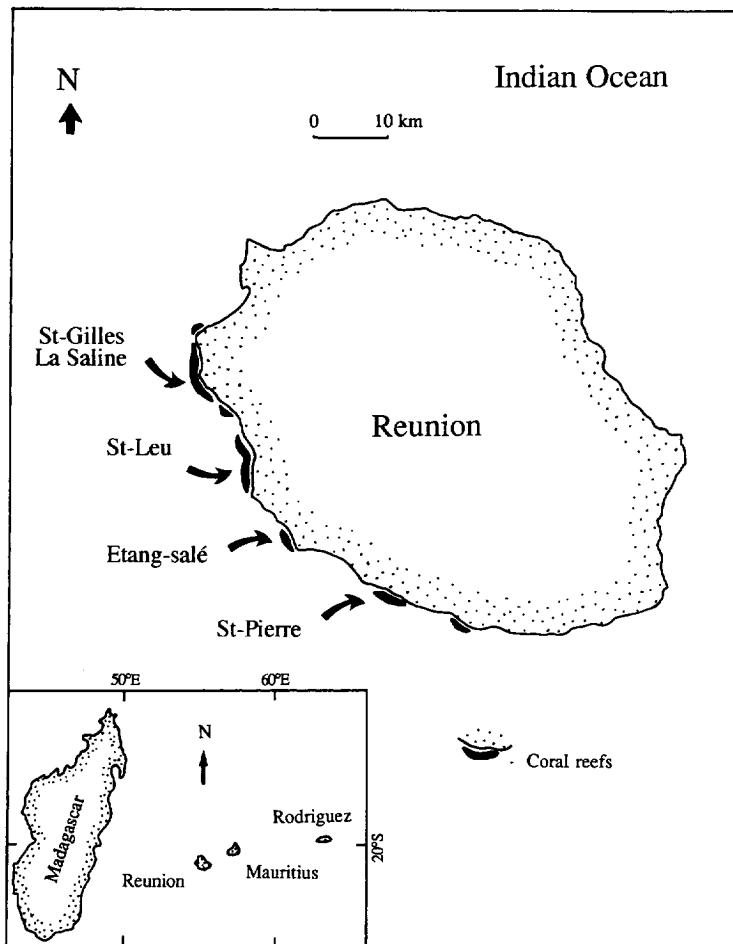


Fig. 1. Location of the four most developed fringing reefs around Reunion Island in the south-west Indian Ocean.

the direct action of the southeast trade winds, which, however, generate a rough choppy sea on this coast. Moreover, the reefs are often exposed to a strong oceanic swell generated by polar depressions. Finally, during the austral summer, hurricanes cause very heavy swells. Thus, the Reunion coral reefs lie in exposed conditions, especially towards the south end of the island (Faure & Montaggioni, 1970). Tides are semi-diurnal and the maximum range during spring tides is about 0.8 m. On the reefs, the tidal phenomenon may be hidden by meteorological factors (direction of the wind, atmospheric pressure, strong wave action, etc.). Thus, the reef flat is rarely totally exposed during low tides, during which fish communities were not surveyed.

The inter-reefs study (large spatial scale) was carried out on the reef flats of the four most developed fringing reefs of the island: the Saint-Gilles/La Saline reef complex, Saint-Leu, Etang-salé and Saint-Pierre (Fig. 1). Although some important parts of the Saint-Gilles/La Saline reef complex are subject to eutrophication caused by submarine groundwater discharges enriched in nutrients (Cuet et al., 1988), this reef is generally considered the most “healthy” of the island (Cuet & Naim, 1989). The fringing reefs of Saint-Leu and Saint-Pierre suffered badly from hurricane Firinga, in January 1989, which caused a 100% coral mortality on these reef flats (Cuet & Naim, 1989; Letourneur et al., 1993). Accumulation of organic matter, presumably from a sugar cane refinery, was used to explain the high level of degradation of coral communities of the fringing reef of Etang-salé (Cuet & Naim, 1993).

Water depth does not exceed 2 m on any of these reef flats. Fish surveys were performed along four transects at each of St-Gilles/La Saline and St-Leu, along three transects at St-Pierre and along two transects at Etang-salé (the number of transects being dependent upon on the reef length). Each of the 13 transects was perpendicular to the coast, and crossed three morphological zones, as defined by Montaggioni & Faure (1980). From the coast to the ocean, these were: the back-reef zone, the inner reef flat and the outer reef flat. Although the composition of each of these morphological zones differs according to the reef, the following characteristics can be considered as representative. The back-reef zone is mainly detrital with few coral colonies and constitutes the deepest part of the reef flats. The inner reef flat is a complex mosaic of narrow coral strips, large transverse strips alternating with narrow and shallow sand channels and/or scattered coral heads. However, at Etang-salé, about half of this zone is composed of large colonies of *Porites lutea* Milne-Edwards & Haime forming micro-atolls. Finally, the outer reef flat is a more or less horizontal furrowed platform with surge channels and residual pools.

On a smaller spatial scale (intra-reef study), two transects, named Trois Chameaux and Planch'alizés, were studied on the St-Gilles/La Saline reef complex. The precise location of these transects is given in Chabanet & Letourneur (1995). They were divided into 10 stations (50 m wide and 50 m long) from the shore to the ocean. The reef complex of St-Gilles/La Saline may be divided into a non-eutrophic sector (Trois Chameaux, St-Gilles reef) and an eutrophic sector (Planch'alizés, La Saline reef) (Cuet et al., 1988). At Plan-

ch'alizés, the concentration of nutrients in the reef waters is twice that at Trois Chameaux. Fleshy algae are abundant at Planch'alizés and, since the 1980s, have set up new facies on the reef flat (Naim, 1993). It is thought that submarine groundwater discharge is mainly responsible for the high concentration of nutrients.

2.2. Sampling techniques

The reliability and limits of visual methods for the study of reef fish communities have been previously reviewed (GBRMPA, 1978; Barans & Bortone, 1983; Harmelin-Vivien et al., 1985). Visual observations permit surveys of fish communities without disturbance, and are efficient for monitoring communities in long term studies.

For the intra-reef study, only presence-absence of fish species were recorded. By snorkelling, the author swam slowly and randomly for 30 min in each of the 10 stations of the Trois Chameaux and Planch'alizés' transects. This type of survey was carried out each month from February 1989 to July 1990 to determine the spatial organization of fish communities on a small spatial scale.

For the inter-reefs study, two types of data were recorded. Firstly, the presence or absence of species was noted within each of the three morphological zones of each of the thirteen transects during a 30-min sampling period. Secondly, fish abundance was recorded on a log abundance scale (following a geometric progression of base 2) within a band 50 m long and 2 m wide, parallel to the coast, in each morphological zone of the St-Gilles/La Saline, St-Leu and Etang-salé reefs. Three replicates were performed in each zone at these reefs. As the visibility at St-Pierre was too low to make precise counts, another quantitative method was adopted (Letourneur, 1991; modified from Williams, 1982). Five abundance categories were used: Category 1 = 1 fish observed, Category 2 = 2–5 fishes, Category 3 = 6–10 fishes, Category 4 = 11–30 fishes and Category 5 = 31–100 fishes. Each species recorded was assigned to one of the five categories, depending on its total abundance observed during a 30-min sampling period. Using the available dietary data of coral reef fishes (Hiatt & Strasburg, 1960; Hobson, 1974; Harmelin-Vivien, 1979), the fishes censused were assigned to one of seven trophic categories, taking into account possible ontogenic changes of diet: herbivores, omnivores, sessile invertebrate feeders, diurnal carnivores, nocturnal carnivores, piscivores and zooplanktivores. The qualitative and quantitative data were recorded in summer and winter 1989 and in summer and winter 1990. The results of temporal fluctuations of the ichthyofauna of the Trois Chameaux and Planch'alizés' transects and of the four reefs will be analysed in the companion paper (Letourneur, 1995).

2.3. Data analysis

The qualitative data recorded for the intra-reef study on the two transects from February 1989 to July 1990 were pooled in a presence-absence matrix (307

stations \times 202 species), which was analysed using the hierarchical clustering method. In addition, the presence-absence matrices of Trois Chameaux (153 stations \times 183 species) and Planch'alizés (154 stations \times 174 species) were analysed using the correspondence analysis technique (Benzecri, 1973) from the SAS procedure (SAS, 1989).

For the inter-reefs study, qualitative data from the four reefs, from summer 1989 to winter 1990, were examined as five presence-absence matrices: one for each reef and one pooled across all reefs (164 stations \times 189 species). Quantitative data (mean of the median of the log abundance categories) were similarly examined as abundance \times site matrices, except the data from St-Pierre, which were not pooled due to the different technique used. For this reef, a matrix of abundance was established using, for each species, the median value of its abundance category.

All of these matrices were analysed by hierarchical clustering and by correspondence analysis. In every case, results obtained with the second technique were visually more explicit (Letourneur, 1992). Thus, the results of correspondence analyses will be presented hereafter. The Mahalanobis' distances between centres of gravity of groups of similar stations (Mahalanobis, 1936) were calculated for all matrices to quantify the differences between the groups. The null hypothesis, i.e. homogeneity of dispersions, was tested using Wilks' test (Wilks, 1932).

The spatial patterns of the distribution of fish communities were also analysed using two-way ANOVAs (reef \times morphological zone). One was performed on species richness data, another on total abundance data. In addition, the data of the most abundant species were also analysed with this technique. The data sets of each season were analysed separately in order to avoid falsely significant results, because of artificially high degrees of freedom if pooled data were used. The results of ANOVAs of summer 1989 only will be presented hereafter and significant changes in patterns between seasons will be mentioned. When ANOVAs detected significant differences, a posteriori Student-Neuman-Keuls' tests were used in order to separate differences between reefs and morphological zones.

3. Results

3.1. Intra-reef distribution

The correspondence analysis indicates a continuum in the spatial distribution of fish species ("Guttman effect") on the two transects at Trois Chameaux and Planch'alizés of St-Gilles/La Saline (Fig. 2). The first axis separates progressively the ichthyofauna from stations subjected to high hydrodynamic conditions (reef front) from the stations with calm conditions (in proximity to the shore). The second axis separates the fish communities from stations with high topographic complexity (transverse stripes and scattered coral colonies) from the fish com-

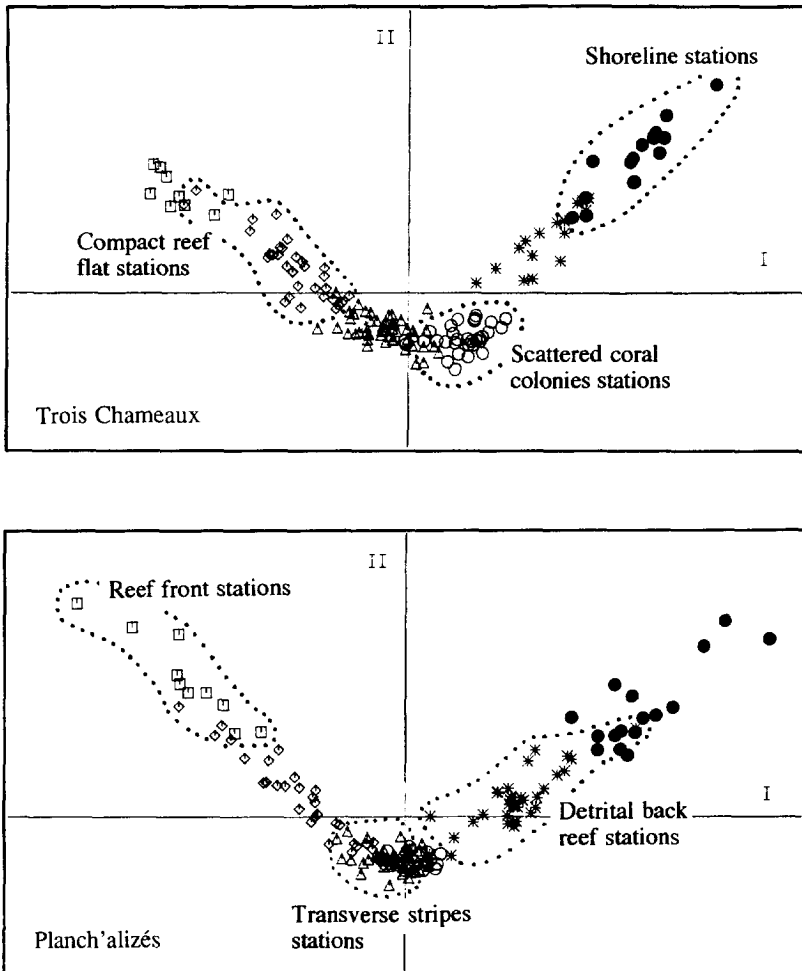


Fig. 2. First factorial plane of the correspondence analyses of the Trois Chameaux and Planch'alizés transects at St-Gilles/La Saline.

munities associated with stations with lower structural complexity (mainly reef front and close to the shoreline). Examination of the absolute contributions of the species to the first and second axis allows the determination of the most representative species of each group of stations (Benzecri, 1973). The stations close to the shoreline are represented by the presence of *Gerres acinaces* and *Cymolutes praetextatus*. *Siderea grisea*, *Parupeneus rubescens* and *Canthigaster valentini* are the most representative species of the detrital back reef; and *Sargocentron diadema*, *Aulostomus chinensis*, *Heniochus monoceros* and *Acanthurus nigricauda* are the most representative species of the scattered coral

colonies stations. The transverse strips are characterised by the presence of *Chrysiptera glauca*, *Stegastes limbatus* and *Stegastes peliciieri*; the compact reef flat by *Apogon taeniophorus*, *Chrysiptera unimaculata* and *Plectroglyphidodon leucozonus* and, on the reef front, *Kuhlia marginata*, *Pempheris adusta* and *Abudefduf sexfasciatus* are the most representative species.

Transitions in species composition between the different zones are more or less pronounced. Partitions between fish communities of the zones close to the shoreline and that of the detrital back-reef, and between the communities of the latter and the scattered coral colonies zone are marked (Fig. 2). Conversely, transitions between the different zones of the bioconstructed reef flat are more progressive, indicating a higher similarity between the fish communities in the different zones of this area.

The hierarchical clustering shows three main fish communities (Fig. 3): a

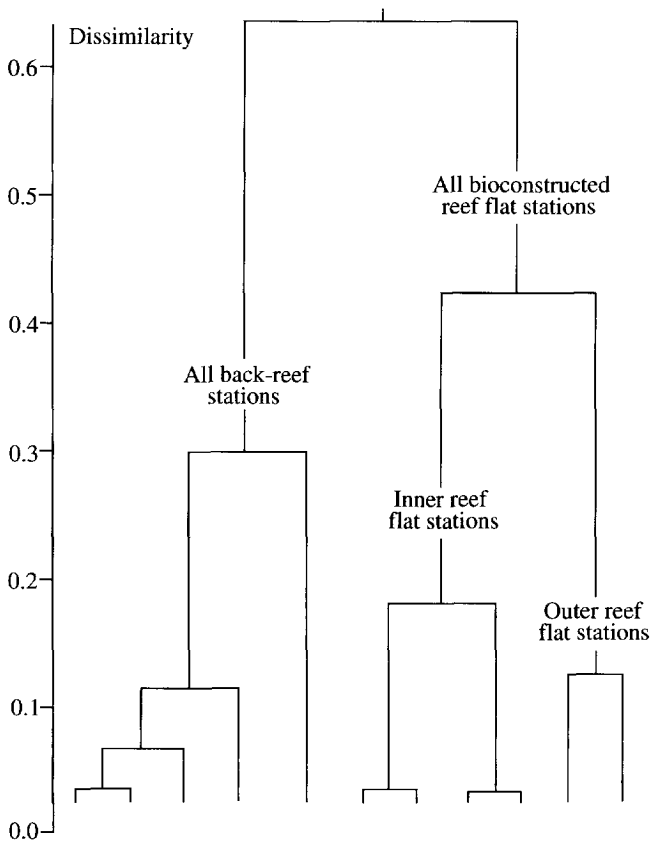


Fig. 3. Dendrogram from hierarchical clustering of the 307 censuses of Trois Chameaux and Planch'alizés transects at St-Gilles/La Saline.

back-reef community including the communities of the zones in proximity to the shoreline and the detrital back-reef, an inner reef flat community including the scattered coral colonies and transverse stripes communities, and an outer reef flat community including the compact reef flat and reef front communities.

Both correspondence analysis and hierarchical clustering do not suggest any marked difference between the ichthyofauna of the two transects. Nevertheless, the total species richness per census is significantly higher (*t*-test, $p < 0.05$) at Trois Chameaux (104.1 ± 8.2 species) than at Planch'alizés (94.9 ± 6.2 species). On the other hand, the mean species richness per census is always higher on the stations of scattered coral colonies. This is significantly higher (*t*-test, $p < 0.05$) at Trois Chameaux (55.9 ± 5.7 species) than at Planch'alizés (48.4 ± 4.0 species).

3.2. Inter-reefs distribution

3.2.1. Within-reefs organization

During the 2 yr of the study, 217 species of coral reef fishes belonging to 44 families were recorded (see Appendix). The most dominant families in number of species were the Labridae (33 species), the Pomacentridae (27), the Chaetodontidae and Acanthuridae (16 each), the Tetraodontidae (11) and the Mullidae (10).

The results obtained for the smallest spatial scale (intra-reef) are still valid for the larger one (inter-reefs). Indeed, the inter-reefs study confirmed the occurrence of three fish communities on Reunion reef flats: a back-reef, an inner and an outer reef flat community (Fig. 4). The significance of the two axes is similar to that of

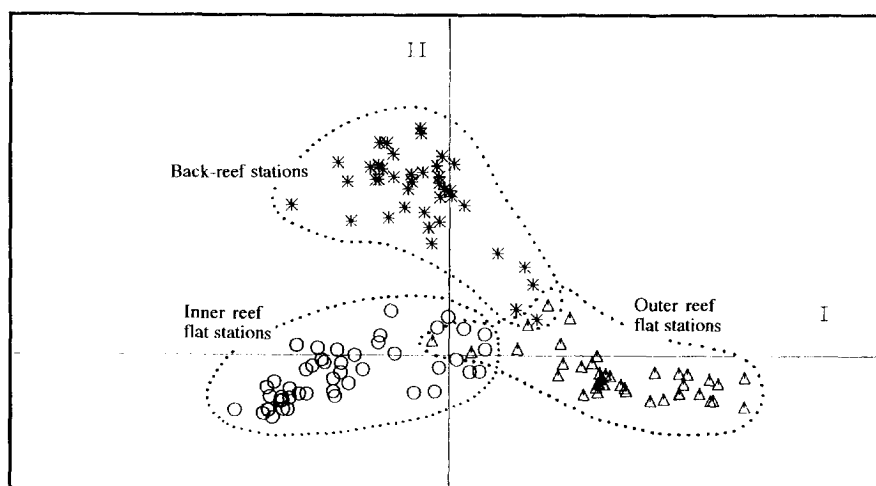


Fig. 4. First factorial plane of the correspondence analyses monitored on the quantitative data of the total ichthyofauna recorded on the reef flats of St-Gilles/La Saline, St-Leu and Etang-salé. The qualitative data, including the reef of St-Pierre, gave a similar pattern (Letourneur, 1992).

Table 1

Mahalanobis' distances between centres of gravity of back-reefs, inner and outer reef flats obtained with qualitative and quantitative data

	Back-reefs vs. inner reef flats	Back-reefs vs. outer reef flats	Inner reef flats vs. outer reef flats	F
Qualitative data	24.77	37.53	19.13	169.5**
Quantitative data	35.06	46.59	19.36	147.8**

F was calculated with Wilks' test (null hypothesis = homogeneity of dispersions, ** = $p < 0.01$).

the small scale study, with hydrodynamic conditions on the first axis, and substratum heterogeneity on the second. The Mahalanobis' distances are small between the inner and outer reef flat zones (Table 1), showing a relative similarity in their ichthyofauna. In contrast, these distances are high between the back-reef zone and the other two zones, indicating the dissimilarity of the back-reef ichthyofauna from that of the inner and outer reef flat zones.

The highest values of both total species richness and mean species richness per census were observed on the inner reef flat, while the lowest values for these parameters were observed in the back-reef zone (Table 2). The most characteristic species of each fish community were determined by their absolute contribution to the first and second axis of the correspondence analysis. The most representative species in the back-reef zone were *Siderea grisea*, *Halichoeres scapularis*, *Rhinecanthus aculeatus* and *Ostracion cubicus*. On the inner reef flat, *Chaetodon trifascialis*, *Stegastes nigricans* and *Zebrasoma scopas* were the most representative species. *Chrysiptera unimaculata*, *Plectroglyphidodon imparipennis*, *Plectroglyphidodon leucozonus* and *Thalassoma purpurum* were the most representative species of the outer reef flat. In contrast, *Cheilinus trilobatus*, *Stethojulis albobittata*, *Thalassoma lunare*, *Scarus sordidus* and *Naso unicornis* were found in all zones of the four reefs. The highest number of individual fishes was recorded on the inner reef flat, although the difference from the outer reef flat is not significant (Table 2).

The trophic structure of the ichthyofauna differed in the three morphological zones (Fig. 5). On the back-reef zone, the herbivorous fishes (37.2% of fish abundance), mainly schooling juveniles of *Acanthurus triostegus* and *Siganus*

Table 2

Total number of species, mean species richness and mean abundance per census (\pm SD) on back-reefs, inner and outer reef flats

	Back-reefs	Inner reef flats	Outer reef flats
Total number of species	142	177	156
Mean species richness	24.9 \pm 4.7	44.7 \pm 8.4	31.9 \pm 6.0
Mean abundance	69.0 \pm 37.6	236.7 \pm 73.6	204.7 \pm 80.7

Underlining indicates means that are not significantly different (t -test, $p > 0.05$).

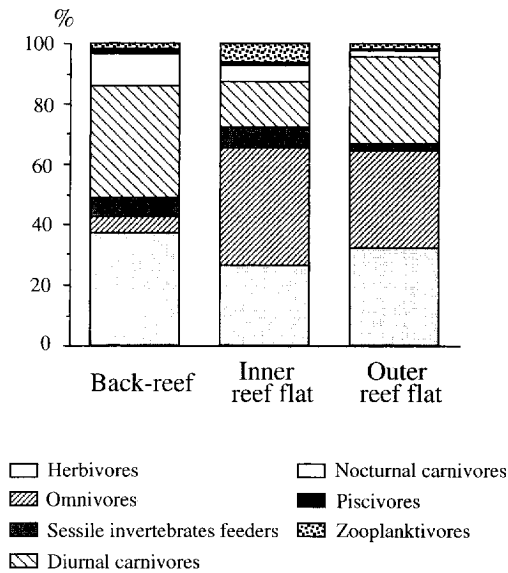


Fig. 5. Trophic structures of the total fish assemblage in the three morphological zones expressed in percentage of total abundance.

sutor, and the diurnal carnivorous fishes (37.3%), like the mullids *Parupeneus barberinus*, *Parupeneus macronema* and *Parupeneus rubescens*, dominated. The relative importance of omnivorous fishes was higher on the inner reef flat (39.5%, mainly due to *Stegastes nigricans*) than on the outer reef flat (32.3%, mainly due to *Chrysiptera unimaculata* and *Plectroglyphidodon leucozonus*). Conversely, the proportion of herbivorous and diurnal carnivorous fishes are higher on the outer reef flat (32.1 and 29.0%, respectively) than on the inner reef flat (26.1 and 14.9%, respectively). In these two zones, the most abundant herbivorous species are *Acanthurus nigrofuscus*, *Acanthurus triostegus* and *Ctenochaetus striatus*, while the most abundant diurnal carnivorous species are *Halichoeres marginatus*, *Thalassoma harwicki* and *T. lunare*.

3.2.2. Between-reefs differences

For each reef, the smallest Mahalanobis' distance was observed between inner and outer reef flat zones (Table 3). Nevertheless, the Mahalanobis' distances between two zones are always higher on the Saint-Gilles/La Saline reef complex than on the other reefs, indicating a higher separation of the three main fish communities on this reef.

The highest values of total species richness and mean species richness per census were recorded on the Saint-Gilles/La Saline reef complex, and the lowest values were on the Saint-Pierre reef (Table 4). A marked north-south decrease in species richness (total, and mean per census) was apparent. The total number of

Table 3

Mahalanobis' distances between centres of gravity of back-reefs, inner and outer reef flats stations, obtained with qualitative and quantitative data

	Back-reefs vs. Inner reef flats	Back-reefs vs. Outer reef flats	Inner reef flats vs. Outer reef flats	F
<i>Saint-Gilles/La Saline</i>				
Qualitative data	74.69	104.92	67.74	121.6**
Quantitative data	162.05	188.12	75.21	260.5**
<i>Saint-Leu</i>				
Qualitative data	49.64	59.54	19.29	67.8**
Quantitative data	38.03	29.35	22.16	50.4**
<i>Etang-salé</i>				
Qualitative data	34.22	61.66	32.68	28.6**
Qualitative data	80.41	78.11	10.09	27.7**
<i>Saint-Pierre</i>				
Qualitative data	19.86	44.24	14.86	28.1**
Quantitative data	24.80	38.18	7.92	20.1*

F was calculated with Wilks' test (null hypothesis = homogeneity of dispersions, * = $p < 0.05$, ** = $p < 0.01$).

individuals is highest at Saint-Leu and lowest at Etang-salé (Table 4). Although the sampling method utilized at Saint-Pierre was different, the abundance of fishes per unit surface area was smaller than at Etang-salé. Thus, the abundance of fishes is higher on the northern reefs (St-Gilles/La Saline and St-Leu) than on the southern ones (Etang-salé and St-Pierre).

The percentages of herbivorous fishes are similar on the four reefs (28.8% on Etang-salé compared to 31.9% on St-Leu) (Fig. 6). The proportion of diurnal carnivorous fishes increases from the north (21.5% on St-Gilles/La Saline) to the south (28.5% on St-Pierre). Conversely, the proportion of omnivorous fishes decreases from the north (31.4% on St-Gilles/La Saline) to the south (22.6% on St-Pierre), except at St-Leu (36.2%).

Table 4

Total number of species richness and mean abundance per census (\pm SD) on the four reefs (counts on 100 m² on St-Gilles/La Saline, St-Leu and Etang-salé, codified abundance on St-Pierre)

	St-Gilles La Saline	St-Leu	Etang-salé	St-Pierre
Total number of species	192	169	156	111
Mean species richness	42.0 \pm 10.9	33.9 \pm 9.4	32.2 \pm 9.9	27.3 \pm 6.5
Mean abundance	185.2 \pm 86.8	208.1 \pm 117.1	127.1 \pm 59.5	164.8 \pm 53.4*

* = The abundance of fishes on St-Pierre was not compared with those of the others reefs, due to the different sampling technique utilized on this reef.

Underlining indicates means that are not significantly different (t -test, $p > 0.05$).

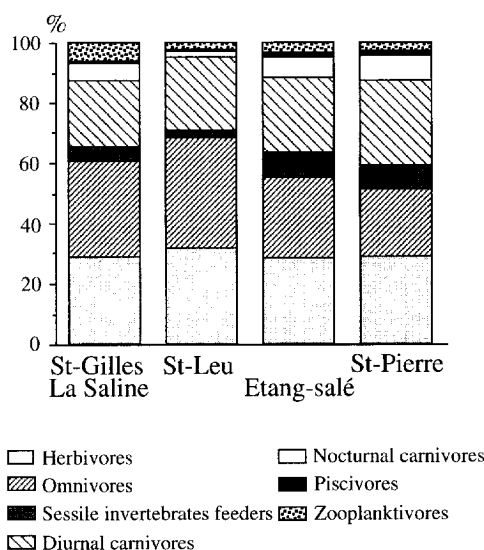


Fig. 6. Trophic structures of the total fish assemblage in the four reef flats expressed in percentage of total abundance.

3.2.3. Between-reefs and zones differences

The total number of species and the mean species richness per census decreases from the north to the south within each of the three morphological zones (Table 5). Nevertheless, this north-south gradient was more pronounced in inner and outer reef flat zones than in the back-reef, especially for the total species richness. On the bioconstructed zones (inner and outer reef flats), the abundance of fishes is higher on the northern reefs than on the southern ones (Table 5). However, this north-south partition is not so apparent on the back-reef zone.

The factors "reef" and "morphological zones" were significant for species richness, total abundance of fishes and number of individuals of some of the most abundant species (Table 6). The results presented only small changes over seasons and expressed the strong influence of the morphological zone which was significant in numerous cases. The mullids *Mulloidides flavolineatus*, *Parupeneus barberinus* and *Parupeneus macronema*, and the rabbitfish *Siganus sutor* were the only fishes to be significantly more abundant on back-reef zones than on bioconstructed ones (Table 6). The latter species was more abundant on the back-reef zone of St-Gilles/La Saline, but was not so abundant in other back-reef zones. Reef was also an important factor for the distribution of some abundant species, such as *Epinephelus merra*, *Chaetodon trifasciatus* or *Acanthurus nigrofasciatus*, but any of these species were more abundant on Etang-salé than on St-Leu or St-Gilles/La Saline.

Greater similarity was observed between the trophic structures of a particular

Table 5

Total number of species, mean species richness and mean abundance per census (\pm SD) (counts on 100 m² on St-Gilles/La Saline, St-Leu and Etang-salé, codified abundance on St-Pierre) on the three zones of the four reefs

	St-Gilles La Saline	St-Leu	Etang-salé	St-Pierre
<i>Total number of species</i>				
Back-reef	95	92	80	79
Inner reef flat	150	133	119	91
Outer reef flat	132	115	101	67
<i>Mean species richness</i>				
Back-reef	30.5 \pm 2.7	24.6 \pm 7.6	23.6 \pm 2.1	21.0 \pm 7.7
Inner reef flat	55.3 \pm 5.5	44.4 \pm 5.2	45.0 \pm 7.7	34.1 \pm 6.7
Outer reef flat	40.1 \pm 4.9	32.7 \pm 6.0	28.0 \pm 4.1	26.8 \pm 3.5
<i>Mean abundance</i>				
Back-reef	83.9 \pm 56.6	70.1 \pm 49.0	52.9 \pm 26.7	114.8 \pm 36.3*
Inner reef flat	247.4 \pm 75.5	303.6 \pm 77.0	159.3 \pm 31.4	197.0 \pm 68.3*
Outer reef flat	224.3 \pm 45.9	250.4 \pm 93.5	169.3 \pm 34.5	182.5 \pm 45.1*

* = The abundance of fishes on St-Pierre was not compared with those of others reefs due to the different sampling technique utilized on this reef.

Underlining indicates means that are not significantly different (*t*-test, *p* > 0.05).

morphological zone between the four reefs than between the different zones within a reef, except for the inner reef flat of Etang-salé and St-Pierre (Fig. 7). The trophic structures on outer reef flat zones are the most similar, except at Etang-salé, and those of the back-reef zones differ the most. A north-south partition appears on each morphological zone: the reef flats of St-Gilles/La Saline and St-Leu in the north and the reef flats of Etang-salé and St-Pierre in the south (Fig. 7).

4. Discussion

Although the spatial distribution of fishes within a reef has been quantified in several studies, most studies are restricted to one fish species or family and/or restricted to only one reef (Vivien, 1973; Galzin & Legendre, 1988; Fowler, 1990). Information on the spatial organization of fish communities from both different zones and different reefs are rare. However, Russ (1984a,b), who described the spatial patterns of the herbivorous fish communities in both several habitats and on several reefs of the Great Barrier Reef of Australia, presented comparable data. The present study suggests that when spatial and temporal monitoring are combined, the spatial patterns appeared persistent over time indicating that spatial variation may be of greater importance than temporal fluctuations (Choat

Table 6

Summary of two-way ANOVAs involving species richness, total abundance and number of individuals of the most abundant species in summer 1989

Fish taxa	Source of variation			S-N-K Test	
	Reef (R)	Zone (Z)	R × Z	Reef	Zone
HOLOCENTRIDAE					
<i>Myripristis murdjan</i>	*(1)	*(1)	ns	SG = ES > SL	IRF > ORF > BR
<i>Sargocentron diadema</i>	ns	***	ns		IRF > ORF = BR
SERRANIDAE					
<i>Epinephelus merra</i>	***	**	*(1)	SG > SL = ES	BR = IRF < ORF
MULLIDAE					
<i>Mulloides flavolineatus</i>	*(2)	*** (2)	ns	ES > SG > SL	BR > IRF > ORF
<i>Parupeneus barberinus</i>	ns	*(3)	ns		BR > IRF = ORF
<i>Parupeneus bifasciatus</i>	*(1)	***	*(1)	SL > SG = ES	ORF > IRF > BR
<i>Parupeneus macronema</i>	ns	** (3)	ns		BR > ORF > IRF
CHAETODONTIDAE					
<i>Chaetodon trifasciatus</i>	***	***	*	SG > ES > SL	IRF > ORF > BR
POMACENTRIDAE					
<i>Dascyllus aruanus</i>	ns (4)	***	ns		IRF > BR > ORF
<i>Plectroglyphidodon dickii</i>	ns (5)	*	ns		ORF > IRF > BR
<i>Stegastes nigricans</i>	ns	***	ns		IRF > ORF > BR
LABRIDAE					
<i>Halichoeres marginatus</i>	ns	***	ns		ORF > IRF > BR
<i>Stethojulis albovittata</i>	*(1)	***	ns	SL > SG = ES	ORF = IRF > BR
<i>Thalassoma hardwicki</i>	ns (6)	***	ns		ORF > IRF > BR
<i>Thalassoma lunare</i>	*(7)	**	ns (8)	SL > SG = ES	ORF > IRF > BR
ACANTHURIDAE					
<i>Acanthurus nigrofuscus</i>	*** (9)	***	ns	SL > SG > ES	ORF > IRF > BR
<i>Acanthurus triostegus</i>	** (1)	** (1)	*(1)	SL > ES > SG	ORF > BR > IRF
<i>Ctenochaetus striatus</i>	ns	***	ns		IRF = ORF > BR
<i>Naso unicornis</i>	ns	ns (8)	ns		
SCARIDAE					
<i>Scarus sordidus</i>	ns	ns (4)	ns		
<i>Scarus</i> spp.	*(3)	ns (5)	ns	SG = SL > ES	
SIGANIDAE					
<i>Siganus sutor</i>	*** (3)	** (1)	** (1)	SG > ES > SL	BR > IRF > ORF
Total abundance	*** (9)	***	ns (8)		
Species richness	***	**	ns		

F-tests have been used to determine the significance of the results. Significance levels: ns $p > 0.05$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$. S-N-K is the Student-Neuman-Keuls test for differences among treatments. SG = St-Gilles La Saline, SL = St-Leu, ES = Etang-salé, BR = back reef, IRF = inner reef flat, and ORF = outer reef flat. Significant changes of this reef and zone pattern with season are mentioned.

(1) ns in the three other seasons; (2) ns in summer 1990; (3) ns in 1990; (4) significant in the three other seasons; (5) significant in winter; (6) significant in summer 1990; (7) ns in winter 1989; (8) significant in 1990; (9) ns in winter 1990.

et al., 1988; Fowler, 1990; Fowler et al., 1992). Considerable variations in the organization of fish communities on Reunion reefs are recorded at different spatial scales. It appears that the within-reefs component, including small and

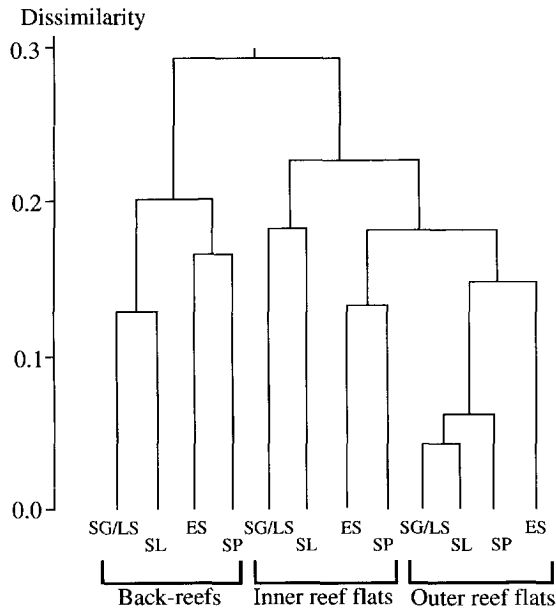


Fig. 7. Dendrogram from hierarchical clustering of the trophic structures in each zone of the four reef flats. SG/LS = St-Gilles/La Saline, SL = St-Leu, ES = Etang-salé and SP = St-Pierre.

large spatial scales, is the major component of the variability in the spatial distribution of fish communities (Williams, 1982; Russ, 1984a,b). Conversely, differences between the reefs are less pronounced than within the reefs, but still present a significant north-south gradient.

4.1. Within-reefs patterns

The differentiation of reef fish communities depends upon the spatial scale on which these communities are studied (Bradbury et al., 1984), but also upon the level of statistical significance chosen. Indeed, Galzin & Legendre (1988) conducted a study at Moorea, French Polynesia, to define the spatial scale at which a community structure could be identified according to the null hypothesis that fish distribution could be random. They concluded that reef fishes were distributed in different communities on a finer spatial scale than the morphological one usually referred to. However, the number of communities identified depended on the α -level of significance used in the statistical analysis. On the same transect, these authors found four fish communities at a 5% α -level of significance, and seven fish communities when they used a 30% α -level (Galzin & Legendre, 1988). The small-scale study on the Trois Chameaux and Planch'alizés' transects suggests similar considerations apply here also. On these two transects, three main fish communities are present: a back-reef zone, an inner reef flat and an outer reef flat

community, organized as a spatial continuum rather than into three totally separate communities. Each of the three main communities appears to include two “sub-communities”. A similar spatial continuum for the coral species on Reunion reefs exists (Faure, 1982).

There are several possible causes that may determine the within-reef distribution of Reunion ichthyofauna. Among them, two non-exclusive hypotheses can be proposed. Firstly, the distribution of reef fish communities may be related to a hydrodynamic gradient. Several authors have explained, at least partially, the structure of reef fish communities by emphasising their exposure to wave energy (Williams, 1982; Russ, 1984a,b; Galzin, 1987). The observed pattern suggests that fishes are sensitive to small differences in the hydrodynamic gradient. Indeed, at Reunion Island, the reef front is characterized by the highest hydrodynamic conditions of the whole reef flat. Although the hydrodynamic conditions decrease on the compact reef flat, wave action in this zone is also very high. Wave exposure in these two zones produces a significant packing down of the coral colonies (Faure, 1982), leading to decreased topographic complexity of the substratum. This effect allows the data to be subject to a second explanation: the organization of fish communities may be closely related to substratum variables. On Reunion reef flats it appears, nevertheless, that the relative importance of hydrodynamic conditions and topographic complexity as factors determining the structure of fish communities varies according to the reef studied (Letourneur, 1992; Letourneur & Chabanet, 1994). The relationship between fish and substratum relationships remains, however, difficult to establish in the present study. The substratum data collected at the same time as the ichthyofauna data were unfortunately too inaccurate to attempt a rigorous explanation. Relationships between fishes and substratum variables are a matter of debate. The correlations between the topographic complexity and the species richness of fish communities are recognized (Risk, 1972; Luckhurst & Luckhurst, 1978; Sano et al., 1984, 1987; Roberts & Ormond, 1987; Harmelin-Vivien, 1989). Conversely, the relationships between topographic relief and abundance of fishes are not as evident. Some authors found a positive correlation between these variables (Sano et al., 1984; 1987), Luckhurst & Luckhurst (1978) found only a low correlation, and Risk (1972) and Talbot et al. (1978) found no significant correlation. The topographic complexity appears to have a marked influence on abundance of territorial and sedentary fish species, such as Pomacentridae (Thresher, 1983; Sale & Douglas, 1984) or Chaetodontidae (Bouchon-Navaro et al., 1985). In this study, *Stegastes nigricans* was closely associated with dead branching corals of the inner reef flat, and the obligate corallivore *Chaetodon trifasciatus* was closely associated with the living corals on the reef flats, mainly on the inner reef flat of St-Gilles/La Saline. Recent investigations (Chabanet, 1994) on both the outer slope and outer reef flat of the St-Gilles/La Saline reef complex have indicated that the correlation between fish abundance and coral cover are marked in shallow waters (outer reef flat), but did not exist in deeper water on the outer slope. Thus, it is evident that the relationships between fishes and substratum variables are complex and require further research.

Despite this complexity, reef morphology appears to be one of the most important factors underlying the organization of fish communities. Substratum type, topographic complexity and availability of shelter and food resources all appear to contribute to this relationship (Luckhurst & Luckhurst, 1978; Choat & Ayling, 1987; Roberts & Ormond, 1987; Harmelin-Vivien, 1989). These factors are particularly important for small, site-attached fish species (Williams, 1991) as are found in the shallow waters of Reunion reef flats. The bioconstructed reef flat, including inner and outer reef flat zones, is characterized by its topographic diversity and complexity (Faure, 1982; Chabanet, 1994) and offers a wide range of shelters and food availability. This may explain the similarities observed between inner and outer reef flat zones. As a consequence of this reef morphology, the fish communities are more diverse and their populations more abundant on inner and outer reef flat zones than in the back-reef zone (Harmelin-Vivien, 1976; Russ, 1984a,b). In the back-reef zone, all of the fish families, except Mullidae, are poorly diversified and their populations are smaller than in the other zones. On Reunion fringing reefs, the back-reef zone is composed of sandy bottom and rubble, with scarce coral colonies, and constitutes a favourable habitat for the mullids, such as *Mulloides flavolineatus*, *Parupeneus barberinus* and *Parupeneus macronema*, which mostly feed on soft-bottom infauna (Harmelin-Vivien, 1979). Another factor determining spatial patterns is likely to be habitat selection by fishes, especially at, or after settlement (Williams & Sale, 1981; Eckert, 1985). Inter-specific interactions such as competition (for food, habitat, etc.) or predation, particularly on young recruits, also probably play a significant role in determining the spatial organization of fish communities (Hixon, 1991).

Degradation of coral may also affect the diversity and abundance of fish communities (Bell & Galzin, 1984; Bell et al., 1985; Bouchon-Navaro et al., 1985; Hourigan et al., 1988). The degradations of Reunion coral reefs, notably due to human activities, have caused pronounced changes in benthic communities, characterized by significant coral injuries and increases in algal communities (Cuet & Naim, 1989; 1993; Naim, 1993; Semple, 1993). These disturbances have probably produced changes in the structure of the ichthyofauna to the detriment of carnivorous fishes (except for the labrids) and to the advantage of herbivores, such as *Acanthurus nigrofusus*, *Ctenochaetus striatus* and *Naso unicornis*, and omnivorous fishes such as *Stegastes nigricans*, mainly on the bioconstructed reef flat. The influence of coral degradation on fish communities is also apparent at a smaller spatial scale. The high coral diversity and vitality and the maintenance of a high morphological complexity at Trois Châteaux, mainly on the zone of scattered coral colonies (Cuet et al., 1988) might explain the significantly higher species richness on this transect compared to Planch'alizés. Nevertheless, despite this significant difference, the structure of fish species on a spatial continuum is clearly noticeable on both transects, suggesting that species richness could be an inappropriate descriptor to demonstrate the effects of eutrophication (Chabanet et al., 1995). The impact of environmental degradations on fish communities on a determined spatial scale, i.e. in a particular zone, may thus disappear at a reef scale, i.e. on a coast-to-ocean transect, underlining the importance of the level of perception used (Bradbury et al., 1984; Galzin & Legendre, 1988).

4.2. Between-reefs patterns

Information on north-south spatial variations of reef fishes is rare, and such variation is monitored over large spatial scales, more than 1000 km, as in the Hawaiian archipelago (Hobson, 1984) or on the Great Barrier Reef of Australia (Fowler et al., 1992). Hobson (1984) suggested the possible influence of gradients of both temperature and larval dispersal by oceanic currents in the determination of significant north-south differences within the Hawaiian Islands. This author also suggested the hypothesis of the role of the variations in the type of islands, from large volcanic islands in the south to isolated atolls in the north. In Australia, Fowler et al. (1992) emphasized the impact of *Acanthaster planci* outbreaks which caused massive coral mortality on the northern zones of the Great Barrier Reef. This phenomenon may be the most important cause of the decrease in abundance of the obligate corallivore *Chaetodon rainfordi* on northern infested zones (Fowler et al., 1992).

In the present study, an important north-south gradient in the separation of fish communities and in the distribution of species richness, abundance of individuals and trophic structures was recorded over a very small latitudinal variation (the distance between the St-Gilles/La Saline and St-Pierre reefs is about 50 km, Fig. 1). This pattern may be caused by two main types of processes: (1) environmental factors, such as reef morphology and/or hydrodynamic conditions, and (2) anthropogenic and/or natural disturbances. The greater width of the reef flat at St-Gilles/La Saline (500 m, compared to 300 m at St-Leu and Etang-salé and 250 m at St-Pierre) might allow a better separation of the three morphological zones. Thus, the fish communities at St-Gilles/La Saline would be in contact on "transition-zones", which are narrow compared to the surface of the three zones. In addition, each morphological zone is wider at St-Gilles/La Saline than on the other reefs, providing a higher number of micro-habitats for fishes. An alternative/complementary explanation may concern the length of the reef (Sale & Douglas, 1984; Galzin, 1987). The reefs at both St-Gilles/La Saline and St-Leu are about 9 km, 1.3 km at Etang-salé and 2 km at St-Pierre. It is likely that hydrodynamic conditions plays important role in the determination of the north-south organization of the fish communities. The swell generated by the southeast trade winds induces strong currents which are higher in the south than in the north (Faure & Montaggioni, 1970). Although the coastal currents of Reunion Island are almost totally undescribed, I suggest that this regular swell determines coastal currents from the south to the north. It is possible that the observed pattern may be partially due to a direct response of fish communities to a gradient in wave exposure, as suggested by Galzin (1987). Nevertheless, observations on fish communities at two reefs of Mauritius Island, the neighbouring island (Fig. 1) submitted to similar oceanographical conditions than those of Reunion, indicated higher values of species richness and abundance of individuals on Mahébourg reef (southeast of the island) subjected to strong hydrodynamic conditions, than on Pointe-aux-Piments reef (NW of the island) subjected to calm hydrodynamic conditions (Letourneur, unpublished data). Furthermore, in the present study, species representative of wave exposed zones, such as *Chrysiptera unimaculata*,

Plectroglyphidodon imparipennis and *Plectroglyphidodon leucozonus*, were not more abundant on the southern reefs than on the northern ones. However, the gradient in hydrodynamic conditions exposure probably induces indirect effects on the observed pattern because it suggests a higher flux of larval recruitment in the northern reefs as fish larvae are less able to swim against these currents.

Degradation of coral colonies may also greatly affect the diversity and abundance of the fish communities. There may be a less separation of fish communities in degraded environments, although the origin of these degradations may differ according to the reef. At St-Pierre, most coral colonies were already dead, mainly due to urban sewage, and largely eroded by an abundant population of the sea-urchin *Echinometra mathei*, chiefly on the outer reef flat (Cuet & Naim, 1989). In addition, the rare living coral colonies on this reef died following hurricane Firinga (January 1989) due to an important silt layer caused by considerable ground erosion (Letourneur et al., 1993). At Etang-salé, the role of both a soft drink factory and a sugar cane refinery was emphasized to explain the significant coral mortalities (Cuet & Naim, 1993). At St-Leu, the high abundance of fishes was due to the proliferation of the omnivorous *Stegastes nigricans*, associated with dead *Acropora pharaonis* colonies. Most of these colonies died following hurricane Firinga, but their habitat complexity was preserved (Cuet & Naim, 1989; Letourneur et al., 1993). These three reefs were thus subjected to different degrees and kinds of natural and anthropogenic disturbances. If we consider species richness and abundance of individuals, this suggests that natural disturbances, despite their roughness, might have less consequences on fish communities than anthropogenic ones; the combination of both would induce low values of these parameters. Among the most abundant species (Table 6), *Parupeneus bifasciatus* (mullid), *Stethojulis albovittata*, *Thalassoma lunare* (labrids), *Acanthurus nigrofuscus* and *Acanthurus triostegus* (acanthurids) were more numerous on St-Leu than on Etang-salé.

Following hurricane Firinga, dead corals provided new substrata for algal growth and associated microfauna. This could account for the abundance of both these herbivorous acanthurids and small carnivorous labrids on St-Leu. Algal biomass and macro-algal abundance are low on Etang-salé, possibly due to sedimentation and/or sea-urchin abundance (Cuet & Naim, 1993). The maintenance of scarce small living *Acropora pharaonis* colonies might explain the relative abundance of the obligate corallivore *Chaetodon trifasciatus* on Etang-salé; whereas living branching corals totally disappeared following the hurricane on St-Leu (Letourneur et al., 1993). On the reef of St-Gilles/La Saline, both the topographic complexity and the coral vitality were greater than on the other reefs (Cuet & Naim, 1989). This probably explain the significant higher abundance of *Chaetodon trifasciatus* on this reef compared to the three others. It is also probably the case for the grouper *Epinephelus merra* which prefers a complex substratum, adapted to its "sit and wait" behaviour (Harmelin-Vivien, 1979).

The processes which may explain spatial patterns are often closely related and their respective roles are difficult to determine (Sale, 1991). Different hypotheses, and combination among them, were proposed, with regards on ecological

preferences of the most abundant species. Although environmental factors, i.e. hydrodynamic conditions and reef morphology, probably play important roles in the north-south pattern, they seemed to be of a lower importance than anthropogenic and/or natural disturbances. However, the relative contribution of each of these different factors on Reunion reefs can not be yet clearly determined, except for some abundant species, and none of them may yet be quantified. As well as for within-reefs patterns, the examination of these hypotheses needs to be among the main goals of future research on Reunion reef fishes. A knowledge of these different phenomena would allow the clarification of the relative importance of the different proposed factors, and to integrate them with patterns of temporal fluctuations, which will be described in the companion paper (Letourneur, 1995).

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Appendix

List of the fish species recorded on the reef flats of St-Pierre (SP), Etang-salé (ES), St-Leu (SL) and St-Gilles/La Saline (SG) from summer 1989 to winter 1990. For the latter reef, this includes data from the intra-reef study monitored from February 1989 to August 1990.

Fish species	SP	ES	SL	SG
MURAENIDAE				
<i>Echidna nebulosa</i> (Ahl)	+	+	+	+
<i>Echidna polyzona</i> (Richardson)				+
<i>Echidna zebra</i> (Shaw)		+	+	
<i>Gymnothorax flavimarginatus</i> (Rüppell)			+	+
<i>Gymnothorax meleagris</i> (Shaw & Nodder)			+	+

<i>Gymnothorax undulatus</i> (Lacepède)		+		+
<i>Gymnothorax zonipectis</i> Seale				+
<i>Siderea grisea</i> (Lacepède)	+	+	+	+
<i>Siderea picta</i> (Ahl)		+		
OPHICHTHIDAE				
<i>Myrichthys maculosus</i> (Cuvier)				+
PLOTOSIDAE				
<i>Plotosus lineatus</i> (Thunberg)	+	+	+	+
SYNODONTIDAE				
<i>Saurida gracilis</i> (Quoy & Gaimard)	+	+	+	+
<i>Synodus variegatus</i> Lacepède	+	+	+	+
CLUPEIDAE				
<i>Herklotsichthys quadrimaculatus</i> (Rüppell)	+			+
BELONIDAE				
<i>Strongylura leiura</i> (Bleeker)			+	+
HOLOCENTRIDAE				
<i>Myripristis berndti</i> Jordan & Evermann		+	+	+
<i>Myripristis murdjan</i> (Forsskal)	+	+	+	+
<i>Neoniphon sammara</i> (Forsskal)		+	+	+
<i>Sargocentron diadema</i> (Lacepède)	+	+	+	+
<i>Sargocentron punctatissimum</i> (Cuvier)	+	+	+	+
<i>Sargocentron spiniferum</i> (Forsskal)		+		+
AULOSTOMIDAE				
<i>Aulostomus chinensis</i> (Linnaeus)	+	+	+	+
FISTULARIIDAE				
<i>Fistularia commersonii</i> Rüppell	+	+	+	+
SYNGNATHIDAE				
<i>Corythoichthys schultzi</i> Herald		+		+
<i>Doryrhamphus excisus</i> Kaup		+	+	+
Genus sp.		+		+
SCORPAENIDAE				
<i>Dendrochirus zebra</i> (Cuvier)		+		+
<i>Pterois antennata</i> (Bloch)	+	+	+	+
<i>Pterois miles</i> (Bennett)	+	+	+	+
<i>Scorpaenodes guamensis</i> Quoy & Gaimard		+	+	+
<i>Scorpaenopsis diabolus</i> Cuvier		+		
<i>Scorpaenopsis gibbosa</i> (Bloch & Schneider)		+	+	+
<i>Scorpaenopsis venosa</i> (Cuvier)			+	+
<i>Taenianotus triacanthus</i> Lacepède		+		+
TETRAROGIDAE				
<i>Ablabys binotatus</i> (Peters)				+
CARACANTHIDAE				
<i>Caracanthus madagascariensis</i> (Guichenot)			+	
DACTYLOPTERIDAE				
<i>Dactyloptena orientalis</i> (Cuvier)				+

KUHLLIDAE

<i>Kuhlia marginata</i> (Cuvier)				+
<i>Kuhlia mugil</i> (Schneider)			+	+

SERRANIDAE

<i>Cephalopholis argus</i> Schneider		+	+	+
<i>Cephalopholis boenack</i> (Bloch)				+
<i>Cephalopholis leopardus</i> (Lacepède)				+
<i>Epinephelus fasciatus</i> (Forsskal)		+		+
<i>Epinephelus faveatus</i> (Valenciennes)	+	+	+	+
<i>Epinephelus hexagonatus</i> (Schneider)	+	+	+	+
<i>Epinephelus merra</i> Bloch	+	+	+	+
<i>Epinephelus tauvina</i> (Forsskal)		+	+	+

GRAMMISTIDAE

<i>Grammistes sexlineatus</i> (Thunberg)	+	+	+	+
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PRIACANTHIDAE

<i>Priacanthus cruentatus</i> (Lacepède)		+	+	+
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APOGONIDAE

<i>Apogon coccineus</i> Rüppel				+
<i>Apogon kallopterus</i> Bleeker	+	+	+	+
<i>Apogon taeniophorus</i> Regan	+	+	+	+

CARANGIDAE

<i>Caranx melampygus</i> Cuvier			+	+
<i>Caranx sexfasciatus</i> Quoy & Gaimard		+	+	+
Genus sp.	+	+		+

LUTJANIDAE

<i>Lutjanus fulvus</i> (Schneider)	+	+	+	+
<i>Lutjanus kasmira</i> (Forsskal)	+	+	+	

CAESIONIDAE

<i>Pterocaesio capricornis</i> (Smith & Smith)				+
<i>Pterocaesio tile</i> (Cuvier)		+		

LETHRINIDAE

<i>Lethrinus variegatus</i> Valenciennes				+
<i>Lethrinus</i> sp.				+

PENTAPOTIDAE

<i>Gnathodentex aureolineatus</i> (Lacepède)	+	+	+	+
<i>Monotaxis grandoculis</i> (Forsskal)	+	+	+	+

KYPHOSIDAE

<i>Kyphosus cinerascens</i> (Forsskal)			+	+
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GERREIDAE

<i>Gerres acinaces</i> Bleeker				+
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MULLIDAE

<i>Mulloides flavolineatus</i> (Lacepède)	+	+	+	+
<i>Mulloides vanicolensis</i> (Valenciennes)	+	+	+	+
<i>Parupeneus barberinus</i> (Lacepède)	+	+	+	+
<i>Parupeneus bifasciatus</i> (Lacepède)	+	+	+	+

<i>Parupeneus cyclostomus</i> (Lacepède)	+	+	+	+
<i>Parupeneus indicus</i> (Shaw)	+			+
<i>Parupeneus macronema</i> (Lacepède)	+	+	+	+
<i>Parupeneus pleurostigma</i> (Bennett)		+	+	+
<i>Parupeneus rubescens</i> (Lacepède)	+	+	+	+
<i>Upeneus tragula</i> Richardson			+	
PEMPHERIDAE				
<i>Pempheris adusta</i> Bleeker	+	+	+	+
<i>Pempheris mangula</i> Cuvier	+			+
POMACANTHIDAE				
<i>Centropyge acanthops</i> (Norman)	+			
<i>Centropyge bispinosus</i> (Günther)				+
<i>Pomacanthus imperator</i> (Bloch)				+
CHAETODONTIDAE				
<i>Chaetodon auriga</i> Forsskal	+	+	+	+
<i>Chaetodon blackburni</i> Desjardins	+	+	+	+
<i>Chaetodon guttatissimus</i> Bennett		+	+	+
<i>Chaetodon kleinii</i> Bloch	+	+	+	+
<i>Chaetodon lineolatus</i> Quoy & Gaimard		+		+
<i>Chaetodon lunula</i> (Lacepède)	+	+	+	+
<i>Chaetodon madagaskariensis</i> Ahl		+	+	+
<i>Chaetodon melannotus</i> Bloch & Schneider	+	+	+	+
<i>Chaetodon meyeri</i> Bloch & Schneider		+	+	+
<i>Chaetodon trifascialis</i> Quoy & Gaimard		+	+	+
<i>Chaetodon trifasciatus</i> Mungo Park	+	+	+	+
<i>Chaetodon unimaculatus</i> Bloch	+		+	+
<i>Chaetodon vagabundus</i> Linnaeus	+	+	+	+
<i>Chaetodon xanthocephalus</i> Bebbett		+		+
<i>Heniochus acuminatus</i> (Linnaeus)				+
<i>Heniochus monoceros</i> Cuvier	+	+	+	+
POMACENTRIDAE				
<i>Abudefduf margariteus</i> (Cuvier)				+
<i>Abudefduf septemfasciatus</i> Cuvier	+	+	+	+
<i>Abudefduf sexfasciatus</i> (Lacepède)	+	+	+	+
<i>Abudefduf sordidus</i> (Forsskal)	+		+	+
<i>Abudefduf sparoides</i> (Quoy & Gaimard)	+	+	+	+
<i>Abudefduf vaigiensis</i> (Quoy & Gaimard)		+		+
<i>Abudefduf</i> sp.				+
<i>Chromis dimidiata</i> (Klunzinger)	+		+	+
<i>Chromis viridis</i> (Cuvier)		+	+	+
<i>Chrysiptera glauca</i> (Cuvier)	+	+	+	+
<i>Chrysiptera unimaculata</i> (Cuvier)	+	+	+	+
<i>Dascyllus aruanus</i> (Linnaeus)	+	+	+	+
<i>Dascyllus trimaculatus</i> (Rüppell)		+		
<i>Plectroglyphidodon dickii</i> (Lienard)	+	+	+	+

<i>Plectroglyphidodon imparipennis</i> (Vaillant & Sauvage)	+	+	+	+
<i>Plectroglyphidodon johnstonianus</i> Fowler & Ball	+	+	+	+
<i>Plectroglyphidodon lacrymatus</i> (Quoy & Gaimard)		+	+	+
<i>Plectroglyphidodon leucozonus</i> (Bleeker)	+	+	+	+
<i>Plectroglyphidodon phoenixensis</i> (Schultz)			+	+
<i>Pomacentrus caeruleus</i> Quoy & Gaimard				+
<i>Stegastes fasciolatus</i> (Ogilby)	+	+	+	+
<i>Stegastes limbatus</i> (Cuvier)	+	+	+	+
<i>Stegastes lividus</i> (Bloch & Schneider)		+	+	+
<i>Stegastes nigricans</i> (Lacepède)	+	+	+	+
<i>Stegastes pelicierii</i> Allen & Emery		+	+	+
Genus sp.1 (juvenile)	+	+	+	+
Genus sp.2 (juvenile)		+	+	+
Genus sp.3 (juvenile)		+	+	
Genus sp.4 (Juvenile)	+	+		+
CIRRITHIDAE				
<i>Cirrhitichytys guichenoti</i> (Sauvage)		+		
<i>Paracirrhites arcatus</i> (Cuvier)	+	+	+	+
<i>Paracirrhites fosteri</i> (Schneider)			+	+
LABRIDAE				
<i>Anampses caeruleopunctatus</i> Rüppell		+	+	+
<i>Anampses lineatus</i> Randall				+
<i>Anampses twistii</i> Bleeker			+	
<i>Cheilinus trilobatus</i> Lacepède	+	+	+	+
<i>Cheilio inermis</i> (Forsskal)			+	+
<i>Coris aygula</i> Lacepède	+	+	+	+
<i>Coris caudimacula</i> (Quoy & Gaimard)	+	+	+	+
<i>Coris gaimard africana</i> Smith		+	+	+
<i>Cymolutes praetextatus</i> (Quoy & Gaimard)				+
<i>Epibulus insidiator</i> (Pallas)			+	+
<i>Gomphosius caeruleus</i> Lacepède	+	+	+	+
<i>Halichoeres hortulanus</i> (Lacepède)	+		+	+
<i>Halichoeres marginatus</i> Rüppell	+	+	+	+
<i>Halichoeres nebulosus</i> (Valenciennes)	+	+	+	+
<i>Halichoeres scapularis</i> (Bennett)	+	+	+	+
<i>Hemigymnus fasciatus</i> (Bloch)	+	+	+	+
<i>Labroides bicolor</i> Fowler & Bean				+
<i>Labroides dimidiatus</i> (Valenciennes)	+	+	+	+
<i>Macropharyngodon bipartitus</i> Smith			+	+
<i>Macropharyngodon cyanoguttatus</i> Randall			+	+
<i>Novaculichthys taeniorus</i> (Lacepède)			+	+
<i>Pseudocheilinus hexataenia</i> (Bleeker)				+
<i>Stethojulis albivittata</i> (Bonnaterre)	+	+	+	+
<i>Stethojulis strigiventer</i> (Bennett)	+	+	+	+
<i>Thalassoma amblycephalum</i> (Bleeker)	+	+	+	+

<i>Thalassoma genivittatum</i> (Valenciennes)	+	+	+	+
<i>Thalassoma hardwicki</i> (Bennett)	+	+	+	+
<i>Thalassoma hebraicum</i> (Lacepède)			+	+
<i>Thalassoma lunare</i> (Linnaeus)	+	+	+	+
<i>Thalassoma purpureum</i> (Forsskal)	+	+	+	+
<i>Thalassoma trilobatum</i> (Lacepède)			+	+
Genus sp. (juvenile)	+	+	+	+
SCARIDAE				
<i>Leptoscarus vaigiensis</i> (Quoy & Gaimard)				+
<i>Scarus falcipinnis</i> Playfair		+	+	+
<i>Scarus frenatus</i> Lacepède			+	+
<i>Scarus ghobban</i> Forsskal		+	+	+
<i>Scarus gibbus</i> Rüppel			+	+
<i>Scarus psittacus</i> Forsskal			+	+
<i>Scarus scaber</i> Valenciennes		+	+	+
<i>Scarus sordidus</i> Forsskal	+	+	+	+
<i>Scarus</i> spp. (juveniles)	+	+	+	+
MUGILIDAE				
<i>Liza vaigiensis</i> (Quoy & Gaimard)		+		+
<i>Mugil cephalus</i> Linnaeus		+	+	+
POLYNEMIDAE				
<i>Polydactylus plebeius</i> (Broussonet)				+
SPHYRAENIDAE				
<i>Sphyraena barracuda</i> (Walbaum)				+
BLENNIIDAE				
<i>Cirripectes castaneus</i> (Valenciennes)		+	+	+
<i>Cirripectes polyzona</i> (Bleeker)			+	
<i>Exallia brevis</i> (Kner)		+	+	+
<i>Istiblennius dussumieri</i> (Valenciennes)	+		+	+
<i>Istiblennius periophthalmus</i> (Valenciennes)		+	+	+
<i>Petroscirtes nitratus</i> Rüppel		+		+
<i>Plagiotremus tapeinosoma</i> (Bleeker)		+		
CALLIONYMIDAE				
<i>Callionymus marleyi</i> Regan				+
GORBIIDAE				
<i>Istigobius decoratus</i> (Herre)	+	+	+	+
<i>Valenciennea sexguttata</i> (Valenciennes)		+		+
Genus sp.1		+	+	+
Genus sp.2	+		+	+
ACANTHURIDAE				
<i>Acanthurus blochii</i> Valenciennes	+	+	+	+
<i>Acanthurus dussumieri</i> Valenciennes				+
<i>Acanthurus guttatus</i> Bloch & Schneider			+	+
<i>Acanthurus lineatus</i> (Linnaeus)			+	+
<i>Acanthurus nigricauda</i> Duncker & Mohr	+	+	+	+

<i>Acanthurus nigrofuscus</i> (Forsskal)	+	+	+	+
<i>Acanthurus polyzona</i> (Bleeker)	+	+	+	+
<i>Acanthurus tennentii</i> Günther		+		+
<i>Acanthurus triostegus</i> (Linnaeus)	+	+	+	+
<i>Acanthurus xanthopterus</i> Valenciennes			+	+
<i>Ctenochaetus striatus</i> (Quoy & Gaimard)	+	+	+	+
<i>Naso brevirostris</i> (Valenciennes)			+	+
<i>Naso litturatus</i> (Schneider)		+	+	+
<i>Naso unicornis</i> (Forsskal)	+	+	+	+
<i>Paracanthurus hepatus</i> (Linnaeus)				+
<i>Zebrasoma gemmatum</i> (Valenciennes)		+		
<i>Zebrasoma scopas</i> (Cuvier)	+	+	+	+
<i>Zebrasoma veliferum</i> (Bloch)	+	+	+	+
ZANCLIDAE				
<i>Zanclus canescens</i> (Linnaeus)	+	+	+	+
BOTHIDAE				
<i>Bothus mancus</i> (Broussonet)		+	+	+
SIGANIDAE				
<i>Siganus sutor</i> (Valenciennes)	+	+	+	+
SOLEIDAE				
<i>Pardachirus marmoratus</i> (Lacepède)			+	
BALISTIDAE				
<i>Abalistes stellatus</i> (Lacepède)				+
<i>Balistapus undulatus</i> (Mungo Park)				+
<i>Balistoides viridescens</i> (Bloch & Schneider)			+	+
<i>Pseudobalistes flavimarginatus</i> (Rüppell)		+		+
<i>Pseudobalistes fucus</i> (Bloch & Schneider)				+
<i>Rhinecanthus aculeatus</i> (Linnaeus)	+	+	+	+
<i>Rhinecanthus rectangulus</i> (Bloch & Schneider)	+	+	+	+
MONACANTHIDAE				
<i>Amanes scopas</i> (Cuvier)		+	+	+
<i>Cantherhines dumerilii</i> (Hollard)		+	+	+
<i>Cantherhines pardalis</i> (Rüppell)	+	+	+	+
<i>Oxymonacanthus longirostris</i> (Bloch & Schneider)		+	+	+
<i>Paraluteres prionurus</i> (Bleeker)		+		+
<i>Pergavor janthinosoma</i> (Bleeker)	+	+	+	+
OSTRACIIDAE				
<i>Lactoria cornuta</i> (Linnaeus)				+
<i>Ostracion cubicus</i> (Linnaeus)	+	+	+	+
<i>Ostracion meleagris</i> Shaw	+	+	+	+
TETRAODONTIDAE				
<i>Arothron hispidus</i> Linnaeus	+	+		+
<i>Arothron immaculatus</i> (Bloch & Schneider)	+	+		+
<i>Arothron meleagris</i> (Bloch & Schneider)		+		
<i>Arothron nigropunctatus</i> (Bloch & Schneider)	+	+	+	+

<i>Arothron stellatus</i> (Bloch & Schneider)	+	+	+	+
<i>Canthigaster amboinensis</i> (Bleeker)	+	+	+	+
<i>Canthigaster bennetti</i> (Bleeker)	+		+	+
<i>Canthigaster janthinoptera</i> (Bleeker)	+		+	+
<i>Canthigaster smithae</i> Allen & Randall			+	
<i>Canthigaster solandri</i> (Richardson)	+	+	+	+
<i>Canthigaster valentini</i> (Bleeker)	+	+	+	+
DIODONTIDAE				
<i>Diodon hystrix</i> Linnaeus		+		+

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