Environmental Biology of Fishes **37**: 109–120, 1993.

Impact of hurricane Firinga on fish community strucrure on fringing reefs of Reunion Island, S.W. Indian Ocean

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Received 27.5.1992 Accepted 16.11.1992

Key words: Cyclone effect, Coral reefs, Ichthyofauna, Recovery

Synopsis

The reef flats of Saint-Pierre and Saint-Leu (Reunion Island, Indian Ocean) suffered badly from hurricane Firinga on 29 January 1989. The high degree of silting due to increased run-off killed the coral colonies. Fish communities were surveyed at four periods following the hurricane (March and September 1989, March and September 1990). An increase in both species richness (31 to 47 spp. per census) and abundance (169 to 265 individuals per census) of fishes was observed with time, along with changes in their trophic structure. This positive succession may be linked to the disappearance of the silt layer from reef flats since September 1989. Nevertheless, there were differences in fluctuations and trophic structure of the fish community between back-, inner- and outer-reef flats. Finally, differences in recovery between the two reefs are related to the overall environmental degradation of the Island, chiefly by human perturbation, prior to the hurricane.

Introduction

Most coral reefs in the world are located in areas which are potentially subjected to the impact of hurricanes. Hurricanes appear to play a significant role in determining the structure of shallow water reef assemblages (Endean 1976). The effects of hurricanes or tropical storms on geological features (Stoddart 1971, Flood & Jell 1977, Kahn 1984), hermatypic corals (Woodley et al. 1981, Dollar 1982, Williams 1984, Laboute 1985, Harmelin-Vivien & Laboute 1986) and other reef organisms (Yoshioka & Yoshioka 1987, Moran & Reaka-Kudla 1991) have been documented. Some information on the effects of hurricanes on reef fish communities are available for the Caribbean (Kaufman 1983, Bouchon et al. 1991, Fenner 1991), for Hawaii (Walsh 1983, Pfeffer & Tribble 1985) and the Great Barrier Reef in the Pacific (Lassig 1983), but none for the Indian Ocean, except for a preliminary study on the influence of hurricane Firinga on reef fishes from Reunion Island (Letourneur 1991). Reef fish communities seem to be differently affected by hurricanes depending on the rate of damage on the corals, the size or stage in the life cycle of the fishes and their habitats.

On 29 January 1989, hurricane Firinga passed across Reunion Island with maximum measured wind velocity of 216 km h^{-1} in the south (SMRR

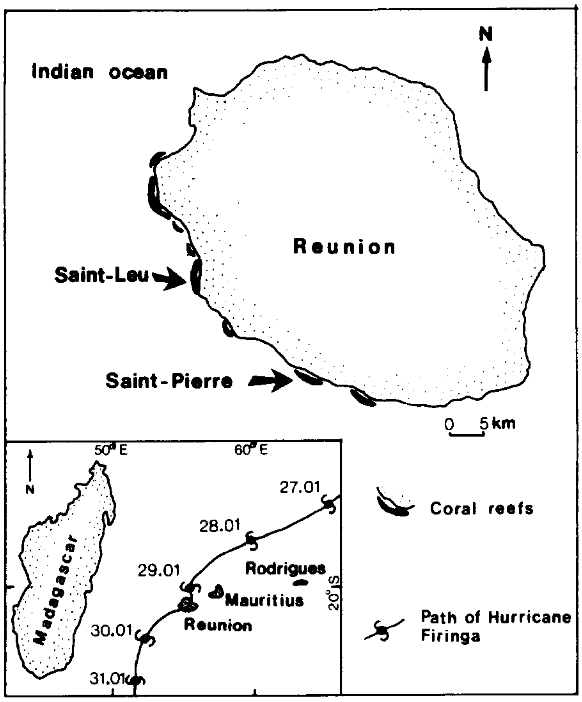

Fig. 1. Location of coral reefs around Reunion Island in the south-west Indian Ocean, and path of hurricane Firinga, January 1989.

1989)[1] (Fig. 1). This wind velocity was probably exceeded locally due to the high and contrasting relief of the Island (3069 m). Some wind gusts were estimated at over 240 km h^{-1} in the south and south-west parts of the Island, where rainfall caused considerable erosion. In the vicinity of Saint-Pierre, numerous domestic animals were killed and carried by rivers and torrents onto the fringing reef flat, along with quantities of terrigeneous material. Because of the decomposition of dead animals, diving was prohibed on the reef flat of Saint-Pierre for several weeks after the hurricane.

The present study was conducted over a 18 month period to assess the fish communities on coral reef flats after a major cyclonic event in the south-west Indian Ocean. We have tried to answer the following questions: (1) What was the temporal development of the fish community on Reunion fringing reef flats after the hurricane (i.e., an increase or decrease in species richness and density, a change of trophic structure)? (2) Did the level of degradation of coral communities prior to the hurricane influence this development?

Materials and methods

Study areas

All the reef formations of Reunion Island, western Indian Ocean (21°70′S, 55°32′E) are fringing reefs (Montaggioni & Faure 1980). Before hurricane Firinga, the fringing reef of Saint-Leu was generally in good health, with numerous large living colonies of *Acropora pharaonis* coral (Faure 1982, Cuet & Naim 1989). In contrast, the fringing reef of Saint-Pierre has been badly degraded by human disturbance, mainly from urban sewage and wastes from sugar cane plantations (Cuet & Naim 1989).

Fish surveys were conducted along two transects at Saint-Leu and along three transects at Saint-Pierre. Each transect was perpendicular to the coast and crossed three geomorphological zones defined by Montaggioni & Faure (1980), which were from the coast to the ocean: the back-reef (BR), the inner reef flat (IRF) and the outer reef flat (ORF).

Sampling technique

Visual counts are commonly utilized to survey fish communities on coral reefs (Sale & Sharp 1983, Galzin 1987a, b, Fowler 1987, Bortone et al. 1989). The reliability and limits of visual methods were discussed in synthetic papers (Barans & Bortone 1983[2], Harmelin-Vivien et al. 1985). Visual counts permit surveys of fish communities without perturbation and are efficient for monitoring communities in long term studies. Because the turbidity of water over the reefs was too high after the hurricane

[1] SMRR, 1989. Cyclone tropical Firinga: du 25 janvier au 7 février 1989. Service Météorologique Régional de La Réunion. 51 pp.

[2] Barans, C.A. & S.A. Bortone (ed.). 1983. The visual assessment of fish populations in the southeastern United States. 1982 Workshop, South Carolina Sea Grant Consortium, Tech. Rep. 1. 52 pp.

to make precise counts of individual fish, a semi-quantitative method was adopted (Letourneur 1991; modified from Williams 1982). Six abundance categories were used: 1= 1 fish observed; 2= 2–5 fishes; 3= 6–10; 4= 11–30; 5= 31–100; 6= 101–300. The senior author swam slowly in each geomorphological zone of each transect for 30 minutes. The area censused during this period was approximately $200 m^2$ (100 m long and 2 m wide). Each species was assigned to one of the six abundance categories, depending on its total abundance during the 30 min sampling period. Based on dietary data of coral reef fishes (Harmelin-Vivien 1979, Sano et al. 1984), each fish species censused was assigned to one of seven trophic categories: herbivore, omnivore, sessile invertebrate feeder, diurnal carnivore, nocturnal carnivore (these two last categories mostly prey on mobile invertebrates), piscivore and zooplanktivore (diurnal and nocturnal species combined). Visual surveys were performed in March and September 1989, and in March and September 1990 on each reef.

Data analysis

The median value by abundance category was used to estimate the total number of individuals in each survey. Mean abundance estimates were calculated for all surveys, for each geomorphological zone, and for each reef. Number of species and individuals in each trophic category were used to determine the fluctuation of the trophic structure of the fish community. Significant variation in mean species richness and mean fish abundance between the four periods studied, the two reef flats and the different geomorphological zones was tested using Student's t-tests (means not significantly different when $p > 0.05$).

Results

In March 1989, one month after Firinga, when diving was permitted again, a thick silt layer (due to the cyclonic rainfall on the island) was observed on Saint-Pierre and Saint-Leu reef flats. Siltation was less on the outer-reef flats which were directly exposed to the action of the ocean waves. Silting apparently killed most coral colonies living on both reef flats. Nevertheless, hurricane Firinga did not cause significant physical damage to the structure of the coral reef. Thus, the biological composition of the benthic reef environment changed drastically due to coral mortality, but its architectural complexity was preserved. Six months later, in September 1989, the silt layer was almost totally washed out by the waves and currents, but a thin layer remained, settled in algal turf and easily resuspended by wave agitation. The low, but persistant, siltation level did not change between September 1989 and September 1990.

Global variation of the reef fish community

During this 18 month study, 153 species of coral reef fishes belonging to 36 families were recorded on the two reefs (Table 1). The total number of species increased between March 1989 and September 1990 (Table 2). Both mean species richness and mean abundance per census steadily increased during this time and the differences were statistically significant between March 1989 and March 1990. An increase in species richness was particularly evident among Chaetodontidae, Pomacentridae and Labridae (Table 1). In contrast, a few families like the Mullidae, showed a slight decrease in their species richness. Six families (Mullidae, Chaetodontidae, Pomacentridae, Labridae, Scaridae and Acanthuridae) accounted for most individuals regardless of season (from 87.7 to 90.5% of the total fish abundance, Table 3). Between March 1989 and September 1990, an increase in the abundance of Chaetodontidae (+124%), Pomacentridae (+137%), Labridae (+180%) and Scaridae (+547%) was observed. The density of Acanthuridae, mainly *Acanthurus triostegus*, decreased six months after the hurricane, and later increased. The most abundant acanthurid species in September 1990 were *Acanthurus nigrofuscus*, *Ctenochaetus striatus*, *A. triostegus* and *Zebrasoma scopas*. The density of Mullidae (chiefly *Parupaeneus bifasciatus* and *P. macronema*) varied

Table 1. Fish species recorded on the reef flat of Saint-Leu (L) and Saint-Pierre (P) between March 1989 and September 1990 (mean abundance per census, – = not observed). Identification and systemic order of families following Smith & Heemstra (1986).

Taxa	March 1989		September 1989		March 1990		September 1990	
	L	P	L	P	L	P	L	P
Muraenidae								
Echidna nebulosa	1.2	–	–	–	–	0.8	0.6	0.4
Gymnothorax meleagris	–	–	0.2	–	–	–	–	–
Gymnothorax undulatus	–	–	–	–	–	0.4	–	–
Siderea grisea	0.6	–	–	–	–	0.4	–	0.4
Genus sp.	–	–	–	0.1	–	–	–	–
Plotosidae								
Plotosus lineatus	–	–	–	–	–	0.4	1.3	0.4
Synodontidae								
Saurida gracilis	1.2	0.6	0.6	–	1.2	0.8	1.2	0.4
Synodus variegatus	–	0.6	–	–	–	0.1	0.2	–
Atherinidae								
Genus sp.	–	–	–	–	–	0.9	–	–
Belonidae								
Ablennes hians	–	–	–	–	0.2	–	–	–
Strongylura leiura	–	–	–	–	0.2	0.1	–	–
Holocentridae								
Myripristis murdjan	0.6	0.6	0.6	–	2.7	1.8	2.7	1.3
Neoniphon sammara	–	–	–	0.1	–	–	–	–
Sargocentron diadema	1.8	1.2	–	–	0.6	1.3	0.6	0.4
Sargocentron punctatissimum	–	1.8	–	0.9	0.6	2.4	0.6	1.9
Aulostomidae								
Aulostomus chinensis	–	–	0.6	–	1.2	0.4	1.2	0.5
Fistulariidae								
Fistularia petimba	1.2	–	–	–	0.6	1.3	0.6	0.9
Syngnathidae								
Doryrhamphus excisus	–	–	–	–	–	0.1	–	–
Scorpaenidae								
Dendrochirus zebra	–	–	–	–	–	0.1	0.2	–
Pterois antennata	–	–	–	–	–	0.4	0.2	0.4
Pterois volitans	–	–	1.2	0.4	–	0.1	0.6	0.1
Scorpaenodes guamensis	–	–	–	–	–	0.4	–	–
Synanceia verrucosa	–	–	–	–	–	0.1	–	–
Serranidae								
Epinephelus faveatus	–	–	–	0.9	0.6	–	–	–
Epinephelus hexagonatus	–	–	–	–	–	1.2	–	0.4
Epinephelus merra	2.3	1.6	1.8	1.3	1.8	2.1	1.2	3.3
Grammistidae								
Grammistes sexlineatus	–	–	–	–	0.6	0.8	0.6	0.4
Priacanthidae								
Priacanthus cruentatus	–	–	–	–	–	–	0.6	–
Apogonidae								
Apogon kallopterus	0.6	0.8	–	–	0.6	1.3	0.6	0.4
Apogon taeniophorus	–	1.7	–	1.7	0.8	1.9	–	3.3
Lutjanidae								
Lutjanus fulvus	1.3	6.0	1.2	2.9	–	0.8	–	–
Lutjanus kasmira	–	1.3	–	–	–	–	–	–
Lethrinidae								
Gnathodentex aureolineatus	–	0.8	1.3	0.4	1.3	0.4	1.8	–
Mullidae								
Mulloides flavolineatus	1.3	1.2	1.3	–	6.4	3.4	–	3.4
Mulloides vanicolensis	–	1.2	–	–	1.9	0.8	–	–
Parupeneus barberinus	12.2	4.2	1.8	3.2	1.2	1.2	–	0.8
Parupeneus bifasciatus	10.5	3.7	5.2	2.2	6.5	6.2	9.3	6.6
Parupeneus cyclostomus	0.6	–	0.6	–	1.2	0.4	–	–
Parupeneus indicus	–	0.1	–	0.3	–	–	–	–
Parupeneus macronema	11.3	2.1	4.4	1.3	9.9	8.8	5.2	5.2

Taxa	March 1989		September 1989		March 1990		September 1990	
	L	P	L	P	L	P	L	P
Parupeneus pleurostigma	–	–	–	–	0.3	0.1	–	–
Parupeneus rubescens	1.2	2.4	0.6	2.3	1.2	3.8	1.2	3.4
Pomacanthidae								
Centropyge bispinosus	–	–	–	0.1	–	–	–	–
Chaetodontidae								
Chaetodon auriga	1.2	2.3	2.3	1.3	2.3	1.9	2.3	1.6
Chaetodon blackburnii	–	–	–	0.1	–	0.4	–	0.8
Chaetodon guttatissimus	–	–	–	–	–	–	0.2	–
Chaetodon kleinii	0.6	0.4	0.6	–	0.6	–	–	–
Chaetodon lunula	–	0.7	0.6	2.3	1.8	2.2	0.6	2.3
Chaetodon madagaskariensis	–	–	–	–	0.2	–	0.3	–
Chaetodon melannotus	–	0.4	–	–	0.6	0.8	–	0.4
Chaetodon trifasciatus	–	–	1.2	1.0	0.6	–	1.2	0.1
Chaetodon vagabundus	1.8	2.3	2.9	4.6	2.4	4.7	6.5	4.1
Chaetodon xanthocephalus	–	–	–	–	0.2	–	–	–
Heniochus monoceros	–	–	–	0.4	0.6	0.8	1.2	0.4
Carangidae								
Atule mate	–	–	–	0.1	–	–	–	–
Caranx sexfasciatus	–	–	–	–	1.2	–	–	–
Genus sp.	–	2.2	–	–	–	–	–	–
Cirrhitidae								
Cirrhitichthys guichenoti	–	–	0.2	–	–	–	–	–
Paracirrhites arcatus	–	–	0.6	–	–	–	1.3	0.1
Pempheridae								
Pempheris adusta	–	–	–	–	0.6	–	1.3	1.3
Pomacentridae								
Abudefduf septemfasciatus	0.6	0.4	1.2	1.3	–	0.4	1.2	1.3
Abudefduf sexfasciatus	–	–	–	0.1	–	–	–	–
Abudefduf sordidus	–	–	–	0.4	1.2	–	0.6	0.1
Abudefduf sparoides	1.9	2.3	1.2	3.4	1.3	4.8	1.9	5.3
Chromis dimidiata	–	–	–	0.1	–	0.1	0.3	–
Chrysiptera glauca	2.5	4.1	4.0	6.8	1.8	4.6	3.8	4.8
Chrysiptera unimaculata	1.2	1.2	0.6	3.4	2.7	2.6	5.8	5.3
Dascyllus aruanus	3.3	0.4	1.2	1.0	1.9	–	2.7	–
Dascyllus trimaculatus	–	0.4	–	–	–	–	–	–
Plectroglyphidodon dickii	0.6	1.2	–	–	0.6	–	1.3	–
Plectroglyphidodon imparipennis	1.2	0.7	1.9	1.4	1.2	5.0	1.9	1.7
Plectroglyphidodon johnstonianus	0.6	–	1.2	–	–	–	0.6	–
Plectroglyphidodon lacrymatus	–	–	–	–	0.6	–	0.6	–
Plectroglyphidodon leucozonus	1.9	4.0	6.7	7.9	14.2	23.8	21.7	22.5
Plectroglyphidodon phoenixensis	–	–	0.2	–	0.2	0.1	–	–
Stegastes fasciolatus	–	–	4.0	3.3	1.8	2.3	5.9	2.8
Stegastes limbatus	0.6	–	6.7	2.5	7.3	2.9	8.0	7.4
Stegastes lividus	–	–	–	–	1.9	–	0.6	–
Stegastes nigricans	44.2	4.0	66.7	9.6	66.7	4.8	67.3	5.3
Stegastes pelicieri	–	–	1.9	–	1.9	–	1.2	–
Genus sp. 1 (juvenile)	–	–	0.6	0.4	–	–	0.6	–
Genus sp. 2 (juvenile)	–	–	0.6	–	–	–	0.6	–
Genus sp. 3 (juvenile)	–	–	–	–	–	–	0.6	–

Table 1. Continued.

Taxa	March 1989 L	March 1989 P	September 1989 L	September 1989 P	March 1990 L	March 1990 P	September 1990 L	September 1990 P
Labridae								
Anampses caeruleopunctatus	–	–	–	–	0.6	–	0.6	–
Cheilinus trilobatus	1.2	1.2	3.8	1.4	5.9	1.9	9.3	3.3
Coris aygula	–	–	1.2	–	1.2	0.8	2.5	1.7
Coris caudimacula	–	–	–	1.0	–	–	–	–
Coris gaimard africana	–	–	–	–	1.2	0.2	–	–
Epibulus insidiator	–	–	–	–	0.3	–	–	–
Gomphosus caeruleus	2.6	1.6	3.1	0.4	2.3	–	3.8	–
Halichoeres hortulanus	–	–	0.6	0.4	–	–	0.6	0.1
Halichoeres marginatus	1.2	0.7	4.6	2.3	7.9	4.3	9.9	4.8
Halichoeres nebulosus	–	0.4	–	1.0	1.2	1.7	–	1.3
Halichoeres scapularis	0.6	0.4	0.6	0.9	0.6	–	1.9	2.6
Hemigymnus fasciatus	–	–	0.2	–	0.3	–	0.2	–
Labroides bicolor	–	–	–	–	–	–	0.2	–
Labroides dimidiatus	–	–	–	–	0.3	0.4	1.2	0.5
Macropharyngodon cyanoguttatus	–	–	–	–	–	–	0.3	–
Novaculichthys taeniourus	–	–	0.2	–	–	–	–	–
Stethojulis albovittata	5.0	4.2	1.9	3.2	10.0	9.8	4.4	4.7
Stethojulis strigiventer	0.6	0.7	–	–	–	0.9	1.2	0.4
Thalassoma amblycephalum	–	–	1.8	–	0.6	1.2	3.7	2.5
Thalassoma genivittatum	–	–	–	–	1.2	1.6	1.2	–
Thalassoma hardwicke	9.9	1.7	11.3	1.4	7.9	0.8	13.3	0.8
Thalassoma lunare	6.6	2.0	9.3	2.9	10.7	11.5	13.9	11.1
Thalassoma purpureum	–	–	4.6	1.4	4.7	3.9	4.7	2.9
Thalassoma trilobatum	–	–	–	–	0.6	0.2	–	–
Genus sp. (juvenile)	–	–	–	–	–	0.4	4.0	–
Scaridae								
Scarus falcipinnis	–	–	0.3	–	0.3	–	0.8	–
Scarus frenatus	–	–	–	–	–	–	0.2	–
Scarus ghobban	–	–	–	0.4	–	–	0.2	–
Scarus scaber	–	–	3.9	–	1.3	–	1.3	–
Scarus sordidus	1.9	0.4	6.7	0.4	2.9	0.4	10.7	0.8
Scarus spp. (juveniles)	0.6	0.4	6.7	–	5.2	1.2	7.2	0.8
Mugilidae								
Genus sp. 1	–	–	–	–	–	0.4	–	–
Genus sp. 2	–	–	0.6	0.4	0.6	–	–	–
Polynemidae								
Polydactylus plebeius	–	–	–	–	1.3	–	–	–
Blenniidae								
Cirripectes castaneus	–	–	–	–	1.3	–	2.1	–
Exallias brevis	–	–	0.6	–	–	–	–	–
Istiblennius dussumieri	–	–	–	0.9	1.3	–	–	0.4
Plagiotremus tapeinosoma	–	–	–	–	–	–	0.2	–
Gobiidae								
Istigobius decoratus	–	–	–	–	–	0.4	–	–
Genus sp.	–	–	–	–	–	–	0.2	–
Acanthuridae								
Acanthurus blochii	0.6	1.7	1.9	1.3	0.2	0.4	–	0.4
Acanthurus nigricauda	–	–	–	–	–	0.2	–	–
Acanthurus nigrofuscus	18.7	7.4	6.6	4.9	18.1	12.5	33.8	12.0
Acanthurus polyzona	–	0.9	0.2	0.4	0.2	–	0.2	0.1
Acanthurus tennenti	–	–	–	0.1	–	–	–	–
Acanthurus triostegus	27.7	46.4	11.3	16.5	18.8	14.3	9.8	13.2
Ctenochaetus striatus	6.6	2.4	18.7	4.3	16.1	4.4	26.3	3.8
Naso unicornis	2.3	2.6	3.3	1.4	8.5	2.7	6.0	1.7
Zebrasoma scopas	0.6	1.6	1.9	0.4	2.4	0.4	2.7	1.7
Zebrasoma veliferum	–	–	0.2	–	0.2	–	0.2	–
Zanclidae								
Zanclus canescens	0.6	0.4	0.6	–	1.8	0.8	3.7	0.2
Siganidae								
Siganus sutor	–	1.7	0.6	–	0.6	0.8	1.2	–
Balistidae								
Balistapus undulatus	–	–	–	0.1	–	0.1	–	–
Rhinecanthus aculeatus	1.9	1.9	2.7	3.1	2.7	5.4	3.3	4.7
Rhinecanthus rectangulus	0.6	–	–	–	0.3	–	0.6	–
Monacanthidae								
Amanses scopas	0.6	–	0.3	–	–	–	–	–
Cantherhines dumerilii	–	–	–	–	–	–	0.3	–
Cantherhines pardalis	–	–	–	–	1.8	0.4	1.2	0.4
Oxymonacanthus longirostris	–	–	–	–	–	–	0.6	–
Paraluteres prionurus	–	–	–	–	–	–	0.3	–
Pervagor janthinosoma	–	0.4	0.6	–	0.6	–	1.2	0.4
Ostraciidae								
Ostracion cubicus	0.6	0.7	1.2	–	1.2	1.6	3.1	1.6
Ostracion meleagris	0.6	–	1.8	–	0.6	0.4	0.8	0.4
Tetraodontidae								
Arothron immaculatus	–	–	–	0.1	–	0.1	–	0.5
Arothron nigropunctatus	–	0.4	–	–	0.6	–	–	–
Arothron stellatus	–	–	–	–	–	0.4	–	–
Canthigaster amboinensis	–	–	0.6	1.3	1.2	–	0.6	0.5
Canthigaster bennetti	–	–	–	–	–	–	0.3	–
Canthigaster janthinoptera	–	–	–	–	–	–	0.3	–
Canthigaster valentini	1.8	0.4	1.8	–	1.8	0.8	1.9	0.9

with season, but were not apparently influenced by the hurricane (Table 3).

Temporal variation between geomorphological zones

Within each of the three geomorphological zones, back reef (BR), inner reef flat (IRF) and outer reef flat (ORF), the fish species richness increased between March 1989 and March 1990 (Fig. 2a). This trend continued in September 1990 except in the back reef zone. During each sampling period, the highest species richness was observed on the inner reef flat. Nevertheless, the percent increase in species richness differed with geomorphological zone. After 18 months, it was highest on the inner reef flat (+83%), intermediate on the outer reef flat

Table 2. Temporal variation of the ichthyofauna on the reef flats of Reunion Island between March 1989 and September 1990. Underlining indicates means which are not significantly different (t-tests); standard deviation in parentheses; number of samples = 15 during each period.

	March 1989	September 1989	March 1990	September 1990
Total number of species	68	92	118	110
Mean species richness per census	30.8 (±6.0)	35.0 (±9.7)	45.8 (±13.2)	46.7 (±13.3)
Mean abundance per census	168.9 (±55.5)	172.1 (±121.1)	236.0 (±98.8)	264.5 (±157.9)

(+48%), and lowest on the back reef (+29%). Just after the hurricane, the species richness was relatively similar within the three zones, whereas between zone differences became greater with time.

The highest mean abundance of fishes was always observed on the inner reef flat, except in March 1989 just after the storm, where it was slightly higher on the outer reef flat (Fig. 2b). Statistically lower mean fish abundance was always recorded on the back reef zone. The mean abundance of fishes per sampling steadily increased between March 1989 and September 1990 on IRF (186.4 to 351.1 individuals per census, increase of 88%) and on ORF between September 1989 and September 1990 (193.9 to 292.2 individuals, increase of 51%). In the back reef zone, the temporal variation of the mean abundance of fishes per sampling was lower than in the other zones, and fluctuated without a well defined trend. Thus, increases in species richness were observed in all geomorphological reef flat zones from March 1989 to September 1990, while increases in mean abundance of individuals were observed mainly on the inner and outer reef flats.

The trophic structure of the fish community on the back reef differed from those observed on the inner and on the outer reef flats, with a higher proportion of diurnal carnivorous fishes, like the Mullids (i.e., *Mulloides flavolineatus* and *Parupeneus macronema*, Fig. 3). Conversely, percentages of herbivorous and omnivorous fishes were lower on BR than on IRF and ORF. No progressive temporal change appeared in the trophic structure of the back reef ichthyofauna, but a predominance of a seasonal trend was evident. The March samples contrasted with those of September with an increase in the number of herbivorous and diurnal carnivorous fishes. Fishes assigned to these two trophic categories also increased slightly with time within each season. The trophic structures of the ichthyofauna on IRF and ORF zones were more similar with a dominance of omnivorous fishes, mostly pomacentrids. A post-hurricane succession occurred on the inner reef flat, with a continuous increase in the number of herbivores, omnivores and diurnal carnivores (Fig. 3). In addition, the relative proportions of the different trophic categories

Table 3. Mean number of individuals per census for the six most abundant fish families on the two reef flats studied after hurricane Firinga; standard deviation in parentheses; number of samples = 15 during each period.

	March 1989	September 1989	March 1990	September 1990
Mullidae	26.0 (±11.1)	11.6 (±2.3)	26.7 (±2.0)	17.6 (±1.9)
Chaetodontidae	4.9 (±1.3)	8.5 (±0.9)	10.4 (±0.5)	11.0 (±1.3)
Pomacentridae	38.7 (±20.0)	70.2 (±28.6)	78.4 (±26.9)	91.9 (±35.4)
Labridae	20.3 (±7.4)	29.8 (±13.5)	48.6 (±9.0)	56.8 (±20.1)
Scaridae	1.7 (±0.9)	9.2 (±8.4)	5.7 (±4.1)	11.0 (±9.4)
Acanthuridae	59.8 (±3.3)	36.7 (±7.4)	49.7 (±14.8)	56.0 (±23.1
Percent total abundance for the six families	87.7	90.5	87.1	88.1

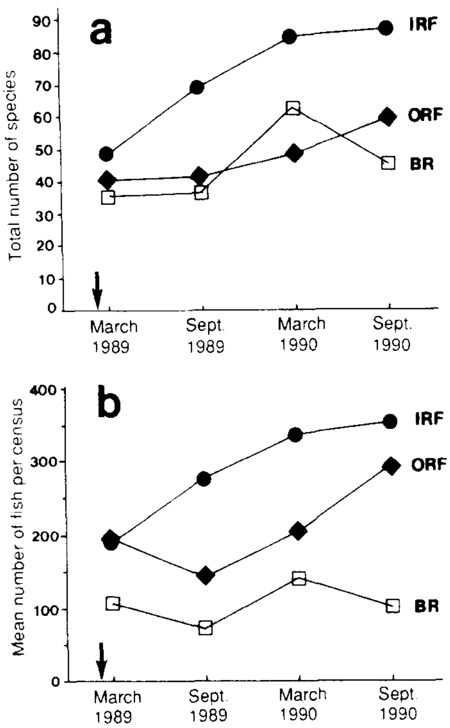

Fig. 2. Variation in total species richness (a) and mean abundance of fish per census (b) on the three geomorphological zones of Reunion reef flats after hurricane Firinga. BR = back reef. IRF = inner reef flat. ORF = outer reef flat. Arrow = date of hurricane Firinga (29 January 1989).

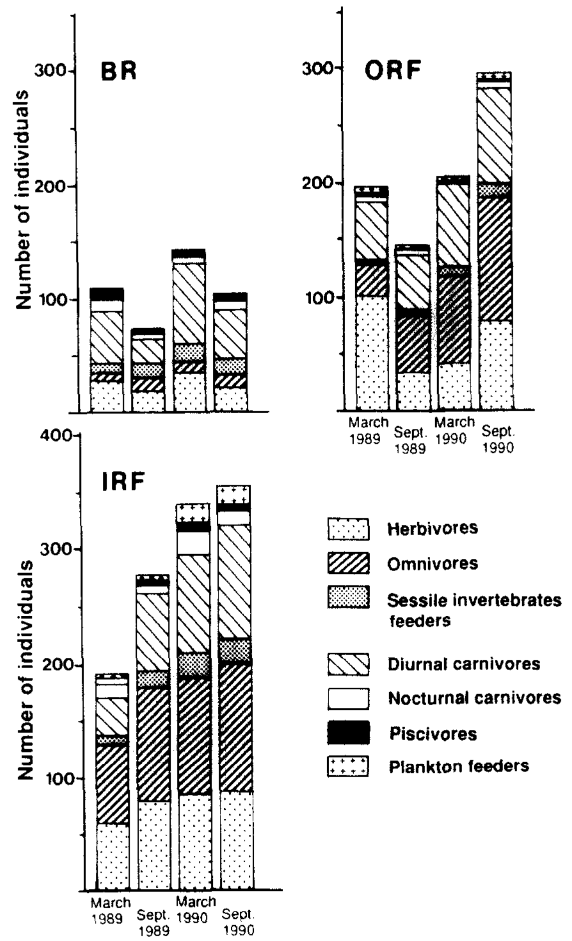

Fig. 3. Changes in trophic structure of the total fish community in the three geomorphological reef zones expressed in number of individuals. BR = back reef. IRF = inner reef flat. ORF = outer reef flat.

remained stable with time on IRF. On the outer reef flat, the trophic structure of the fish community changed noticeably between March 1989 and the other periods. Just after the hurricane, herbivores were dominant on ORF and omnivores not as numerous. Six months later (September 1989), a remarkable decrease in herbivores occurred, mainly due to a diminution of the surgeonfish, *Acanthurus triostegus*, population. Then, a steady increase in the abundance of herbivorous, omnivorous and diurnal carnivorous fishes occurred. The main increases in abundance between March 1989 and September 1990 were observed for omnivorous fishes on ORF (+288%, mainly due to *Plectroglyphidodon leucozonus*) and IRF (+60%, mainly due to *Stegastes nigricans*), and for diurnal carnivorous fishes on IRF (+206%, mainly due to *Thalassoma lunare,*

Table 4. Mean species richness per census on the two reef flats studied. Underlining indicates means which are not significantly different (t = tests); standard deviation in parentheses; n = number of samples during each period.

	March 1989	September 1989	March 1990	September 1990
Saint-Leu (n = 6)	27.0 (±3.7)	34.7 (±10.3)	34.0 (±23.4)	50.7 (±16.4)
Saint Pierre (n = 9)	34.7 (±5.4)	35.3 (±8.9)	45.7 (±15.3)	42.7 (±7.0)

T. harwickei and *Halichoeres marginatus*) and ORF (+70%, mainly due to *Thalassoma lunare, T. purpureum* and *Halichoeres marginatus*).

Differences in variation between the two reefs

The total number of fish species recorded during this study was a little higher on Saint-Leu (129 species) than on Saint-Pierre (117 species). The total species richness increased on the two reef flats between March 1989 and March 1990 (Fig. 4); this increase continued on Saint-Leu, but a decrease was observed on Saint-Pierre between March 1990 and September 1990. The increase in total fish species richness was higher on Saint-Leu (52 to 90 species, increase of 90%) than on Saint-Pierre (59 to 72 species, increase of 22%). The increase in mean species number per census was statistically significant on the two reef flats between March 1989 and September 1990 (Table 4). Except for March 1989 ($p < 0.05$), the mean species richness was not significantly different between Saint-Leu and Saint-Pierre. The mean abundance of fishes per sample increased from March 1989 to September 1990 on both reefs, but was not statistically significant due to the high variance of the data (Table 5). This increase was high (+72%) and constant on Saint-Leu, but low (+34%) and variable on Saint-Pierre. Mean abundance of fish per sampling was always higher on Saint-Leu with significant differences between reefs in March 1989 and 1990.

The trophic structure of the ichthyofauna remained unchanged with time on the reef flat of Saint-Leu; but it changed with time on the reef flat of Saint-Pierre, the main change occurring between March and September 1989 (Fig. 5). The change involved a decrease in the abundance and percentage of herbivorous fishes and an increase in the relative abundance and proportion of both omnivorous and diurnal carnivorous fishes.

Discussion

A survey of the literature indicates conflicting information of hurricane effects on reef fish communities. High fish mortality directly provoked by hurricane waves was rarely reported (Pfeffer & Tribble 1985). Most studies related little direct influence of hurricanes on adult reef fish communities, the main feature being the temporary re-distribution of individuals into non-damaged habitats (Lassig 1983, Walsh 1983). Hurricanes seemed to affect primarily juvenile fishes and reduced further settlement on affected reefs (Lassig 1983, Bouchon et al. 1991). Some authors reported changes in trophic structure of fish communities after hurricanes, generally a short-term increase in the abundance of predators and a long-term increase in the abundance of herbivores, but without any quantification of such phenomena (Woodley et al. 1981, Kaufman 1983).

The present study indicates an increase in both species richness and abundance of fishes during the 18 month period following hurricane Firinga. This trend was highest on the inner reef flat, and lowest in the back reef zone. But, as size classes have not been differentiated, we could not determine the relative proportion of adults and juveniles in the post-hurricane differences of the fish community. The overall increase in species richness and abundance of the fish fauna was higher in the reef flat of Saint-Leu which was less degraded by human activity prior to the hurricane. The trophic reorganisation of the fish assemblage differed between reefs and geomorphological zones. The back reef zones were less affected by the hurricane than the other zones.

Because only qualitative observations on pre-hurricane fish communities were available for these two specific reefs, results cannot be quantified in terms of true community recovery. However, quantitative studies conducted prior to the hurricane on fish communities on other Reunion reef flats located to the north (Letourneur 1992), allow us to suggest interpretations on pre- versus post-hurricane situations. The fish communities of the St-Leu and St-Pierre reef flats studied were more diversified and numerous before the hurricane (Y.L. personal observation).

Three hypotheses may be advanced to explain the low species richness and the low fish abundance observed in March 1989 just after the hurricane, and to account for their subsequent increase: (1) a high mortality of fishes directly attributable to hurricane

Firinga on 29 January 1989; (2) a habitat shift of fishes related to coral mortality; (3) an escape of fishes after silt deposition on the reef flats.

The first hypothesis should be rejected because the observed mortality of fishes on Reunion reef flats after hurricane Firinga was not great, as documented by Walsh (1983) and Fenner (1991) for other reefs after hurricanes. The second hypothesis could partly account for the decrease observed with the movement to nearby, undamaged habitats by reef fishes living in close association with living corals. This may have occurred on the Saint-Leu reef flat, where the living coral coverage was high prior to the hurricane. It is not suitable for Saint-Pierre, where most corals on the transects studied were dead before the hurricane (Cuet & Naim 1989). Coral-associated fish species of the families Chaetodontidae, Cirrhitidae and Monacanthidae were, in fact, scarcer on Saint-Leu and Saint-Pierre reefs after the hurricane than on northern, unaffected reefs. Nevertheless, the post-hurricane increase in coral mortality was not sufficiently high to completely account for the decrease in fish abundance and species richness, and it could not account for their subsequent increase on both reefs, because the living coral coverage remained extremely low thereafter.

The third hypothesis represents the most probable explanation for the observed circumstance. The disappearance in September 1989 of the silt layer washed out by waves and currents allowed some fishes to recolonize the reef flats. The architectural structure of the reef flat was not deeply altered by the hurricane, and once the silt layer was removed, most habitats were again available. The outer slopes were the principal refuge area for fishes just after the hurricane (Letourneur 1991). In Hawaii, Walsh (1983) also reported an evacuation of resident fishes from the shallow reef flat to deeper areas after a storm. The outer reef flat, which is exposed to ocean waves, suffered less from the siltation. The outer reef flat may also have constituted a refuge for some species, especially for members of the Scaridae and Acanthuridae which are generally mobile fishes. They can quickly leave an area exposed to a hurricane, and quickly recolonize it. The high abundance of herbivores on the outer reef flat just after the hurricane may be due to their migration from the other reef flat zones. Their further increase on the inner reef flat was linked to their return from their temporary refuge areas (outer slope and outer reef flat). The increase on the outer reef flat in the omnivorous pomacentrids *Plectroglyphidodon leucozonus* and *Chrysiptera unimaculata,* which live in surge zones (Allen 1975), may be related to the development of algal turf on newly dead corals.

The inner reef flat, where the biotic and topographic structure of reef communities were the most complex before the hurricane (Montaggioni & Faure 1980), was the most altered. On the unaffected reefs to the north, the inner reef flat supported a far more diverse and abundant fish community than the outer reef flat and the back reef (Letourneur 1992). Just after the hurricane, the numbers of species and individuals on IRF were similar to those observed on the other two zones, but the long-term, post-hurricane recovery of the fish fauna was highest on IRF. The abundance of the pomacentrid *Stegastes nigricans* increased between March and September 1989 on the inner reef flat, but remained stable thereafter. This dominant species on IRF did not respond as might be expected owing to the increase in available space for algal turf cultivation after the hurricane. This contradicts the observations on some pomacentrid populations in Jamaica which increased in response to an increase in space available after a hurricane (Williams 1984). Our results suggest that the recruitement rate, which is an important factor controlling the abundance of some *Stegastes* spp. populations (Wellington & Victor 1985), was low on Reunion reef flats after the hurricane. Therefore, dead coral colonies overgrown by turf algae, and not colonized by Pomacentridae, allowed an increase in abundance of herbivorous and some diurnal carnivorous fishes. Kaufman (1983) observed a cessation of territorial activity of *Stegastes planifrons* in Jamaica after hurricane Allen. We did not observe this behavior on Reunion reef flats; the herbivorous fishes continued to be vigorousely attacked by *S. nigricans* after hurricane Firinga.

Most species that increased in abundance after the hurricane feed mainly on algae, like the omnivorous *Stegastes nigricans, Plectroglyphidodon leuco-*

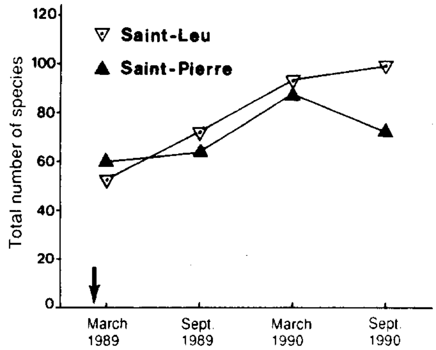

Fig. 4. Changes in total species richness on Saint-Leu and Saint-Pierre reef flats. Arrow= date of hurricane Firinga (29 January 1989).

zonus, Chrysiptera glauca (Pomacentridae) and all the herbivorous Acanthuridae and Scaridae, or on small invertebrates associated with algae, like *Thalassoma lunare, T. hardwicke, Stethojulis albovittata* (Labridae). The most abundant Chaetodontidae, *Chaetodon vagabundus* and *C. auriga,* have a highly diversified diet including algae (Harmelin-Vivien & Bouchon-Navaro 1983). Differences in trophic structure of the ichthyofauna between the three geomorphological zones on Reunion reef flats were related: first to their specific food resources; and second to the range of damage induced by the hurricane. Nowhere was an increase in fish predators observed, probably because few fish were directly killed by the hurricane and because shelters were not drastically reduced. On the back reef, seasonal variation in community parameters predominated over hurricane induced variation. No change in trophic structure could be detected despite an increase in sedimentation rate, because the back reef zone was already composed of sand substrates with scarce coral colonies. Mullids, which mostly feed on soft-bottom infauna (Harmelin-Vivien 1979), re-

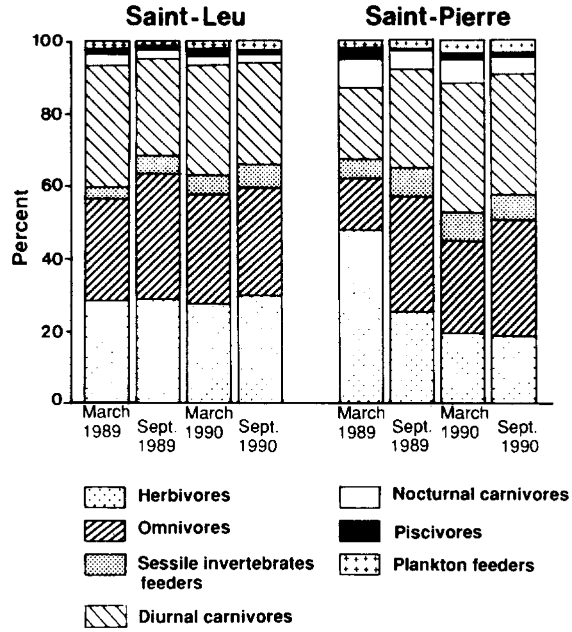

Fig. 5. Trophic structure of the total fish community on Saint-Leu and Saint-Pierre reef flats expressed in percentages of total number of individuals.

mained abundant in the back reef. In contrast, hurricane Firinga induced important modifications of food resources on the inner and outer reef flats with the death of most coral colonies. Dead coral colonies provided new substrata for algal growth and its associated microfauna (Naim 1980). This could account for the increase in herbivores (Scaridae, Acanthuridae) and omnivores (Pomacentridae) which depend on algal turf, and in diurnal carnivores (Labridae) which feed on small invertebrates.

Differences in recovery between Saint-Leu and Saint-Pierre reef flats were probably linked to differences in their previous degradation levels and habitat complexities. The biotic diversity and topographic relief of the reef flat environment were

Table 5. Mean abundance of fishes per census on the two reef flats studied. Underlining indicates means which are not significantly different (t-tests). Standard deviation in parentheses, n = number of samples during each period.

	March 1989	September 1989	March 1990	September 1990
Saint-Leu (n = 6)	201.9 (±53.9)	221.3 (±151.1)	282.5 (±103.7)	346.6 (±178.9)
Saint-Pierre (n = 9)	135.8 (±32.6)	122.9 (±40.9)	189.5 (±66.6)	182.4 (±66.1)

greater in Saint-Leu than in Saint-Pierre before the hurricane, and remained greater afterwards. The large colonies of *Acropora* on Saint-Leu reef flat were killed, but not reduced to rubble, by the hurricane. On the Saint-Pierre reef flat the initial architectural complexity was less than at Saint-Leu; most coral colonies were already dead and largely eroded by a numerous population of the sea-urchin *Echinometra mathaei*. Thus, habitat complexity, which is a recognized factor for explaining reef fish diversity and abundance (Risk 1972, Roberts & Ormond 1987), may account for the greater post-hurricane increases in species richness and abundance of fishes observed on Saint-Leu reef flat.

The main factor explaining the low diversity and abundance of fishes on Reunion Island reef flats just after hurricane Firinga was probably the occurrence of a thick silt layer which overlaid most reef habitats. Its removal several months after the hurricane helps account for the further increase in species richness and abundance of the reef ichthyofauna. The changes in the trophic structure of the fish community were related to the modification of food resources which enhanced the populations of fishes depending on algae or algal-associated microfauna for their food. Differences in the post-hurricane fish communities between the two reefs surveyed were related to levels of habitat complexity and mainly linked to their pre-hurricane level of degradation.

Acknowledgements

This research was supported by the Laboratory of Marine Biology of the University of Reunion (grant from University of Reunion – French Ministry of the Environment No. 87 379), by the ENVIREG program of the Regional Council of Reunion Island and the European Economic Community (DAPE number 91 0243). We are grateful to J.A. Fagerstrom for critically reviewing an earlier draft of the article. We thank P. Chabannet and two anonymous reviewers for constructive comments on the manuscript.

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