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Odile Naim, Pascale Chabanet, T. Done, Catherine Tourrand, Yves Letourneur. Regeneration of a reef flat ten years after the impact of the cyclone Firinga (Reunion, SW Indian ocean). 9th International Coral Reef Symposium, Oct 2000, Bali, Indonesia. pp.547-554. hal-00913738

HAL Id: hal-00913738

<https://hal.science/hal-00913738>

Submitted on 6 Dec 2013

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Regeneration of a reef flat ten years after the impact of the cyclone Firinga (Reunion, SW Indian ocean)

O. Naim¹, P. Chabanet¹, T. Done², C. Tourrand¹ and Y. Letourneur¹

ABSTRACT

Changes in composition of corals, algae and fishes at St-Leu, La Reunion, appear to be successional in character, the presence and abundance of each group facilitating the presence and abundance of others by changing the local community structure and resource base. This was shown in a study following Cyclone Firinga in 1989. Before the cyclone, large colonies of *Acropora muricata*, dominated the coral zone, forming with *Porites lobata*, *Pavona divaricata* and large tables of *Acropora cytherea*, a coral community of 30-40% coverage with relatively low diversity. Immediately after the cyclone, only 2 coral species survived, but the growth rate of living coral later exceeded its previous maximum due to the low tendency for competition for space, reaching more than 6% per year. By 2000, the coral richness on St-Leu (51 species) was comparable to that recorded 20 years earlier. For fish, total species richness and the mean species number / census slightly increased between 1993 and 2000, but there were important differences among sites and times that were mainly due to change in individual numbers inside the territories of the damselfish *Stegastes nigricans*, which in turn were linked to the changing coral and algal cover. Variations in fish density were related to variation of benthic cover, including corallivorous Chaetodontidae, that useful as bioindicators of coral reef health.

Keywords Cyclone, Communities, Recovery, Corals, Fish, Diversity, Chronic disturbance

Introduction

Most natural systems are exposed to major disturbances: fires in plant assemblages, hurricanes and winds throws in forests, waves on beds of intertidal animals, storms over coral reefs. These major disturbances, which are heterogeneous in time and space, generate patchiness in natural systems. But, as they renew limiting resources, they promote local coexistence of species. Then, migration between patches ensures the global persistence of species that might be extinct locally (Andrewartha and Birch 1954).

Tropical cyclones that induce massive mortality of coral reef organisms, as well as some biotic factors, can exert strong control the dynamics of coral reef communities (review Stoddart 1971, Harmelin-Vivien 1994, Endean 1976). In Reunion, cyclones sporadically damage the reefs. In the last sixty years, only one (in 1948) had strongly affected the communities of St-Leu reef flat (Gruchet pers.comm.). Forty one years later, on 29 January 1989, hurricane Firinga, generated more than 99% of mortality of the total coral coverage (Naim et al. 1997). The principal cause of mortality appeared to be the impact of sediment accumulation on coral polyps, as a result of a massive erosion and concomitant run-off of soil.

Recurrent patchy disturbances are also characteristic of most natural systems. These chronic disturbances are considered to be intermediate disturbances that favour fugitive species against competitively superior species (Hutchinson 1951, Huston 1979, Connell 1976). In

consideration of these two types of disturbance, we analysed changes over a decade on two sites: 'St-Leu Oceanic' under oceanic influence (SLO), and 'St-Leu Terrestrial' under chronic terrigenous influence when rain falls (SLT). In particular, we wished to determine the existence and importance of successional processes, wherein earlier changes in the community facilitate later stages. Accordingly, coral and fish recovery was followed from 1993 to 2000. We describe zonation patterns and community succession of the scleractinian corals and algae, and their associated reef fish, based on numerical analysis of species abundance.

Materials and methods

Geographical location, climate

Lying at 21°07' S and 55°32' E, Reunion constitutes the western member of the Mascarene archipelago. This young volcanic island (2.1 MY) has a mountainous topography (highest point: 3,069 m) contained within a coastline of only 210 km, and a total area of 2,512 km². Ten to 12 km of intermittent fringing reefs are found on the west and south coast (see Montaggioni and Faure 1980, Faure 1982, Wells 1988).

The dominant winds blow from the South East all the year round. These winds that are particularly strong during the dry season (austral winter, April to September), can blow uninterruptedly for several days or even weeks. They generate swells that predominantly affect the SE part of the island. During this period, water is cool (mean: 22.5°C). During the rainy season (austral summer, October to March), calm periods are more frequent and longer, and the reef waters warmer (mean 28.0°C).

¹ Laboratoire d'Ecologie Marine, Université de la Réunion, 97715 Saint Denis messag, Cedex 9, Reunion.

² Australian Institute of Marine Science, PMB #3, Townsville MC, Qld. 4810, Australia

However, during this season, severe hurricanes are common. Moreover, a heavy swell of remote origin (the "Roaring Forties") is often observed in Reunion, although this phenomenon is largely independent of local meteorological conditions. The tide regime is typically semi-diurnal and the reef flats of Reunion are microtidal environments (max. range < 1 m).

The study site

The fringing reef of St-Leu lies on the west coast of the island. The adjacent watershed is very steep and, the coastal plain is narrow (< 1 km), and the small town of St-Leu is densely populated. Numerous ravines and drains direct freshwater into the back reef area. The beach composed by mixed coral and basalt fragments is interrupted in many places by the walls of houses built on the natural dunes.

Two reef flat sites (less than 100 m apart in 1-2 m of water) were selected for study: the SLT site – close to the shore - appears to be subject to chronic disturbance, as run-off of fresh water lade with silt routinely reaches the site. Freshwater comes south from the ravine des Poux, and north from a freshwater outlet. The SLO site, 100 m further seaward, is exempt of these impacts, and is situated on a transit zone of oceanic waters just inshore of a shallow outer reef flat (< 1 m).

Calm periods are rare, even in summer. Water masses enter and leave the narrow reef flat as breaking surf, refraction and diffraction resulting in high current velocities which appear to be more governed by wind set-up and swells than tide flow. Sea-grass beds are totally absent.

Storm data and impact on the reef

According to the American classification of hurricanes (Vernon F.Dvorak), Firinga was a "force 5" cyclone. On the 29th of January, south of the island, whirling winds reached 216 km.h⁻¹ and generated 2.8 m high swells. On the same station, 1,030 mm/24 h of torrential rains were recorded (SMRR 1989). Before the impact of Firinga, only qualitative assessment has been made between 1985 to 1989, on coral communities of the studied site. The dominant pattern of the coral communities was large plurimetric colonies of *Acropora muricata*, dominating the coral zone, forming with *Porites lobata*, *Pavona divaricata* and large tables of *Acropora cytherea*, a relatively low diverse coral community, of 30-40% coverage.

The high cyclonic run-off brought sediment and mud on the reef that overwhelmed the coral colonies. This sediment disappeared within six months putting in light the high cleaning capacity of swells in this area. Among corals, only two species survived (Naim et al. 1998), using two different strategies: *Porites lutea* of which large colonies recuperated their zooxanthellae after a bleaching period of 2 or 3 months after the impact, and *Pavona divaricata* which retained centimetric patches of living in areas of coral that were otherwise dead over contiguous areas of square metres. Secondary effects on fish (Letourneur et al. 1993), and evolution of the reef

between 1989 and 1993 have been described (Naim et al. 1997).

Sampling methods

The numerical description is based upon several currently sampling methods. For corals, 50 m long line transects were run, parallel to the substrate. The horizontal spacing between the transects was 20 m. Every sub-sample of 10 m is considered separately. Any coral species that underlay the line was recorded and its projected length on the line was measured to the nearest centimetre.

For fish communities, the sampling was carried out by visual observations. The line coral transect was used as the centre of 50 x 4 m belt transect where all the individuals species observed were recorded. A series of transverses were conducted in order to count the individual species with respect to their behaviour (Galzin 1985, Chabanet et al. 1997).

In the following are presented the results of three measuring campaigns, carried out during the hot seasons of 1993, 1997, and 2000.

Results

The chronic disturbance

To quantify the chronic disturbance affecting the SLT site, we took the average annual quantity of precipitation on the site and the number of rainy episodes per year (Table 1). A rainy episode was defined by a single day having 60 mm of rain or more, or ≥ 45 mm if total monthly rainfall is ≥ 80 mm. By these criteria, freshwater disturbance was maximum during the 93-96 period, intermediate during the 89-92 period, and minimum during the 97-99 period (half of the maximum).

Table 1 : Average annual precipitation (mm per year), percentage/maximum in period 93-96, number of rainy episodes per year

	Average annual precipitation (mm per year)	% /max 93-96	Number of rainy episodes per year
1989-1992	439.3	65.8	1.3
1993-1996	667.1	100.0	2.0
1997-1999	365.0	54.7	1.0
1989-2000	490.5	73.5	1.4

Geomorphology of the reef flat

Reef flat depth ranges from 1.3 m deep on the back reef zone to less than 0.2 m on the surf-swept outer reef. The shoreline is dominated by intertidal beach rocks and sand. Basalt boulders also line parts of the shore, particularly around ravine mouths.

Considering the distribution, of the coral substratum (dead and alive) in 2000, from the shore to the reef front (Fig.1), we can see that, although the two sites are clearly

different in their topographical characteristics, the general picture of the zonation pattern is very similar. From shore to 40-50 m the shoreline, is the back reef zone, 1.3 m deep. Then, at 40-50 m the beach, appears a coral zone made of a continuous bank, parallel to the shore, dominated before the cyclone impact by branching staghorn corals (standing coverage: 30 to 80%). Sediment is there, made of coarse sand mixed with staghorn rubble, with occasional pavement. On the ocean margin of the coral zone (100-110 m from shore), the depth decreases sharply from 0.8 to 0.2 m: this very shallow portion grade from scattered small coral heads into an area covered by decimetric flat fragments of dead corals. This portion separates the coral zone from the reef front. The fore reef platform is very narrow, and rarely accessible due to high swell. It has a rudimentary spur and groove structure and supports massive corals. During low spring tides, upper parts of corals are exposed to desiccation. All the following results will concern the coral zone.

Algae

On the reef flat, fleshy macroalgae and turfs invaded all the reef substrates 2 months after the impact of the cyclone. In 1993, the primary producers, mostly represented by macroalgae (57% of the total algal coverage), still occupied 50 % of the substrates (details on algae in Naim et al. 1997). These algae continued to occupy around half of the substrates all along the year until April 1995. In those days, they lost ground with the set-up of the trade winds and did not come back the next summer. From this period, on both sites, visible algae were only represented by damselfish turfs, rare calcareous algae (generally sciaphilous on this reef) and sporadic small bluegreen algae.

Corals

On SLT, in 1993, the living coral coverage was estimated to 2% on the coral zone (Fig. 2). Then, the coral coverage increased to 12% in 1997 and to 30% in 2000 (Table 3). Average growth rate began very low at 0.4% per year during the period 89-93, increased to 2.3% per year for the next four years and reached 6.1 % per year during the period 97-00.

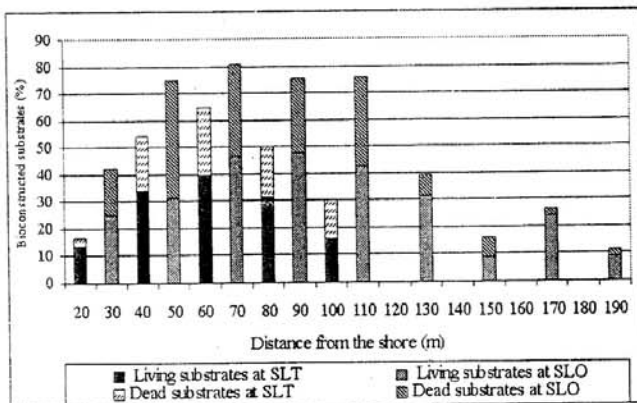


Fig.1 Distribution of the coverage (expressed in percentage) of the built substrates from shoreline to reef front on the SLT and SLO sites, in 2000

Table 2 Algal coverage, expressed in percentage of coverage (standard deviation), measured in 1993, 1997, 2000 hot seasons on the coral zone, on SLO, SLT and Saint-Leu total (SL). M= macroalgae, T= Stegastes territories turfs, CA= calcareous algae

		1993	1997	2000
SLO	M	-	0.0	0.3
	T	-	8.3	15.1
	CA	-	0.0	0.0
	Total	-	8.3 (6.1)	15.5 (11.8)
SLT	M	28.2	0.0	0.5
	T	15.9	3.7	7.6
	CA	5.7	0.0	0.0
	Total	49.8 (26.6)	3.7 (6.1)	8.6 (18.9)
SL	Total	-	6.0 (6.0)	12.0 (16.0)

On SLO, in 1993, no quantitative data is available except those coming from quadrats: the coral coverage was estimated to 12%. In 1997, the coral coverage increased to 21% and to 42% in 2000. Average growth rate on SLO stayed nearly constant, about 2.5 % per year, from 1989 to 1997, then strongly increased to 6.9% during last three years.

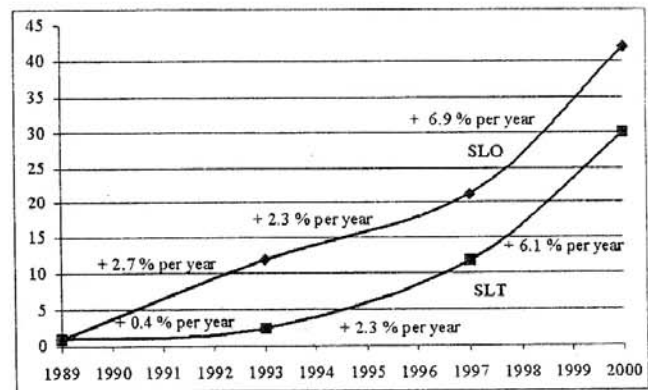


Fig. 2 Temporal variation of the growth rate of the coral coverage on the two sites SLO and SLT

Living coral coverage tended towards zero in 1989 and during 1989-93 the growth rate of coral coverage on SLT was 1/7 of the rate on SLO. Then, from 1993 to 2000, the growth rate became the same on the two sites, although 1/3 lower during the 1993-97 period than during the 97-00 period.

For coral species richness, there was a net increase between 1993 and 1997, although the richness in 1993 may have been under-estimated due to the juvenile status of corals (Table 3). On St-Leu (SLT + SLO), the coral species richness in transects reached 29 species in 1997 and 31 in 2000, when in qualitative assessments we recorded 51 species. Most were recorded at both sites, but the following were censused only on SLO: the Fungiid *Herpolitha limax*, the Faviids *Montastrea annuligera* and *Leptastrea purpurea*, the Mussid *Acanthastrea echinata* and the Dendrophylliid *Turbinaria* sp.

Table 3 Coral coverage = CC, expressed in % (standard deviation), specific richness = Rs, Shannon-Weaver index = H'(1) calculated with LN, H'(2) calculated with log, Equitability (Pielou index) = J', measured in 1993, 1997, 2000 hot seasons on the coral zone, on SLO, SLT and Saint-Leu total (SL)

		1993	1997	2000
SLO	CC	12.0	21.1 (11.8)	42.0 (12.5)
	Rs	-	23	29
	H'(1)	-	1.73	1.47
	H'(2)	-	0.75	0.64
	J'	-	0.55	0.44
SLT	CC	2.4 (3.6)	11.8 (8.7)	30.0 (18.6)
	Rs	10	21	23
	H'(1)	1.68	1.89	1.20
	H'(2)	0.73	0.82	0.52
	J'	0.73	0.62	0.38
SL	CC	7.2	16.5 (11.3)	36.0 (16.8)
	Rs	-	29	31
	H'(1)	-	1.95	1.41
	H'(2)	-	0.85	0.61
	J'	-	0.58	0.41

Considering the diversity and the equitability (estimated by the Shannon-Weaver and Pielou index), one can see that the diversity is relatively stable on SLO, while fluctuating on SLT. The equitability is decreasing with time. The general variation of the Shannon-Weaver index show that the coral community is losing diversity between 97-00, which appears to be the result of the increase of the coverage of the highly competitive branching *Acropora muricata* that tends to overgrow the most massive and low-growing colonies as those of Faviids, Mussids, young Poritids, but also other smaller species of Acroporids (notably *A. humilis*, *A. haimeii*)

Fish

The total species richness and the mean species number / census slightly increased between 1993 and 2000, in all the zones (except for the total species richness in SLO), but this increase is not significant (Student's test, $p > 0.001$). However, mean abundance per census decreased between 1993 and 2000 in SLT (-35%) and steadily increased in SLO (+ 55%), but the difference was significant only in SLO. The differences observed in our data are mainly due to drastic change in individual number inside the territorial damselfish *Stegastes nigricans*. Variations inside this population are responsible of the diversity evolution inside the fish community of St-Leu. Indeed, this diversity remained low on the two sites until 1997, and after this date, started to increase on SLT and decrease on SLO (Table 4). Variations of diversity observed in fish communities are directly linked to the variations of the *S. nigricans* population. When the number *S. nigricans* increased, total fish diversity decreased, and *vice versa*.

For the main fish families censused, our results show that Chaetodontidae are increasing both in SLT and SLO (x 9.8 and x 3.6 respectively) (Table 5). The two sites do not display the same patterns when the other main families

are considered. In SLT, the trend tends toward a decrease of Acanthuridae (x 1.8), Scaridae (x 2.5) and Pomacentridae (x 2.2). Among Pomacentrids, the decrease involved mainly *Stegastes*: 91.0% in 1993 to 42.3% in 2000. Conversely, as *Stegastes* decreased, other Pomacentrids increased, and particularly *Plectroglyphidodon dickii*, *P. johnstoniamus* and *Dascyllus aruanus*. In SLO, fish abundance increased through time. This trend is mainly attributable to Acanthuridae (x 1.6) and Pomacentridae (x 4.1).

Table 4 Variations between 1993 and 2000 on SLT (site under terrigenous influence) and SLO (site under oceanic influence) of fish variables (standard deviation) : total species richness, mean species number / census, mean individuals number / census and diversity (Shannon index). -: not observed.

		1993	1997	2000
Total species richness	SLT	42	40	44
	SLO	-	39	37
Mean species number	SLT	27.3 (3.2)	31.1 (3.6)	33.7 (3.1)
	SLO	-	28.9 (4.1)	30.3 (4.5)
Mean individuals number	SLT	355.7 (70.0)	295.5 (52.0)	263.3 (61.0)
	SLO	-	338.0 (42.0)	756.1 (140.0)
Diversity	SLT	2.84	2.77	4.35
	SLO	-	2.85	2.34

Table 5 Variations of the mean number of individuals (standard deviation) / census between 1993 to 2000 for the six most abundant fish families on SLT (site under terrigenous influence) and SLO (site under oceanic influence)

		1993	1997	2000
Mullidae	SLT	14 (3.6)	12.5 (0.7)	19 (4.0)
	SLO	-	78.3 (41.9)	21.7 (10.8)
Chaetodontidae	SLT	5.7 (3.1)	6 (1.4)	57.3 (3.5)
	SLO	-	5.7 (3.5)	22.3 (5.5)
Pomacentridae	SLT	222.0 (31.1)	199.0 (32.5)	92.3 (78.6)
	SLO	-	175.3 (97.7)	729.0 (106.4)
Labridae	SLT	36.7 (9.1)	22.5 (4.9)	50.7 (14.2)
	SLO	-	15.7 (6.0)	11.7 (1.2)
Scaridae	SLT	16.3 (12.4)	2.5 (2.1)	6.7 (3.8)
	SLO	-	5.3 (5.5)	2.0 (1.0)
Acanthuridae	SLT	56.3 (6.7)	50.5 (12.0)	28.3 (8.5)
	SLO	-	47.3 (35.0)	74.7 (35.3)

The drastic increase of Pomacentrids in 2000 is mainly due to variations on *Stegastes nigricans* density. Their increase seems to be more related to the fact that this species is more often observed in 2000 (558.3 ± 120.0 / census in 2000 versus 154.7 ± 199.6 / census in 1997) than to a real increase of individuals per square meter. In the Pomacentrids, a major increase concerns also

Dascyllus aruanus (5 ± 5 / census in 1997 to 110 ± 24.8 / census in 2000). An opposite pattern is observed for Mullidae in SLO as they decrease through time. This result is mainly due to a school of young *Mulloides flavolineatus* recorded in 1997 and not in 2000.

Discussion

The natural recovery

Until April 1995, the reef flat appeared to be highly controlled by primary producers. The algae could have been favoured by some abiotic factors as nutrient regeneration coming from the organic matter trapped into the dead coral framework (the exogenous nutrient input being very low, see Naim et al. 1997). At this stage, macroalgae did not appear to be controlled by biological factors, except for some (most?) turfs that were highly protected by an abundant population of *Stegastes nigricans*. As the reef is regularly cleaned by swells, it happened that in April 95, the nutrient regeneration would have been insufficient to allow perennially high biomass of primary producers. By then, biological factors could again control algal biomass, particularly herbivory by sea-urchins and fish (Naim et al. 1997).

Algae may have opposed corals by a high competition for space, particularly in the early stages by inhibiting larval settlement. However, by protecting algal turf areas from grazing by sea-urchins, *S. nigricans* may have increased survival in the first stages of the juvenile coral colonies that have been able to settle between the thallus.

Corals: recovery

According one definition of recovery as an increase to at least half of the amount of cover lost in the decline, we can consider that the coral communities of the St-Leu reef flat had recovered, on SLO in 94-95, and, on SLT, in 97-98. However the pattern of coral communities in 2000 was still totally different from the one displayed by the communities before the impact of the cyclone.

Hurricane Firinga allowed the growth rate of living coral to exceed its previous maximum due to the low tendency for competition for space among coral species. During the last 3 years of the study, the average annual growth rate of coral coverage reached more than 6% per year.

By 2000, the coral richness on St-Leu 2000 (51 species) was comparable to that recorded 20 years earlier at la Saline, (50 species, Bouchon 1981).

Before the cyclone, on the coral zone, the coral diversity was apparently lower than nowadays. We consider that St-Leu coral communities have not stabilised and succession will continue to occur. Based on current relative abundance, sizes and growth rates of species, we predict a change towards a reef flat highly dominated by *Acropora muricata* patches, this kind of pattern characterising mature stage of reef flat communities in Reunion.

Corals: differences between the two sites

The principal difference between the two sites appears

in coral coverage that is systematically lower on SLT. This appears to be due to a delay in re-settlement of corals during the period 89-93. Some hypothesis to explain this fact are: (1) there may have been excessive fine sediment trapped in the dead coral framework at SLT (non observed). (2) there may have been more coral larvae inflow at SLO that is under oceanic influence, than on SLT. This hypothesis appears to be corroborated by the existence of supplementary coral species only at SLO. (SLT species are a sub-set of SLO). Among them, some are species whose ranges include middle to deeper sections of the outer reef slope. As Firinga hardly affected the upper part of the outer slope (Engelmann comm.pers.), planulae of the deeper surviving species, like *Herpolitha limax*, *Acanthastrea echinata* that are species from the outer slope in Reunion (Faure 1982) could have colonised preferentially SLO. (3) Lastly, differences in the starting of the coral recovery of these two neighbour sites can be considered to be a result of differences in the intensity, and periodicity of the chronic disturbance to which each is subjected.

Considering coral diversity, the Shannon index was higher in 1997 on SLT than on SLO. From 1997 to 2000, the index decreased slightly on SLO and dropped on SLT. On both sites, the equitability is decreasing with time as *Acropora muricata* increases to high levels on both sites up to 2000 - (SLT: 75%, SLO: 63% of the living coral coverage). Indeed, the process of replacement in succession leads to the local monopolisation of space by the competitively dominant branching coral *Acropora muricata*. This species appears to overgrow other coral species because of a high rate of linear extension vertically and horizontally. Time since disturbance seems to be a good predictor of diversity. On SLT, whereas disturbance by freshwater was maximum during 93-97, the coral diversity censused in 97 was very high, but after three more years, the diversity on SLT dropped as *A. muricata*'s increase reduced the equitability of species abundances.

Fish communities

Hurricanes may affect fish assemblages in their specific composition and density, in their distribution along depth gradients, in their trophic structure and also possibly in growth, reproduction or other behavioral patterns (Harmelin-Vivien 1994). Generally, the decrease of fish density following a cyclone has been explained by a temporary re-distribution of fish into deeper and/or non-damaged habitats rather than by direct mortality (Harmelin-Vivien 1994 review).

In St-Leu, changes in the fishes appear to be more directly related to food supply. Eighteen months after the impact of Firinga, Letourneur et al. (1993) observed an increase in both species richness and abundance of fishes. The density of the herbivorous territorial damselfish *Stegastes nigricans* increased rapidly six months after the cyclone and then remained stable for the following year, whereas the density of other species (e.g. *Thalassoma* spp.) increased gradually during the same 18 month-period. An increase in the abundance of herbivorous and rubble-associated fishes changed the trophic structure of

the fish assemblages. Death of coral colonies caused by the cyclone provided new substrata for the proliferation of turfs and macroalgae that was followed by an increase in herbivorous fish (mainly Acanthuridae, Scaridae and *Stegastes nigricans*) and small carnivorous fish (mainly Labridae, which feed on small invertebrates associated with algae). So, changes in the site's trophic structure were related to modification of food resources rather than drastic physical damage to coral framework structure and complexity (Letourneur et al. 1993).

Four to ten years after the impact of Firinga, species richness stabilized while the number of individuals remained very variable. Variations in fish density were related to variation of benthic cover. In particular, increases of corallivores Chaetodontidae were correlated to the increased percentage of living corals in both sites. We found the obligative coral feeders *Chaetodon trifasciatus* and *C. trifascialis*, to be useful as bioindicators for coral reef health, as advocated by many authors (Reese 1981, Harmelin-Vivien and Bouchon-Navaro 1983, Chabanet 1997, Sano et al. 1984, 1987, Bell and Galzin 1984, Williams 1986, White 1988, Bouchon-Navaro and Bouchon 1989, Roberts et al 1992, Chabanet et al. 1997). We note, however, that in some cases (Bell et al. 1985, Roberts and Ormond 1987, Roberts et al. 1988, Fowler 1990), this correlation can be poor, suggesting that same populations may be limited more by recruitment than by food availability.

By contrast to the Chaetodontidae, where a gradual increase in density was observed in both sites, there were interesting differences between the sites in the Pomacentridae and Acanthuridae. Between 1993 and 2000 at SLT, there was a decrease for both families. At SLO, there was an increase for both families between 1997 and 2000 (unfortunately, no data are available for SLO in 1993). These changes in herbivorous families mirrored changes in algal cover: a decrease through at SLT (50% to 6%) and an increase at SLO (8% to 15%). In particular, the main species within these two families, (*Stegastes nigricans* in the Pomacentridae: *Acanthurus triostegus* and *Ctenochaetus striatus* in the Acanthuridae) use algal turf for food. For *Stegastes nigricans*, the important increase of their population in SLO in 2000 appears to have been caused by a redistribution of territories from SLT to SLO, where very low tides in 2000 had killed patches of *Acropora muricata* branch tips, causing them to be colonised by algal turfs. If corals are killed by any factor, *Stegastes* may be able to immigrate from nearby areas and through its creation of new territories, increase the amount of coral destruction.

Stegastes dominance in the SLO fish community contributed to a decrease in species diversity, both numerically (by decreasing equitability) and behaviourally, by chasing away species, particularly other herbivorous fishes.

Conclusion

The two sites showed changes in composition of corals, algae and fishes that were successional in character, the presence and abundance of each group

facilitating the presence and abundance of others by changing the local community structure and resource base. In the first stages, diversity increased during time on both sites as species colonised bare substrates. Subsequently, cyclone disturbance assumed a major role in increasing qualitative species diversity. There followed a decrease in diversity of both corals and fishes, due, respectively to the rapid growth to numerical dominance of one coral (*A. muricata*) and the numerical and behavioural dominance of one fish (*Stegastes nigricans*). Interestingly, this put the fish community close to that observed before the impact of Firinga. The rapid increase in *A. muricata* in the period 1997-2000 suggests that the community is approaching its pre-Firinga state of heavy dominance by that species.

Acknowledgements This work was supported by the national program 'Recréer la nature' granted by the French Ministry of Environment. We are deeply grateful to Didier M'Radamy and Sirit Coeppicus for help on the field.

Note: the name of the species *Acropora muricata*, has been attributed according to the recent revision of the genus *Acropora* by C. Wallace (1999). The species was previously described in Faure (1982) and Bouchon (1981) as *Acropora pharaonis*.

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