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Initial and mid-term impacts of cyclone Erica on coral reef fish communities and habitat in the South Lagoon Marine Park of New Caledonia

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The cyclone Erica (Class 5) hit the South Lagoon Marine Park of New Caledonia on 14 March 2003, in the midst of a survey conducted on coral reef fish and habitat of Larégnère and Crouy reefs. Such perturbation was exceptional for the area. Nine stations had already been sampled (8–11 March 2003) when the cyclone hit the reefs. These stations were sampled again just after the cyclone (23 March–15 April 2003) and 20 months later (14–16 November 2004). Erica had a significant initial impact on habitat characteristics. The fragile coral forms cover (branching, tubular and foliose) decreased significantly, resulting in a loss of habitat for the fish communities. Species richness and biomass of the commercial reef fish and the Chaetodontidae decreased just after Erica, but not the density. The species assemblage was modified on the stations with the lowest remaining live coral cover. The loss of shelter modified the behaviour of potential prey, which constituted unusual shoals and attracted predators. Twenty months after Erica, the habitat had not recovered and the broken coral colonies were transformed into rubble or colonized by algae. The nature of the mid-term impact on the fish communities was different and more significant than the initial impact. Species richness per station, density and biomass were significantly lower than before and just after Erica. This pattern was confirmed for all the main families, with the exception of Acanthuridae. A different fish assemblage was observed on all stations 20 months after Erica. Herbivorous species and benthic macro-invertebrate feeders associated with rubble replaced the coral associated species that characterized the assemblages before the cyclone. When a Class 5 cyclone affects an area where perturbations of such intensity are uncommon, its impact is immediate and the mid-term consequences are even more significant. A complete modification of the structure of the habitat and the fish assemblages is observed. The consecutive recovery should be a long process.

INTRODUCTION

Coral reefs are remarkable ecosystems because organisms produce their basic physical structure. These building organisms, particularly the stony corals (Scleractinia), create a three dimensional framework that is home for a great biodiversity. Because of their nature and their localization in the tropical region, coral reef habitats are affected by severe physical disturbances caused by cyclones (see the review of Harmelin-Vivien, 1994). Wind, waves and rainfall associated with these meteorological disturbances are important factors structuring coral reef habitats (Harmelin-Vivien, 1994). Coral reef communities are related to habitat structure and consequently affected by these catastrophic disturbances, which are now recognized as controlling parameters in reef community dynamics (Harmelin-Vivien, 1994). The communities are affected by changes in sedimentation processes and increased turbidity due to silted run-offs (Letourneur et al., 1993; Van Woesik et al., 1995; Nowlis et al., 1997), by a decreased salinity due to floods (Van Woesik et al., 1995), and by mechanical damages due to the removal of the reef matrix, scouring and fragmentation (Van Woesik et al., 1995).

Most studies on the effects of hurricanes concerned the habitat and the corals (Adams, 2001). Shallow water

branching coral species (mainly *Acropora*) and soft corals are the most affected communities by storm waves, being smashed to rubble (Hughes, 1994; Van Veghel & Hoetjes, 1995; Jordan-Dahlgren & Rodriguez-Martinez, 1998). Other studies have been conducted on fish communities (Letourneur et al., 1993; Adams, 2001; among others). However, before–after comparisons combining ‘just before’, ‘immediately after’ and ‘after’ data sets are very rare and missing when ecological effects of cyclones can be very patchy.

Cyclone Erica hit New Caledonia on 13–14 March 2003 (Figure 1). Erica (Class 5; Saffir–Simpson scale) had a minimum central pressure of 910 hPa measured in Koné (Mackley, unpublished data). Erica produced winds over 200 km h⁻¹ (maximum recorded 250 km h⁻¹; Mackley, unpublished data), with wind gusts reaching 300 km h⁻¹ in the south of New Caledonia (Ouiné) due to the high and contrasting relief of New Caledonia. The cyclone reached Nouméa on 14 March 2003 at midday. Rainfall over 30 mm was recorded in 12 h (Météo France, unpublished data) and associated run-off was significant. Erica passed directly over the South Lagoon Marine Park on 14 March 2003 with maximum south-south-westerly–south-south-easterly winds. Sediment-laden water in the lagoon was significant for a distance of at least 10 km off the coast

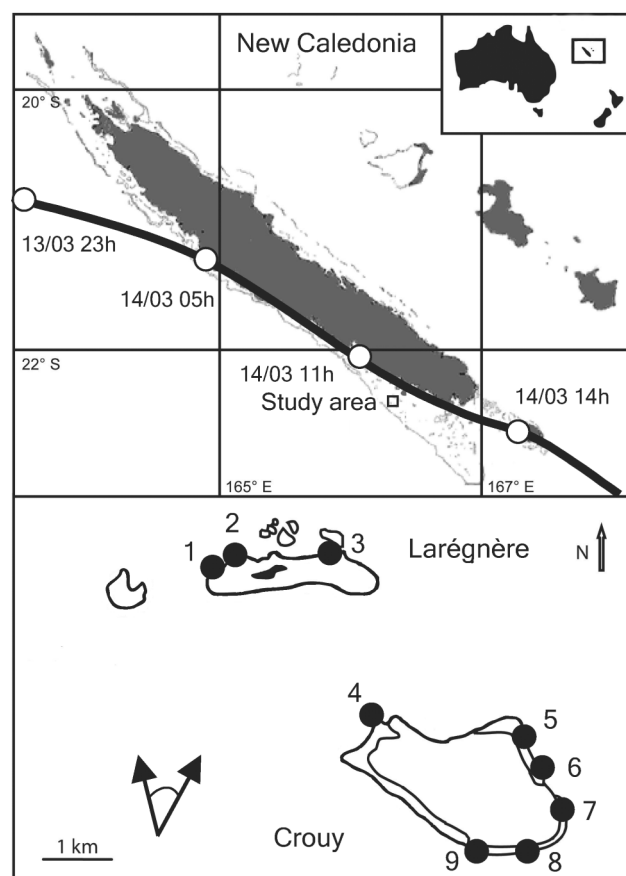


Figure 1. Location of the study area and track of the cyclone Erica. ●, Station sampled before (March 2003), just after (March–April 2003) and 20 months after (November 2004) Erica. The two arrows indicate the direction of the strongest winds.

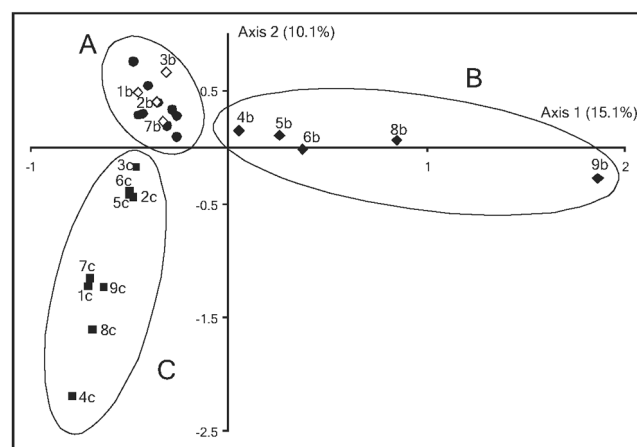


Figure 2. Projection of the samples (stations) on the first two axes determined by the correspondence analysis. ●, before Erica stations; ◇, just after Erica stations of Group A; ◆, just after Erica stations of Group B; ■, November 2004 stations. The percentage of inertia explained by each axis is given. The numbers refer to the stations (Figure 1) and the letters to b, just after Erica; and c, 20 months after Erica.

during the following days. Erica was an exceptional phenomenon for the Nouméa region, which had not been hit by such a cyclone in 34 years (cyclone Colleen in 1969).

Under these circumstances we had a unique opportunity because the cyclone passed in the midst of a survey conducted on coral reefs of the South Lagoon Marine Park. This unexpected phenomenon constrained us from starting our sampling again after the cyclone (Chateau & Wantiez, 2005). However, the data collected before the cyclone allowed us to estimate its initial and mid-term (20 months) impacts on the reef fish communities. Such temporal series can give valuable information on the initial destructive phase and the consecutive mid-term impact following exceptional meteorological perturbations in a well-preserved environment.

MATERIALS AND METHODS

Study sites and sampling methods

The study sites are two coralline islands located in the south-west lagoon of New Caledonia (Figure 1). Larégnère has been a permanent marine protected area (MPA) since 1989 and Crouy is unprotected and located 2 km from the MPA. As part of a research programme on the MPAs of the South Lagoon Marine Park, it was planned to study the habitat and the fish communities of these coralline islands using a systematic sampling protocol (see Chateau & Wantiez, 2005 for details). Six stations had already been sampled in Crouy and three stations in Larégnère (8–11 March 2003), when cyclone Erica affected the South Lagoon Marine Park (14 March 2003). These stations were sampled again just after the cyclone, between 23 March and 15 April 2003, to analyse the initial impact of the cyclone. The same stations were sampled 20 months later, between 14 and 16 November 2004 to quantify the mid-term impact on the communities.

At each station three components of the reef were sampled to get the most accurate image of the communities: the reef flat (1 m depth), the reef crest (1–3 m depth) and the reef slope (2–5.5 m depth). In each habitat, a SCUBA diver randomly chose a point. Commercial fish species and Chaetodontidae were sampled by visual censuses using point counts (see Wantiez & Chauvet, 2003 for details). The diver counted all fish by species, and estimated their size. Chaetodontidae (small species) were sampled in a 3 m radius around the point (28.3 m²), and large commercial species (regardless of individual size) were sampled within the visibility radius (maximum 314 m²). The visibility radius is the maximum distance at which the diver can identify large species without confusion. When visibility was over 10 m, fish beyond 10 m were not sampled. This method minimizes the biases induced by the low detectability of small species, and minimizes the biases induced by the avoidance of the diver by large species easily detectable in a 10-m radius.

The substrate was sampled by the line intercept transect method modified by the Australian Institute of Marine Science (English et al., 1997). At each station and in each habitat (reef flat, reef crest and reef slope), substrate categories were recorded along a 25 m transect laid perpendicularly to the slope and centred on the point count. Thirty substrate categories were recorded.

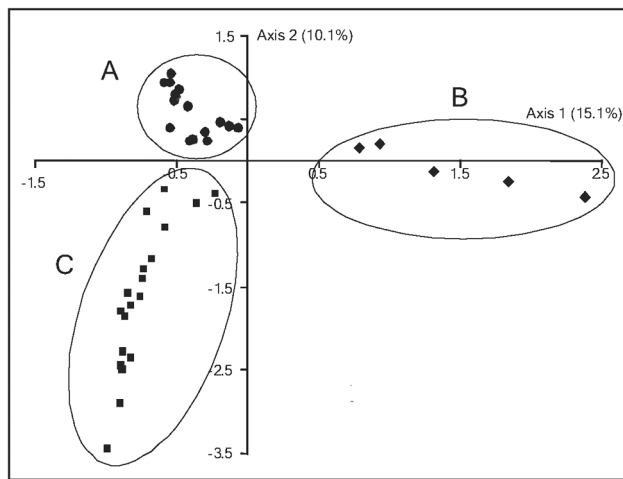


Figure 3. Projection of the species on the first two axes determined by the correspondence analysis. Only species with absolute or relative contributions higher than 10% on one of the first two axes are displayed. ●, Characteristic species of fish communities before Erica, and of Stations 1, 2, 3 and 7 (Group A) just after Erica; ◆, characteristic species of fish communities of Stations 4, 5, 6, 8 and 9 (Group B) just after Erica; ■, characteristic species of fish communities in November 2004 (all stations). The names of the species are given in Table 2. The percentage of inertia explained by each axis is given.

Data analysis

At each station, habitat and fish communities were analysed from the three reef habitats sampled, to get the most accurate image of the station regardless of the tide level at the time of sampling. Within reef habitats, analyses would be strongly influenced by the tide level and would require a sampling of each habitat at the same tide level for all the stations. Consequently, at each station, species richness per station was the total number of species on the three reef components. Density was calculated by:

$$D = \frac{\sum_{k=1}^3 D_k}{3} \quad (1)$$

where D is the density at the station (fish m^{-2}); and D_k is the density of point count k at the station (fish m^{-2}). Density of point count k was calculated as follows:

$$D_k = \frac{\sum_{i=1}^{N_i} n_i}{\pi R_1^2} + \frac{\sum_{j=1}^{N_s} n_j}{\pi R_2^2} \quad (2)$$

where n_i is the abundance of commercial species i at point count k ; N_i is the total number of commercial species censused in a R_1 radius at point count k ; R_1 is the visibility radius ($R_1 \leq 10$ m); n_j is the abundance of Chaetodontidae species j at point count k ; N_s is the number of Chaetodontidae species censused in a R_2 radius at point count k ; and $R_2 = 3$ m.

The weight of fish was calculated from length–weight relationships previously defined (Kulbicki et al., 1993; Letourneur et al., 1998; www.Fishbase.org). Biomass per station was calculated in a similar way to density:

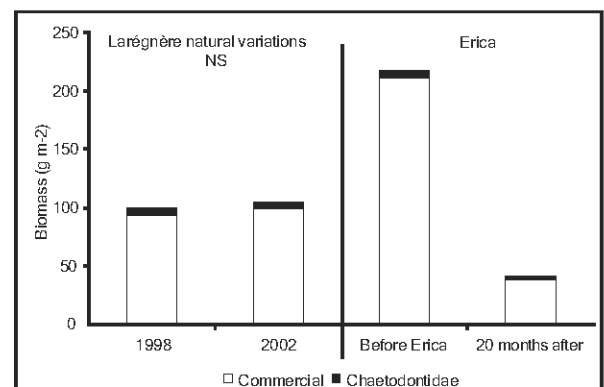
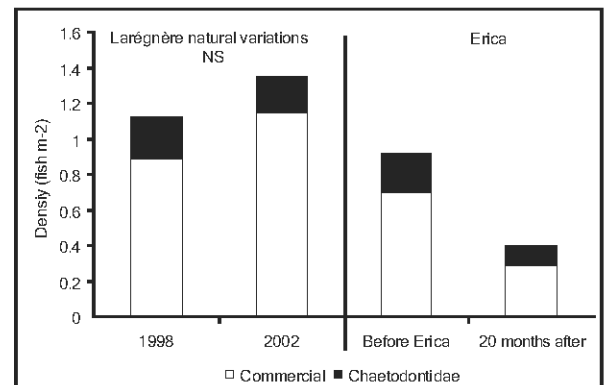
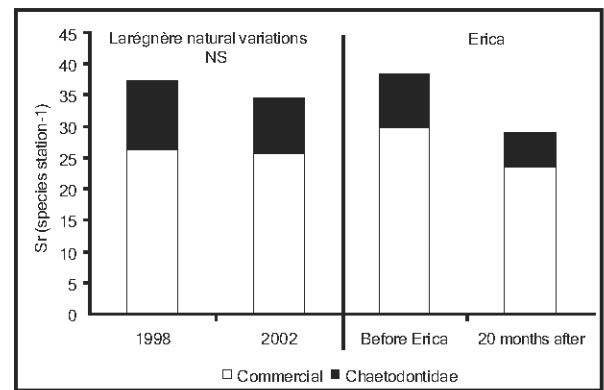


Figure 4. Temporal variations of species richness per station (Sr), density and biomass of fish communities of Larégnère in 1998 and 2002. Data from Wantiez (2004). NS, Wilcoxon sign rank test not significant ($P > 0.05$).

$$B = \frac{\sum_{k=1}^3 B_k}{3} \quad \text{and} \quad B_k = \frac{\sum_{i=1}^{N_i} w_i}{\pi R_1^2} + \frac{\sum_{j=1}^{N_s} w_j}{\pi R_2^2} \quad (3)$$

where B is the biomass at the station (g m^{-2}); B_k is the biomass of point count k at the station (g m^{-2}); w_i is the weight of species i at point count k (g); and w_j is the weight of Chaetodontidae species j at point count k (g m^{-2}).

The percentage of each substrate category at each station was calculated by:

$$\%_i = \frac{1}{3} \sum_{k=1}^3 \frac{L_{ik}}{L_t} 100 \quad (4)$$

where %_i is the percentage of substrate category *i*; L_{ik} is the total length of category *i* at point count *k*; and L_t is the total length of transect (25 m).

Variations of total species richness were tested using a χ^2 -test. When variances were not significantly heterogeneous (Bartlett's test for homogeneity of variance, $P > 0.05$), variations of species richness per station, density, biomass and substrate characteristics were tested using a two-way analysis of variance (ANOVA) without replication (time \times station). When the ANOVA was significant ($P \leq 0.05$), a Tukey–Kramer test was performed to identify the source of the differences between ‘before’, ‘just after’ and ‘20-months after’ data series. When variances were significantly heterogeneous (Bartlett's test for homogeneity of variance, $P \leq 0.05$) variations of species richness per station, density, biomass and substrate characteristics were tested using a Friedman two-way analysis of variance without replication. When the Friedman analysis was significant ($P \leq 0.05$), a Steel–Dwass test was performed to identify the source of the differences. It was chosen to block the spatial factor (stations) using two-way analyses without replication instead of including a site factor and considering site stations as spatial replications. The reason was that the exposure of the stations to the cyclone's strongest winds was not similar between sites (Figure 1). This latter approach would lead to a false site effect.

Changes in fish assemblages were studied using multivariate analyses performed on densities because the individual was considered as the basic functional component in the determination of species structure. As the data matrix was characterized by numerous zeros because of the dominance of a small number of species, a correspondence analysis using a χ^2 similarity coefficient was selected. All species were used in the analysis, since rare species can be indicators of brief environmental perturbations. No transformation was applied to the data because a higher inertia was extracted by the analysis when raw data were used. The projection of the species, with absolute or relative contributions to one of the first two axes of the correspondence analysis greater than 10%, was used to identify the most important characteristic species of the assemblages. Differences between the identified assemblages (species richness per station, density, biomass and habitat) were tested using a Kruskal–Wallis test and multiple comparisons between treatments (Steel–Dwass test).

RESULTS

Initial impact

Cyclone Erica had a significant initial impact on habitat characteristics and destroyed live corals. Broken corals constituted a mean of 6.8% of the substrate of the stations (maximum 33.6%) (Table 1). Branching, tubular and foliose corals were the most significantly affected (65.2% of the coral colonies) and decreased significantly (ANOVA, $P \leq 0.01$), together with dead corals with filamentous algae (Friedman analysis of variance, $P \leq 0.05$) (Table 1). The other substrate categories were not significantly affected (ANOVA and Friedman analysis of variance, $P > 0.05$) just after Erica (Table 1).

Total species richness decreased from 109 species to 84 species (χ^2 -test, $P = 0.06$) and total biomass decreased by

Table 1. Variations of total species richness (*Sr tot*), species richness per station (*Sr*), density (*D*, 10^{-2} fish m^{-2}) and biomass (*B*, g m^{-2}) for the fish community, and benthic habitat characteristics (% cover) on the stations sampled before (March 2003), just after (March–April 2003) and 20 months after (November 2004) Erica.

	1— Before	2— Just after	3— 20 months after	Difference
All species				
Sr tot	109	84	80	χ^2 , $P = 0.06$
Sr	38.44	32.89	29.00	A, * [1 [2] 3]
D	83.56	91.54	39.84	A, ** [1,2] 3
B	217.19	96.19	40.82	F, * [1,2] 3
Serranidae				
Sr tot	8	6	3	χ^2 -test not possible
Sr	2.44	1.89	0.89	F, ** [1 [2] 3]
D	2.89	1.40	0.26	F, ** [1,2] 3
B	3.32	2.36	0.77	F, * [1 [2] 3]
Chaetodontidae				
Sr tot	19	18	14	χ^2 , n.s.
Sr	8.59	6.78	5.44	F, * [1 [2] 3]
D	30.52	21.61	11.00	A, *** [1,2] 3
B	5.59	3.05	3.03	A, ** [1,2] 3
Scaridae				
Sr tot	18	17	14	χ^2 , n.s.
Sr	8.78	7.33	5.78	A, * [1 [2] 3]
D	11.22	42.33	8.85	F, * [1,2] 3
B	16.39	14.52	5.66	F, ** [1,2] 3
Acanthuridae				
Sr tot	14	9	16	χ^2 , n.s.
Sr	4.67	4.33	6.00	A, *** [2 [1] 3]
D	12.49	19.78	6.81	F, ** [1,2] 3
B	17.87	17.79	8.07	F, NS
Live coral				
Br, T and F	23.5	15.3	9.8	A, **
S	5.1	7.8	8.1	F, n.s.
M and E	5.8	6.1	6.6	A, n.s.
Macroalgae	13.6	17.1	20.1	A, n.s.
Other organisms	1.9	2.3	3.7	F, n.s.
RKC	0	6.8	0	Test not possible
DCA	12.7	5.7	4.1	F, *
Sand	6.5	4.2	7.9	A, n.s.
Rubble	18.1	19.6	26.0	A, n.s.
Rock	12.8	15.1	13.7	F, n.s.

Br, branching; T, tubular; F, foliose; S, submassive; M, massive; E, encrusting; RKC, recently killed or broken coral; DCA, dead coral with filamentous algae; χ^2 , chi square test; A, two-way analysis of variance without replication and Tukey–Kramer post-hoc test when differences are significant; F, Friedman two-way analysis of variance by rank and Steel–Dwass post-hoc test when differences are significant. *P*, probability level; n.s., not significant ($P > 0.05$); *, significant ($0.05 \geq P > 0.01$); **, highly significant ($0.01 \geq P > 0.001$); ***, extremely significant ($P \leq 0.001$). The groups between square brackets are not significantly different.

44% just after Erica (Table 1). Conversely, total density did not change significantly (Table 1). Similar variations affected the Serranidae and the Chaetodontidae families (Table 1). The pattern of variations was different for the Scaridae, with a higher density just after Erica (+377%)

Table 2. Species characteristic of the three fish assemblages (A, B and C) identified by the correspondence analysis (Figure 3).

Group A	Group B	Group C
<i>Cephalopholis boenack</i>	<i>Carcharhinus melanopterus</i>	<i>Epinephelus fasciatus</i>
<i>Plectropomus leopardus</i>	<i>Epinephelus cyanopodus</i>	<i>Caesio caerulea</i>
<i>Lutjanus fulviflamma</i>	<i>Scarus</i> spp. juvenile	<i>Gnathodentex aureolineatus</i>
<i>Lethrinus atkinsoni</i>	<i>Scarus globiceps</i>	<i>Scolopsis bilineatus</i>
<i>Lethrinus nebulosus</i>	<i>Scarus psittacus</i>	<i>Parupeneus ciliatus</i>
<i>Parupeneus barberinus</i>		<i>Parupeneus indicus</i>
<i>Chaetodon rafflesii</i>		<i>Parupeneus multifasciatus</i>
<i>Chaetodon speculum</i>		<i>Kyphosus vaigensis</i>
<i>Chaetodon trifasciatus</i>		<i>Chaetodon citrinellus</i>
<i>Chaetodon lunulatus</i>		<i>Chaetodon flavirostris</i>
<i>Chaetodon unimaculatus</i>		<i>Heniochus chrysostomus</i>
<i>Heniochus singularis</i>		<i>Cheilinus trilobatus</i>
<i>Cheilinus undulatus</i>		<i>Choerodon graphicus</i>
<i>Naso unicornis</i>		<i>Acanthurus</i> spp.
<i>Siganus argenteus</i>		<i>Acanthurus nigricans</i>
<i>Siganus doliatus</i>		<i>Acanthurus xanthopterus</i>
		<i>Zebrasoma scopas</i>
		<i>Zebrasoma veliferum</i>
		<i>Siganus spinus</i>

because of the grouping of juveniles in unusual large shoals over the broken branching *Acropora* fields. Erica had no significant initial impact on Acanthuridae populations (Table 1).

Fish assemblages before Erica (Group A) were similar on all stations (Figure 2). Just after Erica, these assemblages were still present on the three stations of Larégnère and one station of Crouy (Figure 2). The three stations of Larégnère were protected from the cyclone's strongest winds and the habitat was less affected (broken corals constituted 3.8% of the substrate). Conversely, the Crouy

station was exposed to the cyclone winds (Figure 1) and severely impacted (broken corals constituted 33.6% of the substrate after the destruction of more than 60% of the colonies) but the live coral cover remained high after the cyclone (31.7%). Group A was characterized by 16 species, particularly coral associated species (Chaetodontidae) (Figure 3; Table 2). The species richness per station and biomass were significantly higher on these stations (Table 3), which were characterized by a significantly higher live coral cover (Table 3). Cyclone Erica had a significant initial impact on the fish assemblages of the other stations (Group B). These stations were exposed to the cyclone's strongest winds, with the exception of Station 4 (Figures 1 & 3). Two predators (*Carcharhinus melanopterus*, *Epinephelus cyanopodus*) and three Scaridae (*Scarus* spp.), particularly important shoals of juveniles, characterized these assemblages (Figure 3; Table 2). The species richness per station was low, the density was high and the biomass intermediate (Table 3). However, these indices were not significantly different from those of Group A (Table 3). The stations where these communities were observed had the lowest live coral cover after the cyclone (Table 3).

Mid-term impact

Habitat did not recover 20 months after Erica, particularly live coral cover (Table 1). The broken branching corals were either transformed into rubble or colonized by macroalgae and coralline algae (Table 1). However, the increases of these categories were not statistically significant (ANOVA, $P > 0.05$).

Twenty months after Erica the fish communities did not recover from its impact. The consequences of the cyclone on the global indices appeared more significant in November 2004 than just after its passing. The total species richness remained low and similar to post-hurricane values (80 species) but species richness per

Table 3. Mean species richness per station (S_r), density (D , 10^{-2} fish m^{-2}) and biomass (B , g m^{-2}) and habitat characteristics (% cover), for the three fish assemblages (Groups A, B and C) identified by the correspondence analysis (Figure 2).

	Group A	Group B	Group C	Difference
S_r	37.54	30.80	29.00	A, * [A[B]C]
D	83.30	98.60	39.84	A, ** [A, B]C
B	176.69	104.70	40.82	K, ** [A[B]C]
Live coral				
Br, T and F	25.9	2.4	9.8	K, ** A[B, C]
S	6.9	5.1	8.1	K, n.s.
M and E	6.3	4.9	6.6	A, n.s.
Macroalgae	10.3	28.5	20.1	A, n.s.
Other organisms	2.1	2.4	3.9	K, n.s.
RKC	3.5	3.1	0	Test not possible
DCA	10.3	6.5	4.1	K, n.s.
Sand	5.3	5.2	7.9	A, n.s.
Rubble	17.3	22.9	26.0	K, n.s.
Rock	12.1	18.9	13.7	K, n.s.

Br, branching; T, tubular; F, foliose; S, submassive; M, massive; E, encrusting; RKC, recently killed or broken coral; DCA, dead coral with filamentous algae; A, one-way analysis of variance and Tukey–Kramer post-hoc test when differences are significant; K, Kruskal–Wallis analysis of variance by rank and Steel–Dwass post-hoc test when differences are significant. n.s., not significant ($P > 0.05$); *, significant ($0.05 \geq P > 0.01$); **, highly significant ($0.01 \geq P > 0.001$). The groups between square brackets are not significantly different.

station was significantly lower than before Erica (Table 1). Density and biomass were significantly lower than both before and just after Erica (Table 1). This pattern was also observed for four families (Serranidae, Chaetodontidae, Scaridae and Acanthuridae), with the exception of Acanthuridae species richness per station, nearly all differences being significant (Table 1).

The absence of recovery was confirmed for the fish assemblages but the nature of the modifications were different than the initial impact. In November 2004, different fish assemblages (Group C) were censused on all stations (Figure 2). Thirteen species, particularly herbivorous species (*Kyphosus vaigensis*, *Acanthurus* spp., *Zebrasoma* spp. and *Siganus spinus*) and benthic macro-invertebrate feeders associated to rubble (*Gnathodentex aurolineatus*, *Parupeneus* spp.) characterized these assemblages (Figure 3; Table 2). This assemblage had significantly lower species richness per station, density and biomass and low branching coral cover characterized the habitat (Table 3).

DISCUSSION

Comparisons of 'snapshots' of pre- and post-hurricane fish assemblages are often inconclusive regarding a storm's impact because the irregular frequency of storms makes it difficult to collect appropriate data to place the hurricane within the context of 'natural' variations in fish assemblage structure (Adams, 2001). This is particularly true for areas where hurricanes are frequent. In the present study, the unique opportunity to compare fish assemblages and habitat characteristics just before and just after Erica gives a good estimation of the immediate impact of the cyclone for an area where cyclones of such strength (Class 5) are exceptional and coral reef ecosystems well preserved. The sampling in November 2004 should also be representative of mid-term impact, 20 months after Erica. 'Natural' variations can be substantial, particularly in the case of significant modifications of the global oceanographic conditions (shift between El Niño and La Niña conditions) (Wantiez, 2004). However, they should be limited during the period of the study when global oceanographic conditions were similar, by comparison with the differences recorded before and after Erica. Several results support this hypothesis. The temporal variations of species richness per station, density and biomass were not significant between 1998 and 2002 in Larégnère (Wilcoxon signed rank test, $P > 0.05$) (Figure 4). Moreover, these variations were of a significantly lower magnitude than the variations observed during this study (Figure 4). Unfortunately, no data series were available for Crouy. However, Kulbicki (1997) indicated that in New Caledonia the variations of fish species richness are low on coral reefs at short and long terms, and variations of density and biomass are also limited in the absence of significant perturbations, particularly for commercial species. Consequently, the 'natural' variations should be minor compared to the mid-term effects of Erica according to the magnitude of the variations detected. The drastic changes of the habitat and its associated ichthyofauna observed by the authors in the area during this study support this hypothesis.

Initial impact

Cyclone Erica was a major perturbation and had a significant initial impact on fragile coral forms, and dead coral skeletons colonized by filamentous algae. These colonies were partly destroyed resulting in a loss of habitat for the fish communities. A review of the major patterns of coral-induced damage to coral reef communities can be found in Harmelin-Vivien (1994). Destruction ranges between 0% and 100%, depending on coral reef characteristics (shape, skeleton, strength and size of colonies, depth, ecological history, habitat location) and cyclone characteristics (intensity, distance between the reef and the cyclone path, direction of cyclone-induced waves). Destruction of live coral are common impacts of tropical cyclones, particularly the branching forms which are the most susceptible to storm waves; on shallow *Acropora* fields of the Great Barrier Reef (5% to 85% of dead colonies, Van Woesik et al., 1995), on Curaçao reefs (7% to 94% of damaged colonies, Van Veghel & Hoetjes, 1995), on Jamaica shallow *Acropora* fields (Hughes, 1994) and on St Lucia coral reefs (5% to 32% of dead corals, Nowlis et al., 1997). However, cyclones do not always cause significant damage to the architectural complexity of the coral reef despite significant coral mortality and drastic changes of the biological composition of the benthic environment, such as in Reunion Island (Letourneur et al., 1993).

The initial impacts of Erica on reef fish populations in the South Lagoon Marine Park were also significant. However, no sign of direct mortality or fish injury was observed during post-hurricane sampling. The impacts were a decrease of fish species richness and biomass, and a modification of community structure when the live coral cover decreased. There are few quantitative data on the initial impact of cyclones on reef fish population. Letourneur et al. (1993) reported more diverse communities before cyclone Firinga (Class 3 with gusts over 240 km/h) in Reunion Island (Indian Ocean). Unfortunately, the pre-hurricane observations were only qualitative. The author indicated that these communities were mainly affected by redistribution of fish into non-damaged habitats after the destruction of the corals and the presence of a thick silt layer due to high sedimentation following cyclonic rainfall (Letourneur et al., 1993). Turpin & Bortone (2002) reported lower biomass after cyclones Erin (Class 2) and Opal (Class 3) on artificial reefs near Pensacola (Gulf of Mexico). Conversely, cyclone Marilyn (Class 2) had no significant influence on the observed decline pattern of all variables over time of the fish communities of Saint Croix (Adams, 2001). On the same island, hurricane Lenny (Class 4) had no effect on fish despite a significant effect on habitats (Adams & Ebersole, 2004). These authors proposed that the apparent resistance of coral reef fish of St Croix to hurricanes was due primarily to the high frequency of disturbances at this location, which was not the case for the present study. Consequently, the impacts of cyclones on fish communities could be linked to their frequency and strength in the area.

The most noticeable initial impact of Erica was a modification of reef fish behaviour consequently to the modification of the habitat and an increased predation due to the loss of shelters. This is a common phenomenon (Harmelin-Vivien, 1994). Erica had partly destroyed habitat shelters

and exposed several species, which probably attracted predators in these affected areas. Thus, unusual groups of aggressive juveniles of *Carcharhinus amblyrhynchos* were observed in the area. Short-term increase in the abundance of predators has been reported in Jamaica (Kaufman, 1983). Potential preys tended to form unusually large compact shoals. Such behaviour was observed by the authors, particularly for juveniles of *Scarus* spp. and small Pomacentridae such as *Chromis viridis*. This phenomenon was not observed when the live coral cover was preserved, on the stations protected from the cyclone winds. Conversely, Kaufman (1983) observed smaller groups of small planktivorous species after hurricane Allen in Jamaica. These differences may be due to the strength of the cyclone and the range of destruction of coral habitat (Harmelin-Vivien, 1994). In St Croix, hurricanes are so frequent that coral reef communities are in a persistent state of early succession. Therefore fish assemblages are adapted to these disturbances and rubble-associated fish are more common (Adams & Ebersole, 2004) which is not the case on the well-preserved coral reefs of the South Lagoon Marine Park of New Caledonia.

Mid-term impact

Twenty months after Erica, live corals had not fully recovered. A large proportion of broken branches suffer immediate mortality after the storm and usually only some branches or fragments will survive, regenerate and grow in their new position (Harmelin-Vivien, 1994). Shallow leeward reefs of the Great Barrier Reef (Australia) did not recover and were already overgrown by turf algae two months after cyclone Joy (Class 4) (Van Woesik et al., 1995). On the Capricorn Bunker Sector of the Great Barrier Reef live coral cover remained low and turf algae dominated the benthos five years after the disturbance before significant recovery (Halford et al., 2004). Reasons for such mortality can be different, ranging from mechanical destruction to stormwater or sediment run-off over the reef. In Jamaica, hurricane Allen inflicted extensive damage on coral reefs because this Class 5 hurricane struck after a long period without a major storm (40 years) (Hughes, 1994), as in New Caledonia. Moreover, recruitment by *Acropora* was minimal and broken fragments survived poorly within a few months (Hughes, 1994). The reef began to slowly recover over the next three years (Hughes, 1994). It was also observed that after a variable lag period the recovery process of coral reefs was well underway in two reefs of the Yucatan Peninsula (Mexico) (Jordan-Dahlgren & Rodriguez-Martinez, 1998). This lag period was longer than 20 months after the hurricanes Gilbert (Class 5) and Keith (Class 4), as in New Caledonia, and only a few dislodged branches of *Acropora palmata* survived (Jordan-Dahlgren & Rodriguez-Martinez, 1998). The increase was detected after 60 months. On the other hand, Fong & Lirman (1995) indicated rapid wound healing of corals and 72% of hurricane generated fragment cemented to the bottom and became new asexual recruits nine months after hurricane Andrew (Class 4) for the Florida Reef Track. The rate of community succession will be slower when the area disturbed is large and the disturbance event extreme (Harmelin-Vivien, 1994).

Twenty months after Erica, the fish community did not recover. The mid term effects on fish populations were different and more significant than the initial effects. The total number of species was similar to initial post-cyclone value, but species richness per station, density and biomass were lower than both before and just after the cyclone. This can be explained by the non-recovery of the habitat, the loss of habitat resulting in a decline in reef fish abundance. On the Great Barrier Reef, the species richness of Chaetodontidae, Scaridae and Acanthuridae, and the abundance of several species of these families had fallen significantly three years after a storm (Halford et al., 2004). These authors observed a partial recovery seven years later. Conversely, data from Letourneur et al. (1993) in Reunion Island indicate an increase of the species richness of commercial fish and Chaetodontidae seven months after hurricane Firinga (from 27 to 36 species) when most habitats were again available, because of the disappearance of a silt layer and the preserved architectural structure of the reef (Letourneur et al., 1993). A significant increase of the abundance of Chaetodontidae and Scaridae was also recorded during the 18-month period following the hurricane but not for Acanthuridae (Letourneur et al., 1993).

Twenty months after Erica, the fish assemblages were also different from those before the cyclone. Herbivorous species and rubble-associated benthic macro-invertebrate feeders replaced the coral associated species that characterized the assemblages before Erica. A long-term increase in the abundance of herbivores was also observed but not quantified in Jamaica after hurricane Allen (Kaufman, 1983). As mentioned by Letourneur et al. (1993) in Reunion Island, the dead broken branching corals were colonized by algae and its associated microfauna and allowed an increase in the abundance of herbivorous and some diurnal carnivorous species. The effects of a hurricane on the reef fish assemblages can also be undetectable such as in St Croix after cyclone Marilyn (Class 2) (Adams, 2001). Such a phenomenon is observed when there is little structural damage to the reef or when the strength of the cyclone is not sufficient to significantly influence fish assemblage in the mid-term (Adams, 2001). When the fish assemblages suffer little, the return to the pre-storm situation seems to occur rapidly (1–1.5 years) but when damage is important a long-lasting shift in trophic structure is observed towards herbivorous and rubble-associated species (Harmelin-Vivien, 1994). The effects of Erica belong to the second category. Despite the high degree of resilience of coral reef communities to major storm activity, recovery can take at least ten years as for the Great Barrier Reef (Halford et al., 2004) when perturbations are uncommon and coral reefs well preserved.

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