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Spatial structure of commercial reef fish communities along a terrestrial runoff gradient in the northern lagoon of New Caledonia

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Synopsis

The spatial distribution of commercial reef fishes from four areas of the northern lagoon of New Caledonia was studied following a terrestrial runoff gradient ranging from very low on the western barrier reef to high on the northern fringing reefs. Species richness decreased from eastern reefs (30.4 species transect^{-1}) to northern fringing reefs (21.4), suggesting a link between terrestrial influence and species richness. Density ranged from 0.49 fish m^{-2} (western reefs) to 0.69 fish m^{-2} (eastern reefs), but did not show any particular trend. Biomasses increased from 148 g m^{-2} on the northern fringing reefs to 447 g m^{-2} on the western reefs. Such high values are likely due to the very low fishing pressure in the whole area. Numerous significant relationships were found between fish descriptors (i.e. diversity, density, biomass and mean weight) and terrestrial influences (i.e. distance to coast, visibility, % of carbonates in the sediment, % of mud, granulometry and color of sediments). Descriptors of total ichthyofauna were all positively correlated with decreasing terrestrial influence. The 6 dominant fish families displayed similar trends and were positively correlated with decreasing terrestrial influence, except for Siganidae which showed the opposite trend. Some of the most common species, such as *Scarus sordidus* and *Siganus doliatus*, had no particular distribution pattern. Size, density and biomass of other species, such as *Lethrinus atkinsoni, Cheilinus undulatus, Hipposcarus longiceps, Scarus microrhinos* and *Acanthurus xanthopterus*, were significantly correlated to parameters characteristic of offshore reefs. Conversely, *Plectropomus leopardus, Scarus ghobban* and *Siganus lineatus* were closely related to coastal reefs. Some species had significant correlations with parameters characteristic of intermediate reefs, such as *Scarus schlegeli* and *Acanthurus nigricauda*. Data for *Plectropomus leopardus* and *Scarus ghobban* suggested a possible ontogenic migration of these two species from the northern fringing reefs, where numerous small individuals were observed, to offshore barrier reefs, where only large individuals were recorded.

Introduction

During the last three decades, numerous studies have been conducted on the structure of coral reef fish communities, focusing mainly on spatial and/or temporal scales. Indeed, understanding how fishes respond to the great heterogeneity of reef substrata over a wide range of spatio- temporal scales is one of the fundamental aims of ecological studies on coral reefs (Sale 1991). Contrary to general opinion, works providing clear data on the ecological processes involved in spatio-temporal distribution of fish communities are not so numerous (Williams 1991). Relationships between fish and substratum variables are a matter of debate. Correlations between topographic complexity and fish species richness are well documented (Luckhurst & Luckhurst 1978, Sano et al. 1984, Roberts & Ormond 1987, Chabanet & Faure 1994). Conversely, correlations between topographic complexity and fish density are not so evident. Some authors found a positive correlation between these variables (Sano et al. 1984), whilst Luckhurst & Luckhurst (1978) found only a low correlation, and Risk (1972) and Talbot et al. (1978) found no significant correlation. Generally, small and territorial fish are the most sensitive to substrate variables. Data for larger species, such as those which are of commercial interest, are rare and often contradictory. In addition, studies investigating the possible role of terrigeneous influence on reef fish communities are not numerous (Williams & Hatcher 1983, Russ 1984, Wantiez et al. 1997). Furthermore, although these works mentioned terrigeneous influence on the ichthyofaunal structure, none of them provided quantification of this phenomenon. In a previous work, correlations between commercial reef fish communities and substrate variables were investigated (Labrosse et al. 1996). Only a low number of significant correlations between fish and substrate descriptors were found. Among them, the diversity of Lethrinidae was positively correlated to sand cover; the diversity of Scaridae was negatively correlated to sand cover; diversity, density and biomass of Acanthuridae were all positively correlated with cover by filamentous algae; whereas diversity of Acanthuridae was negatively correlated with the percentage of living coral (Labrosse et al. 1996).

As part of an on-going study of the commercial reef fish communities of a reef area of nearly 600 km^2 (the entire lagoonal area referred to is about 10 000 km^2), four major reef areas representing a gradient of terrigeneous influence on the northern lagoon of New Caledonia were investigated. In this area, fish communities had never been studied with the exception of a work focusing on soft-bottom fish communities (Wantiez 1992). We will try to answer the following questions: (1) Do commercial fish communities from these four areas show significant segregation in their main descriptors, i.e. diversity, density, biomass and mean weight of fish? (2) Are these fish descriptors correlated to terrestrial influence variables? and, if so, (3) do these correlations explain fish distribution more accurately than those previously established with substrate variables?

Material and methods

Study area and sampling zones

The present work was conducted in the northern lagoon of New Caledonia, between latitudes 19°30′ and 20°30′ S, and between longitudes 163°20′ and 164°10′ E (Figure 1). Human density is very low in that region (about 4 inhabitants km^2) and only small artisanal fisheries exist there. Rainfall in the north of 'Grande Terre' usually varies between 1 and 2 m year^{-1} (Richer de Forges et al. 1987). The term 'Grande Terre' represents, in this context, the northern part of the emerged lands of New Caledonia. Four major lagoonal areas were investigated in this study: the western barrier reefs (hereafter WBR), the eastern barrier reefs (EBR), lagoonal islands (LI), and the northern fringing reefs (NFR). A total of 16 geographical sub-sectors were also defined (Figure 1) in order to allow a finer study of the fish communities in relation to the gradient of terrestrial influence. The WBR includes four sub-sectors (no. 1, 2, 3 and 4), the EBR two (no. 11 and 12), the NFR five (no. 6, 7, 8, 9 and 10), and the LI five (no. 5, 13, 14, 15 and 16) (Figure 1). Each sector may be considered as globally homogeneous in term of reef morphology, exposure to wave energy, etc. Each sector includes a variable number of stations (i.e. replicates), ranging from 9 to 23. Indeed, as recommended by Legendre & Legendre (1984), the sampling effort in each geographical sector was proportional to the estimated surface of reef slopes at the sampled depths (1–7 m on average). Sampling was conducted with the oceanographic vessel 'Alis' between 21 February and 29 April 1995. A total of 255 stations was investigated during this period. The stations, all located on reef slopes, were separated by approximatively 1 km.

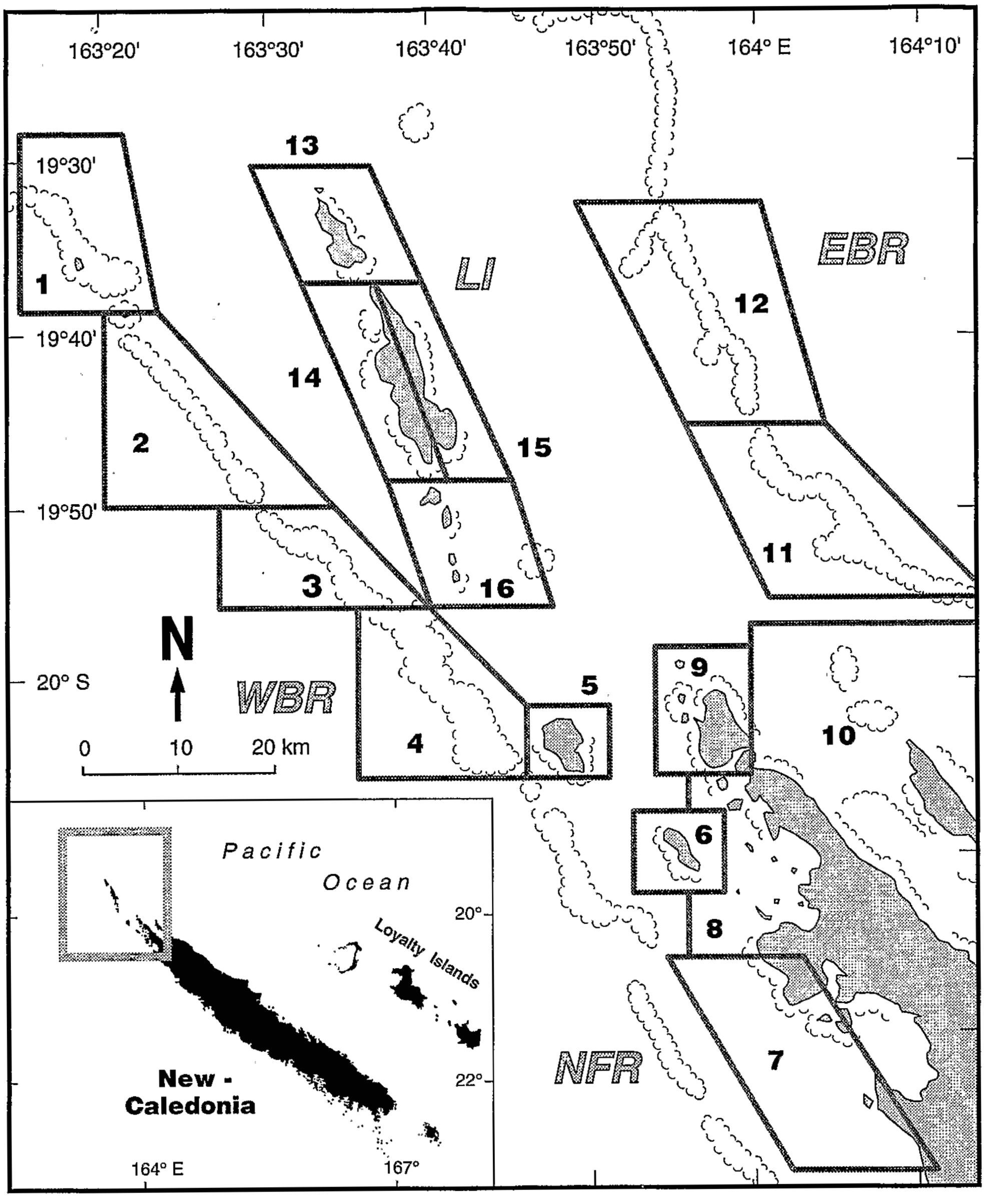


Figure 1. Location map of the study areas in the northern lagoon of New Caledonia, Southwestern Pacific Ocean. The western barrier reefs (WBR) includes sub-sectors 1, 2, 3 and 4; the eastern barrier reefs (EBR) includes the sub-sectors 11 and 12; the lagoonal islands (LI) includes the sub-sectors 5, 13, 14, 15 and 16; and the northern fringing reefs (NFR) includes the sub-sectors 6, 7, 8, 9 and 10.

Fish sampling techniques

Commercial fish communities were studied by visual censuses using the line-transect method (Buckland et al. 1993) at depths which required SCUBA diving equipment. This census method is derived from terrestrial procedures, and its precision and accuracy for underwater-based work have been demonstrated (Ensign et al. 1995, Kulbicki 1997). Several other authors have also used this method (e.g. Thresher & Gunn 1986, Kulbicki 1988, Wantiez et al. 1996, Labrosse et al. 1996). On each station, two divers censused fishes along a 50 m transect, one on each side of the transect. The observers counted all commercial fish, and recorded the estimated perpendicular distance between the fish and the transect line. Distances were noted in 1 m intervals for fishes between 0 and 5 m, in 2 m intervals for fishes between 5 and 10 m, and in 5 m intervals for fishes between 10 and 20 m away from the transect line. Censuses did not take place if visibility was less than 4 m for each side of the transect. Density and biomass estimates (see below) are based on the detectability functions of species. This factor is much better accounted for by the method used than fixed width transects or fixed radius points counts (Kulbicki 1997). The sizes of fish (total length) were estimated in 1 cm classes for fishes ranging from 1 to 10 cm, in 2 cm classes for fishes ranging from 10 to 30 cm, in 5 cm classes for fishes from 30 to 60 cm, and in 10 cm classes for fishes larger than 60 cm. The choice of increasing size classes with fish length follows the recommendations of Bell et al. (1985). Previous studies (Kulbicki 1988, Kulbicki & Wantiez 1990, Kulbicki et al. 1994) indicated that for most species, the difference between observed and actual size was less than 15%.

If fishes were in a school or a group, the number of fishes was estimated and the perpendicular distance of the closest fish and the furthest fish were recorded. Each sighting occurrence will be called a record. Each record contained the species name, the number of fish sighted, the estimated size of fish, and the distance at which the fish were observed from the transect line. Despite usual bias of visual censuses, mainly for cryptic or shy species, this method is particularly efficient in biotopes where human visits (diving, spearfishing, etc.) are rare, because the fish behavior remains natural (Kulbicki 1997). Particular care was also used for species attracted to the divers and to avoid double counts of fish traversing both sides of the transect.

Terrestrial influence: nature of sediments, visibility and distance to 'Grande Terre'

Data on the nature of sediments come from Chevillon & Clavier (1988) and Chevillon (1990, 1996). Although they were not collected in combination with the fish sampling, data on sedimentological structure of the northern lagoon of New Caledonia are very unlikely to have changed significantly over this moderate period of time. Four descriptors of the nature of sediments were considered for each station: (a) the median size of the sediment particles, (b) the percentage of mud, (c) the percentage of carbonates (in fraction < 63 μm) which allows the evaluation of biogenic or terrigeneous origin of the sediments when the terrestrial rocks are not calcareous (as in New Caledonia), and (d) the color, following criteria of the Munsell table. The color is an interesting descriptor for the separation of different sedimentological facies (Chevillon 1990). Several categories were defined for each of these four descriptors.

For median size, six categories were used: (1) pebble, (2) coarse sand, (3) medium sand, (4) fine sand, (5) very fine sand, and (6) mud. For percentage of mud (PM), four categories were used: (1) PM < 10%, (2) 10% < PM < 20%, (3) 20% < PM < 40%, and (4) 40% < PM < 60%. For percentage of carbonates (PC), four categories were also used: (1) 70% < PC < 80%, (2) 80% < PC < 85%, (3) 85% < PC < 90%, and (4) 90% < PC < 95%. For color, six categories were used: (1) white, (2) pale yellow, (3) yellow-orange, (4) light grey, (5) dark grey, and (6) olive. Precise descriptions of all of these different categories were given previously (Chevillon & Clavier 1988, Chevillon 1990, 1996). Results on sedimentological structures are not presented here, as they may be consulted in previous studies (Chevillon & Clavier 1988, Chevillon 1996).

The horizontal underwater visibility for each station censused was measured along the transect line during the dives, and the distance between each station and the closest part of the 'Grande Terre' was measured.

Data analyses

The data of the two observers can not be used as replicates because the environment within a station may be heterogeneous (for example, when the census was done near the basal part of the reef slope, one diver may have counted on the 'reef side' of the transect and the other on the 'sand side'). Data were thus pooled for each transect. Many density estimators, based on the work of Burnham et al. (1980), may be chosen. Among them, as mentioned by Wantiez et al. (1996), the most robust for this type of data is

$$D_i = (2L)^{-1} \Sigma (n_i/d_i),$$

where D_i = density of species i (fish m^{-2}), L = transect length (50 m), n_i = abundance of species i, d_i = average distance of species i to the transect (m). Average distance for species i was calculated as follows:

$$d_i = (n_i)^{-1} \Sigma (n_j d_j),$$

where n_j = number of fish of species i observed at occurrence j, and d_j = distance of fishes of species i to the transect at occurrence j.

The weights of fishes were calculated from length-weight relationships previously defined (Kulbicki et al. 1993). Biomass can be calculated in a similar way to density

$$B_i = (2L)^{-1} \Sigma (w_i/d_i),$$

where B_i = biomass (g m^{-2}), and w_i = weight of species i (g).

These different estimates can be calculated for each species or for all species combined. The most robust estimates for global data were obtained using the sum of estimates per species rather than estimates which consider all species combined (Labrosse et al. 1996). A principal component analysis (PCA) was applied to the 3 'global' fish descriptors (i.e. diversity, density and biomass, which were standardized due to their different natures) of the 255 stations. The heterogeneity of dispersion was tested with random permutations of stations between groups (i.e. the four areas) (Romesburg 1985). One-way ANOVAs were performed on each type of data (species richness, density and biomass), for total ichthyofauna, main families and the most abundant species. When ANOVAs detected significant differences, a posteriori Student-Neuman-Keuls test for comparison of means were used. Descriptors of fish communities and terrestrial influence were fitted by the most significant correlation chosen between the linear, logarithmic, polynomial or exponential regressions. This used mean values for the fish and terrestrial descriptor data of the 16 geographical sectors. The stations within the 16 sectors were pooled because sedimentological data were not always easy to relate specifically to one or another station. In addition, pooling the stations allowed us to smooth some of their heterogeneity. The significance of the correlation index (R) was tested according to the degrees of freedom given by the model chosen (Legendre & Legendre 1984).

Results

Diversity, mean density and biomass of total ichthyofauna and of major fish families

Over the whole area studied, a total of 209 commercial fish species was recorded. The total number of species was lower on eastern (131 species) and western barrier reefs (143) than on lagoonal islands (159) and northern fringing reefs (154) (Table 1). Conversely, the mean species richness per transect was significantly lower on NFR than on both barrier reefs. Mean density of fishes did not differ between areas, except between the EBR and WBR. The bio-

Table 1. Total species richness, mean species richness, mean density (indiv. m^{-2}) and mean biomass (g m^{-2}) per transect on western barrier reef (WBR), lagoonal islands (LI), eastern barrier reef (EBR) and northern fringing reefs (NFR). Results of one-way ANOVA and a posteriori SNK tests (α = 5%). Level of significance of ANOVAs: * = $p < 0.05$, ** = $p < 0.01$ (– = not tested). Confidence intervals at α = 5% level are in parentheses.

	Total	WBR	LI	EBR	NFR	ANOVA	SNK test
No. of stations	**255**	60	76	38	81	–	–
Total nb species	**209**	143	159	131	154	–	–
Mean nb species	**26.1 (1.2)**	28.2 (2.0)	27.7 (2.1)	30.4 (3.2)	21.4 (1.9)	**	EBR=WBR=LI>NFR
Mean density	**0.57 (0.10)**	0.49 (0.07)	0.52 (0.09)	0.69 (0.11)	0.62 (0.24)	*	EBR>WBR
Mean biomass	**276 (81)**	447 (103)	231 (43)	390 (87)	148 (30)	**	WBR=EBR>LI>NFR

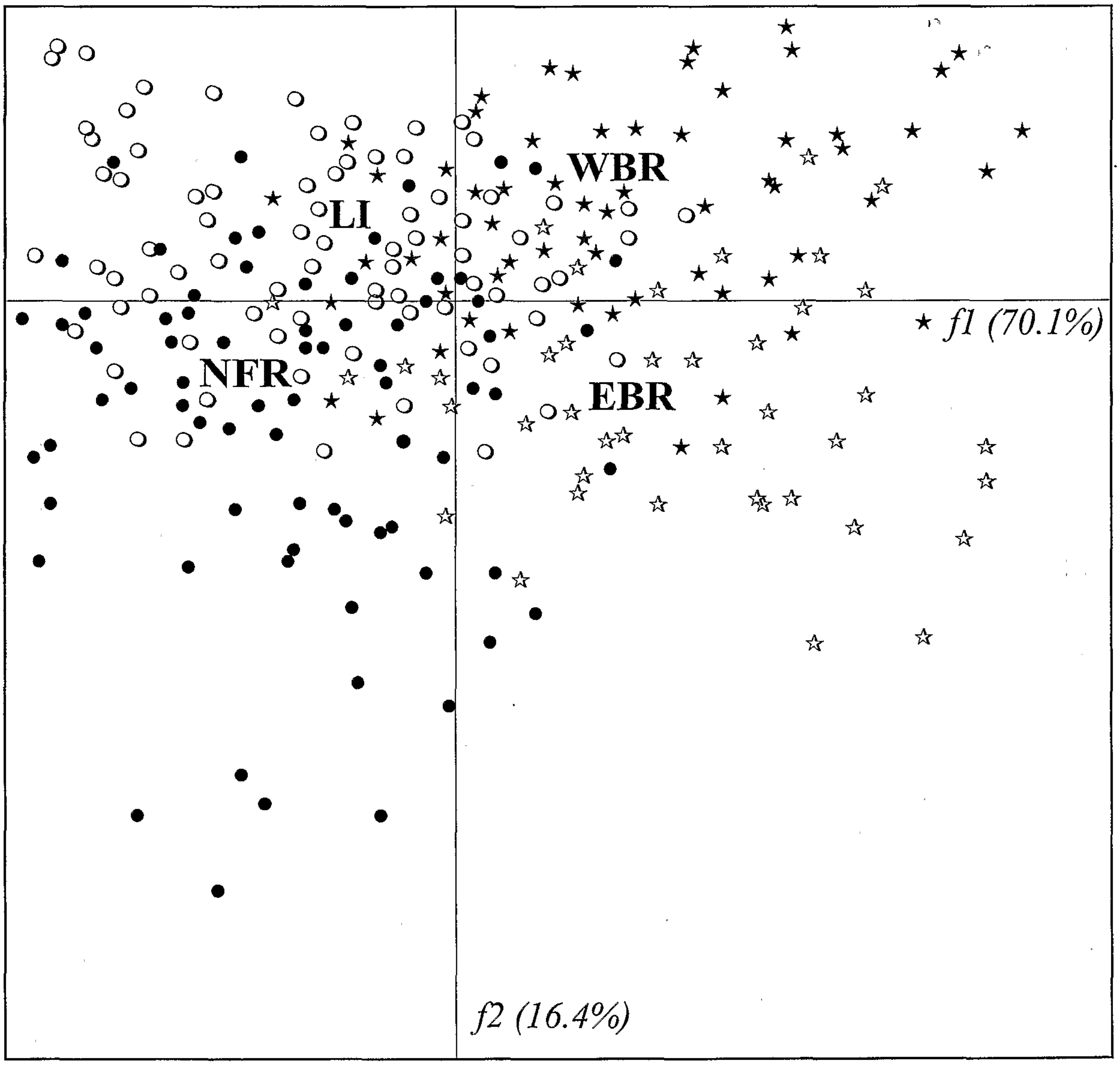


Figure 2. First factorial plane of the Principal Component Analysis monitored on the standardized data of diversity, density and biomass of the commercial reef fishes. The position of the barycenter of each group of stations is mentioned as follow: WBR = western barrier reefs (stations: ★), EBR = eastern barrier reefs (stations ☆), LI = lagoonal islands (stations: ●), and NFR = northern fringing reefs (stations: ○).

mass, ranging from 148 g m^{-2} to 447 g m^{-2}, were high on the four areas, and those of the barrier reefs (WBR and EBR) were significantly higher than those of the two other zones; the mean biomass of the NFR was the lowest recorded. Thus, fish communities significantly differed between areas because each area was characterized by different triplets of data, i.e. mean species richness, density and biomass. This was confirmed by the PCA which also revealed striking differences in fish communities (Figure 2). Axes 1 and 2 explained about 85% of the total inertia. The test of random permutations is highly significant ($p < 0.001$), underlining that fish communities were significantly different between the four areas studied.

The most diverse fish families were Acanthuridae (27 species in total), Scaridae (24) and Serranidae (23); this pattern was similar in all areas (Table

Table 2. Number of species recorded for the major fish families on the western barrier reef (WBR), lagoonal island (LI), eastern barrier reef (EBR) and northern fringing reefs (NFR).

	WBR	LI	EBR	NFR	Total
Holocentridae	3	4	5	4	5
Serranidae	19	20	16	19	23
Carangidae	8	7	3	5	14
Lutjanidae	12	12	9	14	16
Haemulidae	4	6	4	6	7
Lethrinidae	12	12	8	13	16
Mullidae	12	12	10	13	14
Labridae	14	15	11	13	18
Scaridae	20	23	20	19	24
Acanthuridae	19	20	22	22	27
Siganidae	4	9	7	10	11
Balistidae	7	6	7	0	9

2). Differences in diversity of families between zones were generally low. However, the NFR had the highest diversity for four families, LI for three, both WBR and EBR for one.

The highest densities were observed for the families Acanthuridae and Scaridae (0.158 and 0.137 individual m^{-2}, respectively), and at a lower level, Lutjanidae (0.056), Siganidae (0.053) and Lethrinidae (0.042) (Table 3). The dominance of both Acanthuridae and Scaridae was observed in all zones. Lutjanidae and Siganidae displayed significantly higher densities on both LI and NFR than on western and eastern barrier reefs. Conversely, Serranidae were significantly more abundant on both barrier reefs than on the two other biotopes. Density of Lethrinidae was about 2-fold higher on NFR than on the barrier reefs.

The biomasses of the families Scaridae (82.6 g m^{-2}) and Acanthuridae (78.3 g m^{-2}) were the highest over the whole area (Table 4). Biomass of other families, such as Serranidae, Lutjanidae, Labridae, Lethrinidae and Siganidae were lower, and ranged from 8.7 g m^{-2} to 21.6 g m^{-2}. However, this pattern differed strongly according to the area. Biomasses of Acanthuridae were low on LI and NFR (49.0 and 24.1 g m^{-2}, respectively) compared to those of WBR and EBR (129.8 and 175.1 g m^{-2}, respectively). On these barrier reefs, the biomasses of Serranidae and Labridae were relatively high (between 20.4 and 43.6 g m^{-2}), whereas those of Lutjanidae and Lethrinidae were lower, especially on EBR.

Density and biomass of some of the most abundant fish species

Acanthurus xanthopterus was the most abundant acanthurid on both barrier reefs, whereas it presented lower abundances on LI and NFR (Figure 3). However, whereas densities of *A. xanthopterus* were similar on both barrier reefs (SNK-test, $p > 0.10$), biomasses were significantly higher on the WBR than on EBR (SNK-test, $p < 0.001$), suggest-

Table 3. Mean density × 10^4 (fish m^{-2}) of the major fish families on the western barrier reef (WBR), lagoonal islands (LI), eastern barrier reef (EBR) and northern fringing reefs (NFR). Results of one-way ANOVAs and a posteriori SNK tests ($\alpha = 5\%$). Levels of significance of ANOVAs: * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. Confidence intervals at $\alpha = 5\%$ level are in parentheses.

	WBR	LI	EBR	NFR	Total	ANOVA	SNK test
Holocentridae	12 (6)	32 (9)	63 (9)	24 (12)	28 (9)	**	EBR>LI=NFR=WBR
Serranidae	218 (48)	184 (28)	321 (43)	181 (40)	207 (26)	**	EBR>WBR>LI=NFR
Carangidae	18 (8)	15 (7)	2 (1)	26 (8)	16 (8)	**	NFR=WBR=LI>EBR
Lutjanidae	316 (113)	713 (141)	310 (52)	788 (184)	564 (93)	*	LI=NFR>WBR=EBR
Haemulidae	45 (16)	28 (7)	15 (7)	50 (11)	37 (7)	*	NFR=WBR>LI=EBR
Lethrinidae	374 (120)	79 (22)	280 (74)	763 (23)	423 (56)	**	NFR>WBR=EBR>LI
Mullidae	327 (103)	323 (36)	184 (51)	302 (30)	284 (24)	*	WBR=LI=NFR>EBR
Labridae	123 (27)	169 (14)	135 (17)	266 (29)	183 (11)	**	NFR>LI=WBR=EBR
Scaridae	1482 (125)	1593 (114)	1668 (176)	1058 (80)	1368 (57)	*	EBR=LI=WBR>NFR
Acanthuridae	1864 (309)	1336 (118)	3465 (434)	861 (93)	1584 (131)	***	EBR>WBR>LI>NFR
Siganidae	105 (53)	502 (15)	352 (19)	787 (97)	530 (37)	***	NFR>LI>EBR>WBR
Balistidae	22 (7)	8 (2)	70 (5)	19 (10)	22 (5)	**	EBR>WBR=NFR>LI

ing greater mean size and weight on WBR, as found by Labrosse et al. (1996). There was another distribution pattern for *Naso tuberosus* and *N. unicornis*. The former was significantly more abundant on EBR, and the latter on WBR, whereas they were not abundant on other habitats. Similar patterns were observed for the biomass of these species. Other abundant acanthurids have a small size, such as *A. nigrofuscus* (0.035 indiv. m^{-2} all habitats combined) and *Ctenochaetus striatus* (0.033 indiv. m^{-2}). Density and biomass of *Siganus doliatus* were significantly higher on LI than on other habitats, and those of *S. argenteus* were significantly higher on EBR than on other habitats (SNK-test, $p < 0.001$ for each cases). *S. punctatus* presented high biomass but low densities on both barrier reefs. This indicates that these fish reached large mean sizes on these areas (Labrosse et al. 1996). High densities of Scaridae were mainly due to the abundance of *Hipposcarus longiceps, Scarus microrhinos, S. ghobban* (Figure 3), and *S. altipinnis, S. sordidus* and undetermined juvenile scarids (0.018, 0.019 and 0.028 indiv. m^{-2} all zones combined, respectively). *H. longiceps* showed significantly higher densities and biomasses on both barrier reefs than on LI and NFR, whereas *S. ghobban* presented the opposite pattern.

Like herbivorous species, carnivorous ones presented significantly higher densities on some habitats than on others (Figure 4), such as *Lutjanus fulviflamma* and *L. quinquelineatus* on LI and NFR, *Plectropomus leopardus* on NFR, and *Lethrinus nebulosus* on NFR (SNK-test, $p < 0.001$ for each case). Other species, such as *Epinephelus merra* (0.005 indiv. m^{-2} all areas combined), *Lutjanus fulvus* (0.003), *L. gibbus* (0.002), *L. russelli* (0.003), unidentified juveniles of Lethrinidae (0.015), *Lethrinus genivittatus* (0.006) and *Monotaxis grandoculis* (0.004) were among the most abundant carnivorous fishes. These relatively low values underline that densities of carnivorous fishes were lower than those of herbivorous ones. Biomass followed similar patterns. However, some cases require particular attention. Despite significantly higher densities of *Plectropomus leopardus* in LI than in other areas (SNK test, $p < 0.001$), the highest biomass was observed on EBR (SNK test, $p < 0.001$), whereas biomass of other zones did not significantly differ (SNK-test, $p > 0.10$). This was due to the large mean sizes and weight of this species on EBR (Labrosse et al. 1996). A similar trend was observed for *Lethrinus nebulosus*, which was abundant with low biomass on NFR (mainly juveniles), whereas it was not very abundant but presented high biomass on WBR (mainly large adults). On the other hand, the high biomass of *Lutjanus bohar* on WBR, contrasted with its low density, underlining the high mean weight of this species on this biotope (2.29 kg, Labrosse et al. 1996).

Table 4. Mean biomass (g m^{-2}) of the major fish families on the western barrier reef (WBR), lagoonal islands (LI), eastern barrier reef (EBR) and northern fringing reefs (NFR). Results of one-way ANOVAs and a posteriori SNK tests ($\alpha = 5\%$). Confidence intervals at $\alpha =$ 5% level are in parentheses. Significance levels for ANOVA: ns = not significant, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

	WBR	LI	EBR	NFR	Total	ANOVA	SNK test
Holocentridae	0.3 (0.1)	0.8 (0.2)	1.6 (0.3)	0.8 (0.1)	0.8 (0.1)	**	EBR>LI=NFR>WBR
Serranidae	35.0 (0.9)	16.1 (0.7)	31.1 (1.9)	13.0 (1.1)	21.6 (1.0)	***	WBR>EBR>LI>NFR
Carangidae	6.8 (0.4)	3.7 (0.3)	0.6 (0.1)	3.2 (0.3)	3.6 (0.3)	**	WBR>LI=NFR>EBR
Lutjanidae	28.2 (2.1)	15.5 (2.2)	13.8 (1.2)	16.2 (1.9)	18.0 (0.7)	*	WBR>NFR=LI=EBR
Haemulidae	15.3 (0.9)	3.7 (0.8)	5.4 (0.6)	3.7 (0.3)	6.8 (0.7)	**	WBR>EBR>LI=NFR
Lethrinidae	28.3 (1.4)	3.4 (0.3)	7.6 (0.6)	5.2 (0.7)	11.1 (0.8)	***	WBR>EBR>LI>NFR
Mullidae	6.3 (0.3)	7.0 (0.8)	6.1 (0.5)	5.7 (0.4)	6.1 (0.5)	ns	
Labridae	43.6 (1.3)	5.6 (0.4)	20.4 (1.4)	9.8 (0.5)	18.1 (0.9)	***	WBR>ERB>NFR>LI
Scaridae	120.4 (5.8)	96.0 (3.7)	93.2 (3.6)	40.5 (1.5)	82.6 (3.8)	***	WBR>EBR=LI>NFR
Acanthuridae	129.8 (7.7)	49.0 (2.4)	175.1 (8.1)	24.1 (0.7)	78.3 (2.3)	***	EBR>WBR>LI>NFR
Siganidae	6.4 (1.6)	9.9 (1.0)	13.2 (1.2)	7.0 (0.6)	8.7 (1.2)	**	EBR>LI>WBR=NFR
Balistidae	1.3 (0.1)	0.3 (0.1)	2.6 (0.1)	0.7 (1.8)	0.9 (0.1)	*	EBR>WBR=NFR=LI

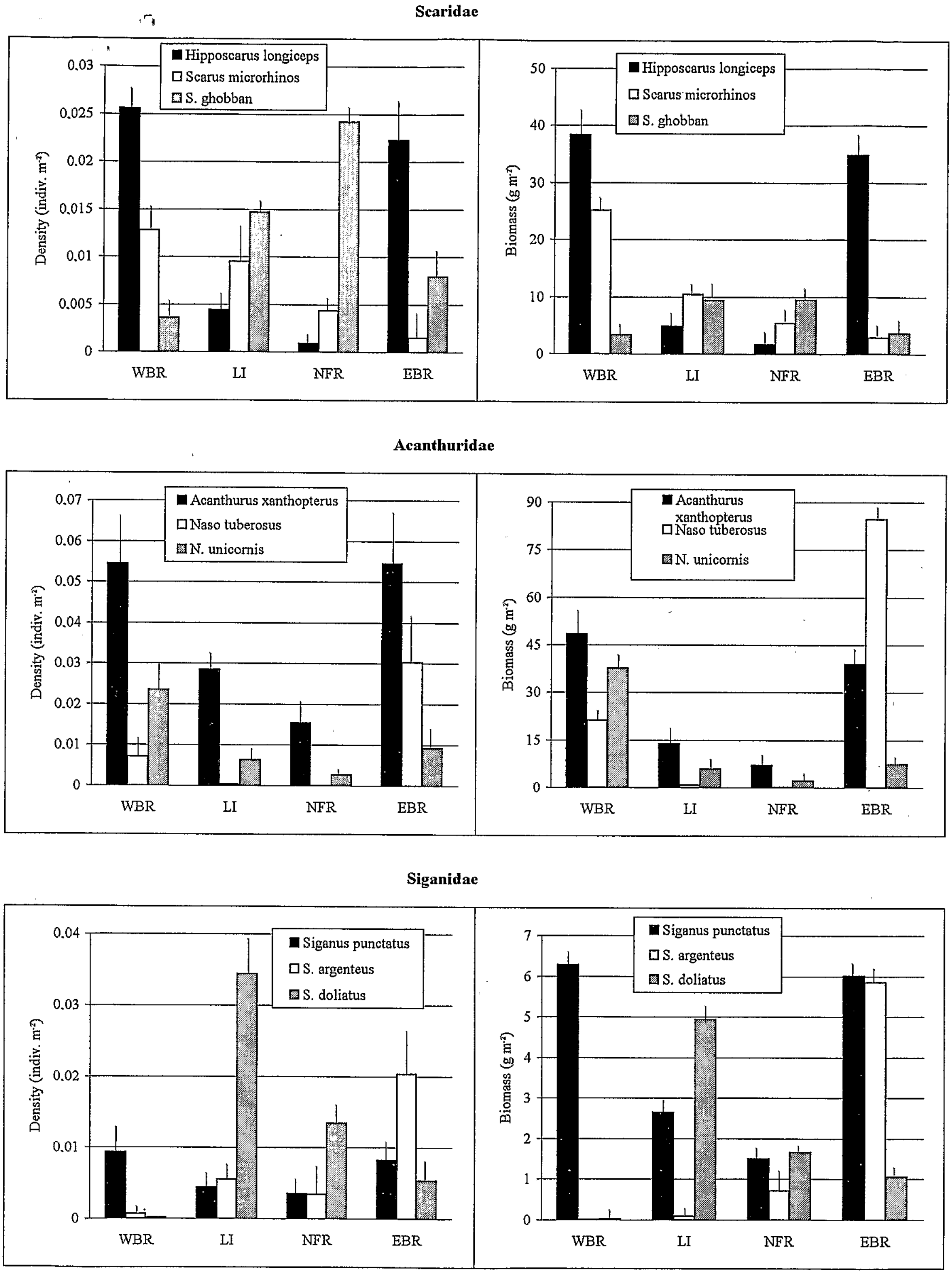
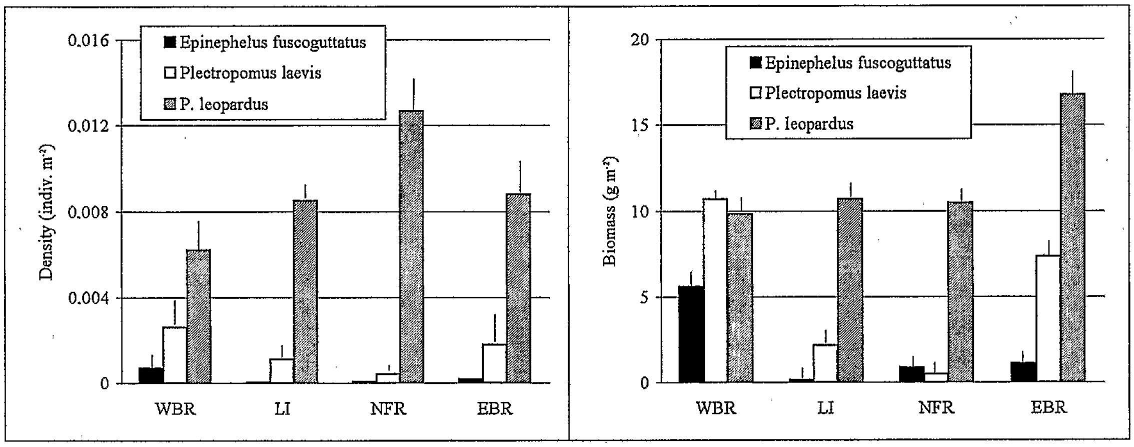
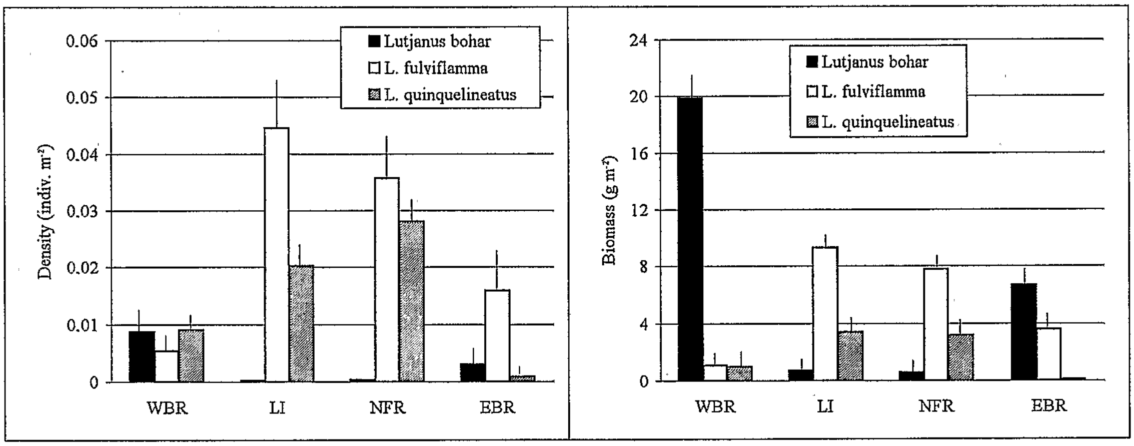


Figure 3. Densities and biomasses of some herbivorous fish species in the western barrier reefs (WBR), the lagoonal islands (LI), the northern fringing reefs (NFR) and the eastern barrier reefs (EBR). Vertical bars indicates confidence intervals at $\alpha = 5\%$ level.

Serranidae



Lutjanidae



Lethrinidae

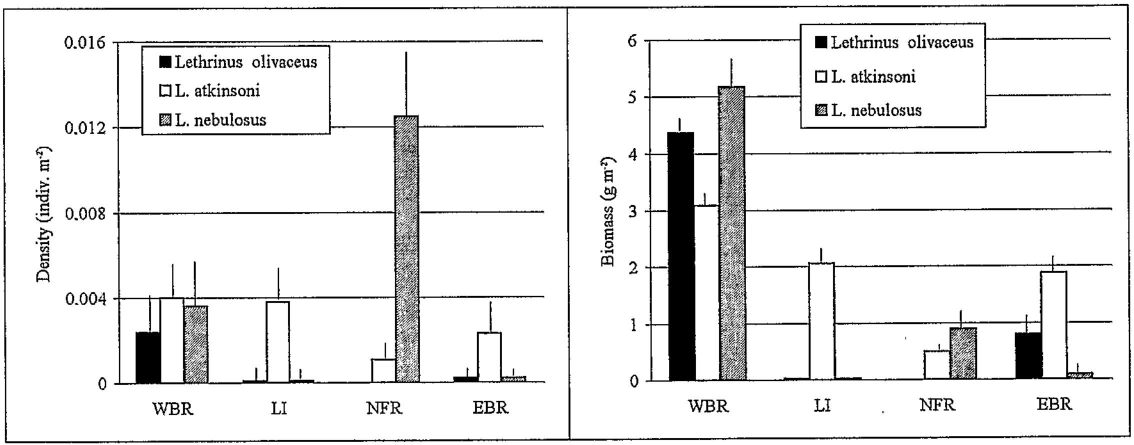


Figure 4. Densities and biomasses of some carnivorous fish species in the western barrier reefs (WBR), the lagoonal islands (LI), the northern fringing reefs (NFR) and the eastern barrier reefs (EBR). Vertical bars indicates confidence intervals at $\alpha = 5\%$ level.

Relationships between fish and terrestrial runoff gradient descriptors

The three descriptors of the total ichthyofauna were correlated with all the terrestrial influence descriptors (except for total density vs. visibility). These correlations were positive for distance to 'Grande Terre', visibility and percentage of carbonates, and negative for percentage of mud, color of sediment, and median particle size (Table 5). The fact that the three first terrestrial descriptors mentioned show similar trends is not surprising, since visibility usually increases with distance to coast, and the farthest reefs are most often characterized by biogenic sediments. Conversely, increasing percentage of mud usually induces darker sediments, which in turn are usually characterized by low median particle size. However, median particle size is not necessarily linked to mud content, as, for example, nearshore sediments may contain high percentage of mud but also large median particle size due to terrestrial debris (Chevillon 1990, 1996). Distance to the coast, visibility, percentage of mud and color of sediment were more significant descriptors than percentage of carbonates and median size in explaining fish distribution (Table 5). Similar trends were found for 5 of the 6 major fish families; Siganidae displayed opposite trends. Acanthuridae, Scaridae and Lethrinidae were the most sensitive families to terrestrial influence, whereas Serranidae was the least sensitive.

Most carnivorous fish species displayed, in general, similar trends of the family to which they belong (Table 6). There were however, several species which showed opposite trends and, in addition, some displayed mixed trends. Thus, *Plectropomus laevis* and *Epinephelus merra* had trends in their responses to terrestrial influence similar to Serrani-

Table 5. Summary of the significance of the relationships between fish and terrestrial influence descriptors for total ichthyofauna and the six major fish families. Significances: ++ = positive correlation at $\alpha = 1\%$ level, + = positive correlation at $\alpha = 5\%$ level, — = negative correlation at $\alpha = 1\%$ level, – = negative correlation at $\alpha = 5\%$ level, and ns = non significant.

		Distance to coast	Visibility	% of carbonates	% of mud	Color of sediments	Median size
Total	Diversity	++	++	+	—	–	—
	Density	+	ns	+	–	–	–
	Biomass	++	++	++	—	—	–
Serranidae	Diversity	ns	ns	ns	–	–	–
	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	++	+	—	—	–
Lutjanidae	Diversity	+	++	++	–	—	ns
	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	+	ns	–	–	–
Lethrinidae	Diversity	+	+	ns	–	—	ns
	Density	ns	++	+	—	—	ns
	Biomass	+	++	+	–	—	ns
Scaridae	Diversity	++	+	+	–	ns	ns
	Density	+	ns	+	–	–	ns
	Biomass	++	++	+	—	–	ns
Acanthuridae	Diversity	++	++	+	—	—	–
	Density	+	++	+	—	—	ns
	Biomass	++	++	++	—	—	–
Siganidae	Diversity	ns	–	–	+	+	+
	Density	ns	ns	–	+	ns	+
	Biomass	ns	ns	ns	+	ns	+

dae as a whole (although more often significant), whereas *E. maculatus* was indifferent in most cases. *P. leopardus* presented different responses to terrestrial influence. Its density decreased with distance to coast, visibility and percentage of carbonates, and increased with percentage of mud and color of sediment. Conversely, the mean weight of this species presented the opposite pattern, whereas biomass was not significantly correlated with a terrestrial gradient, except for visibility. This means

Table 6. Summary of the significance of the relationships between fish and terrestrial influence descriptors for the major carnivorous fish species. Significances: ++ = positive correlation at α = 1% level, + = positive correlation at α = 5% level, — = negative correlation at α = 1% level, – = negative correlation at α = 5% level, dd = dome shaped (i.e. polynomial) correlation at α = 1% level, d = dome shaped correlation at α = 5% level, and ns = non significant.

		Distance to coast	Visibility	% of carbonates	% of mud	Color of sediments	Median size
Serranimodae							
Epinephelus maculatus	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	ns	ns	ns	ns	ns
	Mean weight	ns	–	ns	+	+	ns
E. merra	Density	ns	++	++	—	—	ns
	Biomass	ns	+	+	—	dd	ns
	Mean weight	ns	ns	ns	–	ns	ns
Plectropomus laevis	Density	+	++	++	–	—	ns
	Biomass	+	++	++	–	—	ns
	Mean weight	ns	+	++	ns	—	ns
P. leopardus	Density	—	—	–	++	++	ns
	Biomass	ns	d	ns	ns	ns	ns
	Mean weight	ns	++	+	—	—	—
Lutjanidae							
Lutjanus bohar	Density	++	++	++	—	—	ns
	Biomass	++	++	+	—	—	ns
	Mean weight	ns	++	d	–	ns	—
L. fulviflamma	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	–	ns	ns	ns	ns
	Mean weight	–	–	ns	ns	ns	ns
L. quinquelineatus	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	ns	ns	ns	ns	ns
	Mean weight	ns	ns	ns	ns	ns	ns
Lethrinidae							
Lethrinus atkinsoni	Density	+	+	++	—	—	ns
	Biomass	+	++	+	—	—	ns
	Mean weight	++	++	d	–	ns	—
L. nebulosus	Density	ns	ns	ns	ns	ns	ns
	Biomass	+	+	ns	ns	—	ns
	Mean weight	ns	+	ns	ns	ns	ns
Monotaxis grandoculis	Density	ns	++	ns	–	—	ns
	Biomass	+	++	ns	–	—	ns
	Mean weight	+	++	ns	—	—	ns
Labridae							
Cheilinus undulatus	Density	+	++	+	–	—	ns
	Biomass	ns	++	++	—	—	ns
	Mean weight	ns	++	ns	—	–	—
Choerodon graphicus	Density	—	—	–	++	++	ns
	Biomass	—	—	–	++	++	ns
	Mean weight	ns	—	ns	dd	+	ns

that *P. leopardus* was abundant nearshore but most individuals were juveniles, whereas on offshore reefs density was lower but most individuals were large adults.

Lutjanus bohar displayed trends similar to its family Lutjanidae, *L. fulviflamma* presented only few significant correlations (in addition, opposite to those of its family), and *L. quinquelineatus* was not sensitive to terrestrial influence (Table 6). *Lethrinus atkinsoni, L. nebulosus* and *Monotaxis grandoculis* displayed trends similar to the family Lethrinidae, although *L. nebulosus* did not clearly respond to terrestrial influence. Other carnivorous fishes, such as *Cheilinus undulatus* and *Choerodon graphicus*, were also significantly influenced by a terrestrial gradient, whereby *C. undulatus* presented correlations with descriptors characterizing offshore reefs, and *C. graphicus* presented correlations with descriptors characterizing coastal reefs.

Like carnivorous fishes, some herbivorous fish species presented trends similar to those of the rest of their family, whereas others presented different or undefined patterns (Table 7). Among the Scaridae, *Hipposcarus longiceps, Scarus microrhinos* and, to a lesser extent, *S. altipinnis*, had significant affinities for descriptors characterizing offshore reefs, contrasting with *S. ghobban* which had significant affinities for coastal reefs. For the latter however, trends for density and mean weight were opposed. This may be explained in the same way as for *Plectropomus leopardus*. Other species, such as *S. rivulatus* and *S. schlegeli* displayed dome-shaped correlations, indicating correlations with descriptors characterizing 'intermediate' reefs. Among the Acanthuridae, *Acanthurus xanthopterus* and, to a lesser extent, *Naso tuberosus* and *N. unicornis* were positively correlated with descriptors characterizing offshore reefs. The affinities of *A. blochii* and *A. dussumieri* were not well established, whereas *A. nigricauda* presented significant correlations with descriptors of intermediate reefs. Relationships between the most common Siganidae and terrestrial influence varied according to species. One species had significant positive correlations with characteristics of nearshore reefs (*Siganus lineatus*), another species (*S. punctatus*) with offshore reefs, and a third (*S. doliatus*) had only a few significant correlations with descriptors of intermediate reefs (Table 7).

Discussion

Structure of fish communities

The present work indicates marked differences in the main descriptors of the fish communities of the four major areas sampled. Some of our results show very high values, such as the biomasses on both western and eastern barrier reefs. On the Great Barrier Reef, Williams & Hatcher (1983) indicated that the standing crop found on a mid-shelf reef (237 g m^{-2}) was the highest recorded for a coral reef. This study demonstrated that some coral reefs may support much higher values (mean of 276 g m^{-2}, with a maximum of 447 g m^{-2}). Indeed, the values obtained are likely to be underestimates, as they are only for commercial species. Several explanations may be advanced to explain these values. First, fish sampling was performed mainly on lagoonal inner reef slopes. In New Caledonia, this habitat is usually characterized by higher values of density and biomass than on reef flats or deeper areas (Kulbicki et al. 1991, 1994, Kulbicki 1997), and this might account, at least partially, for these high biomasses. Second, the area sampled is subject to very low human disturbance. For this reason, many species may show significant attraction to the diver (Harmelin-Vivien et al. 1985, Kulbicki 1997). Although observers were submitted to rigorous training to avoid this potential bias, it remains possible that incorrect estimates of the distance at which a fish is first detected occurred, resulting in an overestimate of densities and biomasses. A third explanation for high biomass found might be linked to the very low fishing pressure in the whole area, especially on both barrier reefs. Although data from the local fishery services must be considered with much caution, it is obvious that the 4–8 tons 'officially' caught each year in the whole area (Anonymous[1]) remains negligible compared to the total stock on the reef which

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[1] Anonymous, 1995. Pêches maritime et aquaculture. Les chiffres de 1994. Rap. Serv. Territ. Mar. March. Pec. Mar. 19 pp.

Table 7. Summary of the significance of the relationships between fish and terrestrial influence descriptors for the major herbivorous fish species. Significances: ++ = positive correlation at α = 1% level, + = positive correlation at α = 5% level, — = negative correlation at α = 1% level, – = negative correlation at α = 5% level, dd = dome shaped (i.e. polynomial) correlation at α = 1% level, d = dome shaped correlation at α = 5% level, and ns = non significant.

		Distance to coast	Visibility	% of carbonates	% of mud	Color of sediments	Median size
Scaridae							
Hipposcarus longiceps	Density	++	++	++	—	—	ns
	Biomass	++	++	++	—	—	ns
	Mean weight	+	+	++	–	–	ns
Scarus altipinnis	Density	+	ns	ns	d	ns	ns
	Biomass	++	+	++	d	ns	ns
	Mean weight	dd	+	++	–	—	ns
S. Ghobban	Density	—	—	—	++	++	+
	Biomass	–	–	—	ns	++	ns
	mean weight	–	++	+	–	—	ns
S. microrhinos	Density	++	++	ns	ns	ns	ns
	Biomasss	++	++	+	–	–	ns
	mean weight	+	+	++	—	—	ns
S. rivulatus	Density	ns	ns	d	dd	+	ns
	Biomass	ns	ns	dd	dd	ns	ns
	Mean weight	ns	+	ns	ns	ns	ns
S. schlegeli	Density	ns	ns	ns	dd	dd	ns
	Bimoass	ns	ns	ns	dd	dd	ns
	Mean weight	dd	ns	d	d	d	ns
S. sordidus	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	ns	ns	d	ns	ns
	Mean weight	ns	ns	ns	d	d	ns
Acanthuridae							
Acanthurus blochii	Density	ns	ns	ns	ns	ns	ns
	Biomass	dd	ns	ns	ns	ns	ns
	Mean weight	++	++	++	—	—	ns
A. dussumieri	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	ns	ns	ns	ns	ns
	Mean weight	++	+	++	–	dd	ns
A. nigricauda	Density	ns	ns	ns	d	ns	ns
	Biomass	dd	d	ns	d	ns	ns
	Mean weight	dd	ns	ns	ns	dd	ns
A. xanthopterus	Density	++	++	++	–	—	ns
	Biomass	++	ns	++	–	—	ns
	Mean weight	+	++	++	—	—	ns
Naso tuberosus	Density	ns	ns	++	–	—	ns
	Biomass	ns	ns	++	–	—	ns
	Mean weight	ns	++	++	—	—	ns
N. unicornis	Density	++	++	+	—	—	–
	Biomass	+	++	+	–	—	ns
	Mean weight	ns	+	d	ns	d	–
Siganidae							
Siganus doliatus	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	ns	ns	ns	ns	ns
	Mean weight	dd	dd	ns	ns	+	ns
S. lineatus	Density	ns	ns	ns	ns	ns	ns
	Biomass	ns	ns	ns	ns	ns	ns
	Mean weight	ns	—	—	++	++	++
S. punctatus	Density	++	+	+	—	—	ns
	Biomass	++	++	++	—	—	ns
	Mean weight	ns	ns	+	ns	d	ns

Table 8. Densities (fish m^{-2}) and biomass (g m^{-2}) obtained for some fish taxa in the Indo-Pacific area (values with * considered all fish species, including the non-commercial ones).

Area	Type of reef	Taxa	Density	Biomass	Method (and source)
Hawaii	Fringing	Acanthuridae	0.04	2.7	Rotenone
		Total	3.1*	106*	(Brock et al. 1979)
Chesterfield Islands	Fringing	Serranidae	0.01	3.0	Visual counts
		Lutjanidae	0.002	3.7	(Kulbicki et al. 1990)
		Lethrinidae	0.09	8.4	
		Scaridae	0.18	13.1	
		Acanthuridae	0.16	22.4	
		Siganidae	0.016	1.6	
		Total	2.6*	140*	
Great Barrier Reef	Outer reef	Serranidae		7.7	Explosive
		Lutjanidae		2.8	(Williams & Hatcher 1983)
		Lethrinidae		1.9	
		Scaridae	0.036	9.6	
		Acanthuridae		24.0	
		Siganidae		1.4	
		Total	3.2*	156*	
Mayotte	Barrier	Serranidae	0.038	28.8	Visual counts
		Lutjanidae	0.068	9.1	(Letourneur 1996b)
		Lethrinidae	0.009	2.8	
		Scaridae	0.130	19.9	
		Acanthuridae	0.224	31.3	
		Total	3.7*	202	
Kenya	Fringing	Serranidae	0.005	6.5	Visual counts
		Lutjanidae	0.016	7.8	(Samoilys 1988)
		Lethrinidae	0.007	2.5	
Yap	Atoll	Scaridae		5.05	Exhaustive fishing
		Acanthuridae		5.06	(Smith & Dalzell[4])
Ouvéa	Barrier	Serranidae	0.03	14.2	Visual counts
		Lutjanidae	0.09	24.9	(Kulbicki et al. 1994)
		Lethrinidae	0.1	14.9	
		Scaridae	0.13	55.9	
		Acanthuridae	0.27	56.1	
		Signidae	0.02	3.2	
		Total	0.7	187	
SW of New Caledonia	Barrier	Serranidae	0.016	3.0	Visual counts
		Lutjanidae	0.01	3.0	(Kulbicki et al. 1995)
		Lethrinidae	0.06	8.2	
		Scaridae	0.12	18.7	
		Acanthuridae	0.09	15.3	
		Siganidae	0.02	2.4	
		Total	0.7	182	

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[4] Smith, A. & P. Dalzell. 1993. Fishery resources and management investigations in Woleai atoll, Yap State, Federal States of Micronesia. SPC Inshore Fish. Res. Proj. Tech. Doc., Nouméa 4. 64 pp.

is in the order of 45 000 tons (Labrosse et al. 1996). This low fishing pressure most likely played a highly significant role. Indeed, a comparison between our density and biomass results with those of other coral reef areas (Table 8) indicates that densities were not exceptionally high in the northern lagoon of New Caledonia (Tables 1, 4), but biomasses were much higher in our study than on other coral reefs. This underlines the unusually large sizes, and consequently mean weights, of most species in the sampled areas, in particular the largest species (Labrosse et al. 1996).

Several factors might cause and maintain differences in commercial reef fish community structure. The observed pattern could be the result of (i) differential availability of recruits across the northern lagoon, (ii) habitat selection by recruits, (iii) differential survivorship after settlement, (iv) main lagoonal current, (v) length of the reefs, and/or (vi) coastal pollution due to mining activities. The interactive nature of these four first factors is likely, as observed in various geographical areas (Choat et al. 1988, Doherty & Williams 1988, Sale 1991, Planes et al. 1993, Letourneur 1996a). However, recruitment and settlement processes, and lagoonal currents in the studied area are totally unknown. It is thus impossible to estimate the contribution of each of these factors, either singly or in combination, to overall variability.

The length of reefs may be a complementary explanation, as longer coral reefs usually provide a larger number of micro-habitats for fishes (Sale & Douglas 1984, Galzin 1987, Galzin et al. 1994, Letourneur 1996a). In the northern lagoon of New Caledonia, both western and eastern barrier reefs are very extensive and reticulated, and interrupted only by few passes. Conversely, both lagoonal and fringing reefs are more patchily distributed. However, total diversity and mean diversity per transect did not vary greatly between habitats; the greatest difference occurred for biomass values.

Consequences of the mining activities on coastal communities are weakly documented in New Caledonia. Nevertheless, it is obvious that these activities increase the risks of unusual high terrestrial runoff and hypersedimentation of coastal areas during rainfall episodes, particularly when hurricanes pass over the island. The role of concentrations of heavy metals (mainly nickel, but also chromium and iron) in the coastal sediments and communities was reviewed by Duhet[2]. Invertebrates, such as echinoderms and molluscs, are particularly sensitive to heavy metals. Contamination to superior trophic levels such as fishes exists, but bioconcentration, toxicity, physiological and/or ecological impact are not demonstrated in New Caledonia (Duhet[2], personal communication). Although it remains to be confirmed, it is probably correct to assume that these mining activities do not favour fish communities and the coastal environments in which they live. A first step to test this hypothesis is to analyze the role of terrestrial influence on fish communities and populations.

Influence of terrestrial gradient

Although some works mention the role of terrestrial runoff gradients in structuring reef fish communities (Williams 1982, Williams & Hatcher 1983, Russ 1984, Ayling & Ayling[3], Wantiez et al. 1997), none of them provided quantification of this phenomenon and/or correlations between fish and terrestrial influence descriptors. On the Australian continental shelf, it appeared that mid-shelf reefs support higher diversity, density and biomass than outer and inshore reefs (Williams 1982, Williams & Hatcher 1983, Russ 1984). Although most families of fish followed this trend, some such as Chaetodontidae, Labridae and Acanthuridae increased in diversity from inshore to outer reefs (Williams & Hatcher 1983). These authors also found that the biomass of Acanthuridae was significantly higher on outer shelf reefs, those of Siganidae and Serranidae significantly higher on inshore reefs, whereas biomass of Scaridae and Lethrinidae picked on mid-shelf reefs. Russ (1984) found similar trends in diversity and density of herbivorous grazing fishes.

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[2] Duhet, D. 1992. Les métaux dans l'environnement marin de la Nouvelle-Calédonie. Tech. Rep. ORSTOM-Nouméa. 128 pp.

[3] Ayling, A.M. & A.L. Ayling. 1986. A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Marine Park. Rep. GBRMP Authority. 61 pp.

Within a family, differences in patterns appeared between species. For the Serranidae, *Plectropomus leopardus* peaked in abundance on mid-shelf reefs, whereas *P. maculatus* was more abundant on inshore reefs (Williams & Hatcher 1983, Ayling & Ayling[3]).

In the present study, the role of terrestrial influence descriptors appeared to be statistically significant for the total ichthyofauna and major families, as well as for numerous common species, and strongly contrasts with the low number of significant correlations previously found with substrate variables (Labrosse et al. 1996). A possible explanation to this may be linked to the fact that most of the commercial reef fish species are not sedentary. Relationships between fish and substrate variables have been mainly established for small and/or territorial species, such as Chaetodontidae (Bell & Galzin 1984, Bouchon-Navaro & Bouchon 1989, Roberts et al. 1992) or Pomacentridae (Sano et al. 1987, Williams 1991, Chabanet & Faure 1994). These relationships may be more difficult to demonstrate for mobile species which are more free-ranging. One exception to high mobility are the Serranidae, which are mainly characterized by sit-and-wait type behavior. This was corroborated by the positive correlation found between density of fish of this family and hard substrates, because these fish occurred mainly near coral colonies or rocky shelters (Labrosse et al. 1996). For large commercial species, our work indicates that it may be more efficient to consider variables other than substrate variables, such as terrestrial influence descriptors, in order to define the relationships between commercial reef fish (also including Serranidae) and their environment.

For most species studied, no significant ontogenetic shift appeared in the distribution of individuals. Only two exceptions were found, *Plectropomus leopardus* and *Scarus ghobban*, for which juveniles were more abundant on fringing reefs than in other areas, with larger sized individuals being found offshore. This result suggests either differences in growth rates according to terrigeneous influence or a migration of individuals of these species from coastal fringing reefs to barrier reef as fish size increases. Differential growth rates between habitats have been recorded for reef fishes, such as for *Dascyllus aruanus* in southwestern lagoon of New Caledonia, but links with terrestrial influence did not appear in all cases (Baillon 1990).

Ontogenetic migrations of fishes between habitats are relatively well documented, but involve mainly differences in vertical distribution, with juveniles usually occurring in shallower waters than conspecific adults (Harmelin-Vivien 1984, Galzin 1987). Size differences according to other gradients are less well documented (Ayling & Ayling[3], Kulbicki 1988). On the Australian continental shelf, larger individuals of *Plectropomus leopardus* were found on outer reefs whereas smaller sizes were observed on mid-shelf reefs (Ayling & Ayling[3]). Nevertheless, ontogenetic migrations between these Australian reefs remain unlikely due to the large distances between them, the depth and the unsuitable substrate between reefs. In New Caledonia, the hypothesised ontogenetic migration across the lagoon is partly supported, at least for *P. leopardus*, by catches of individuals of median size over lagoonal soft-bottoms by longlines in both northern (unpublished data) and southwestern lagoons (Kulbicki 1988), and by underwater visual observations similar to ours in the SW lagoon and at Ouvéa (Kulbicki et al. 1994). Although not confirmed, we presume that this habitat partitioning along the terrestrial gradient may be linked to an intraspecific competition for food, possibly in combination with changes in feeding behavior or ecological requirements over the lifespan of these fishes. This also suggests that responses of a fish population or community to terrestrial influence may vary according to an ontogenetic pattern.

Most herbivorous fish families or species usually display higher affinities for clear waters than for turbid ones (Williams & Hatcher 1983, Russ 1984), despite the fact that some species, such as siganids, may show an opposite pattern. Among carnivorous species, some are known to present strong oceanic affinities, such as the voracious piscivore *Lutjanus bohar* (Williams & Hatcher 1983). Our results clearly confirm these trends; indirect measures of terrestrial influence, such as distance to coast or visibility, were in fact as efficient as the direct ones (i.e. percentage of mud, granulometry, a.s.o.) to quantify the role of terrestrial gradients.

In the relatively isolated atoll of Ouvéa, which is about 100 km off northern New Caledonia, the Siganidae are poorly diversified (3 species vs. 11 in northern fringing reefs) and their stocks are not abundant (0.018 indiv. m^{-2} vs. 0.079 indiv. m^{-2}), whereas other herbivores such as Acanthuridae and Scaridae do not differ in diversity and density (Kulbicki et al. 1994). Few differences appear in structure of Acanthuridae and Scaridae population stocks between New Caledonia (large terrigeneous influence) and French Polynesia (low to very low terrigeneous influence), whereas Siganidae strongly decrease in diversity and density (Kulbicki & Rivaton 1997). The duration of larva period of Siganidae is similar to that of other species which have efficiently colonized remote atolls or small islands, such as Ouvéa or French Polynesia. These two examples, combined with those others cited above, illustrate the importance of emerged lands and terrestrial gradients as determining structure of coastal reef fish communities and their ecological and trophic functioning.

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