Fish stock assessment of the northern New Caledonian lagoons: 1 – Structure and stocks of coral reef fish communities

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Abstract — Lagoon fish in New Caledonia are mainly caught by artisanal fisheries and subsistence fishing. Reef fish are the major component of this catch. The present study aimed at estimating these reef fish standing stocks and at finding the main factors influencing the distribution of these fish. Sampling of 904 stations was stratified according to three zones (north, east and west) and three reef types (barrier, intermediate and fringing). Fish communities exhibited strong heterogeneity in their distribution, showing higher biomass (maximum of 447 g·m^{-2}) and total standing stock (43 000 tonnes) in the north zone than in the east and west zones. Similarly, observed patterns were dependent on reef types: higher biomass and total standing stock being observed on barrier reefs than on intermediate or fringing reefs. The total standing stocks, which were about 65 000 t, were mainly composed of herbivorous fish families such as the Acanthuridae and Scaridae. The differences in the patterns of distribution of species, individuals and standing stocks between reef types may be explained by variations in terrestrial influences and reef morphology, whereas differences among zones were most likely due to accessibility of fishing areas and fishing pressure. The latter is almost non-existent in the north zone, which can thus be considered to be almost unexploited commercially. This most likely explains the high proportion, 77 %, of long-lived species in the biomass of this zone. The results might have implications in management of reefs elsewhere in the South Pacific, for which similar data are only scarcely available. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Reef fish / commercial demersal fish / population structure / New Caledonia / SW Pacific Ocean

Résumé — Estimation des stocks de poisson des lagons de Nouvelle-Calédonie : 1 – Structure et stocks des communautés des poissons de récifs. Les poissons de lagon de Nouvelle-Calédonie sont exploités par les pêcheries artisanales, dont les poissons de récifs constituent la majeure partie de ces captures. Ce travail vise à estimer les stocks de ces poissons récifaux et à déterminer les principaux facteurs qui influencent leur distribution. L'échantillonnage de 904 stations a été stratifié en fonction de trois zones (nord, est et ouest) et de trois types de récif (barrière, intermédiaire et frangeant). Les peuplements de poissons ont montré une très forte hétérogénéité dans leur répartition de la biomasse et des stocks. Dans la zone nord, ces valeurs ont été bien supérieures (jusqu'à 447 g·m^{-2}, et stocks de 43 000 tonnes) à celles des zones est et ouest. La distribution de ces peuplements est également fonction du biotope considéré, de plus fortes densités et biomasses étant relevées sur les récifs barrières, par contraste avec les récifs intermédiaires et frangeants. La majeure partie du stock total, qui est de l'ordre de 65 000 t, est constituée d'espèces herbivores d'Acanthuridés et de Scaridés. Les principales causes des différences observés dans la répartition des espèces et des individus, ainsi que des stocks entre types récifaux seraient liées à des différences d'apports terrigènes et de morphologie récifale, tandis que les différences relevées entre les trois zones sont davantage liées à l'accessibilité des ressources et à la pression de pêche. Cette dernière est très faible dans la zone nord, qui peut être considérée comme inexploitée. Cela expliquerait la forte proportion, 77 %, des espèces à longue espérance de vie de la biomasse totale de cette zone. La gestion des pêcheries artisanales dans l'ensemble du Pacifique Sud, où les données sont rarement disponibles, implique la prise en compte de ces observations. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Poissons de récifs / poissons démersaux commerciaux / structure de population / Nouvelle-Calédonie / océan Pacifique

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1. INTRODUCTION

In coral reef ecosystems, fish are usually the most important resource, especially for developing countries in the Pacific and Caribbean where they may constitute the major protein supply. Unfortunately, most coral reefs across the world are increasingly subjected to various types of human pressures [8, 14, 47], which almost always result in a decline in reef health [40]. Despite the lack of data on pristine situations, it is generally accepted that an increase in fish consumption, mainly linked to demography, results in a concomitant increase in fishing pressure on the coral reefs of various geographical areas [16, 17, 19, 41, 44]. In several cases, overfishing has occurred, or will be reached in the very near future, and is considered one of the most serious threats to coral reefs [37, 38, 41]. However, contrary to general opinion, studies on the effects of fishing on fish communities are scarce and are usually too recent to allow a good understanding of these phenomena [15, 16, 19, 43, 44]. Indeed, fishing effects are widely treated as equivalent to overfishing and thus many studies of fishing effects have been based upon studies of localized catastrophic events rather than changes linked to fishing under normal conditions [17]. In addition, most studies have compared variations in density and biomass among sites and years to assess fishing effects on the ichthyofauna, whilst other basic data from the same areas, such as stock estimates, catches or CPUEs, are seldom simultaneously available. Therefore, relationships between ecological and fisheries-dependent data are difficult to establish. The description of such relationships is nevertheless needed to understand how fisheries characterized by complex fish communities may evolve.

We conducted a stock assessment of lagoonal and reefal demersal fish of commercial interest at the request of the Northern Province of New Caledonia in the SW Pacific Ocean. In this province, human density is low, 4.2 inhabitants·km^{-2}, especially when compared to those found on other Pacific islands: 34 inhabitants·km^{-2} in Palau, 132 in Tonga, 271 in Guam and 505 in Nauru [9]. If we consider this low density, the artisanal nature of the local fisheries and the very large area (15 000 km^2) of the lagoons of this province, we can make the hypothesis that, overall, local fish communities of commercial interest are not substantially depleted by fishing activities. However, the fish communities of this province have never been studied, except for two specific and spatially limited works focusing on bait-fishes for tuna fisheries [7] and on soft-bottom fishes [50].

The main objectives of the whole study (e.g. this paper and the two companion ones [22, 27]) were as follows: to define the structure of fish communities at different spatial scales (whole province, three main zones, three main biotopes); to provide estimates of both total and exploitable stocks for the whole community and major fish families; and to analyse the

relationships between field data and the existing and expected socio-economic aspects of the fishery. This is the only way to test our hypothesis that these fish communities are not overfished. The three major biotopes (e.g. coral reefs, near-reef areas and lagoon bottoms) examined in this whole study display considerable differences in their ecological characteristics. This is the reason why they were censused with different methods.

The present paper focuses on reef fish, which were studied by visual censuses, whereas the near-reef and the lagoon bottom areas, which were investigated with line-fishing techniques, are presented in the first companion article [22]. Field techniques provide valuable ecological information but give little information on the relationships between human and fish populations. Despite their fundamental importance, primarily for island nations, the social and economic aspects sensu lato of reef fisheries have been almost systematically neglected or at least underestimated [36]. This lack of information on these aspects may explain many failures in management options on coral reef areas [1, 9, 18, 35]. This topic was studied in the second companion article [27], particulary because in New Caledonia there is strong customary tradition that greatly influences fishing activities. The whole study conducted over a period of two and a half years constitutes one of the largest works of this kind ever conducted in the Indo-Pacific region on multispecific lagoonal and reefal fish communities with different techniques and at such a large spatial scale.

2. MATERIALS AND METHODS

2.1. Study area and sampling zones

New Caledonia is located in the south-western Pacific Ocean (*figure 1*), and coral reefs are well developed around this island. The present work was conducted on the coral reefs of the Northern Province of New Caledonia (*figure 1*). Three main zones were defined according to natural partitions: the north, the west and the east zones. The area studied covers approximately 10 000 km^2 of lagoonal waters, including about 700 km^2 of coral inner reef slopes. The northern limit of this study was 19°30'S.

In each zone, the three existing reef types were sampled. There were, from land outwards to open ocean: the coastal fringing reefs, the intermediate reefs (e.g. the reefs close to lagoonal islets), and the barrier reefs. A regular sampling strategy was adopted on the entire reef system of the area covered. Stations were chosen approximately 0.6 nautical miles apart from one another for each reef type. The sampling effort in each zone and reef type was thus proportional to the length of the coral reefs [28]. In addition, the number of stations was adapted to the estimated surface of reef slopes at the sampled depths (2–8 m on average) [28], resulting in a higher number of samples in areas with low reef slopes than in those with abrupt reef slopes.
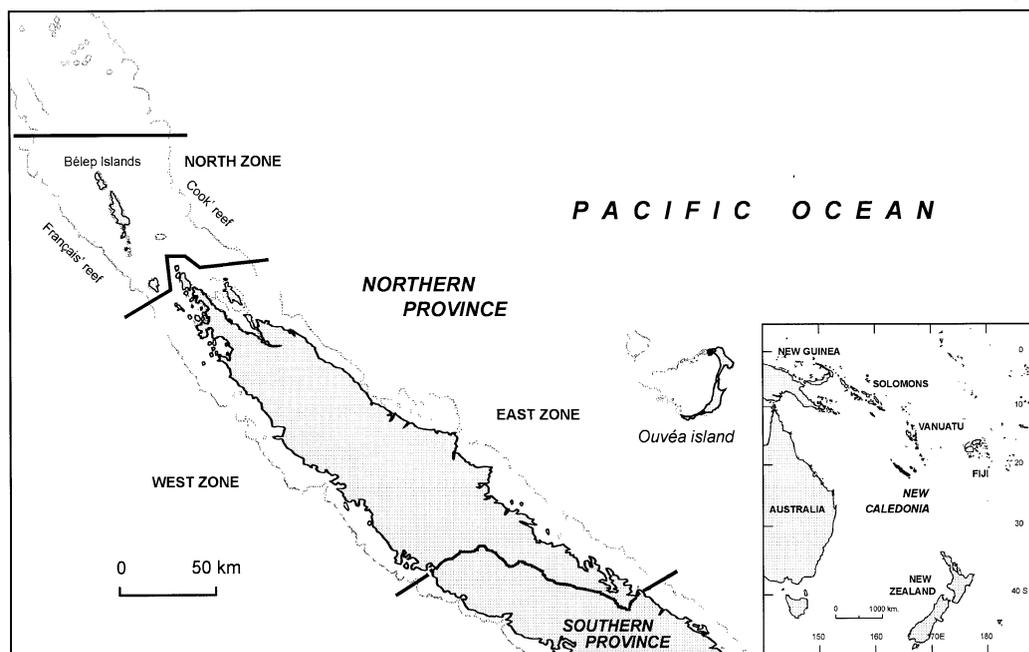
Figure 1. Location of the studied lagoons of the Northern Province of New Caledonia, in the south-western Pacific Ocean.

Sampling was conducted between February and April 1995 using the R/V 'Alis' for the north zone, between July 1995 and January 1996 using a smaller boat and motorized canoes for the west zone, and between March 1996 and February 1997 for the east zone, also using a small boat and motorized canoes. A total of 904 stations were investigated on coral reefs during the whole study.

2.2. Fish sampling technique

In a multispecific context, it is often difficult to define what is precisely a commercial species. In New Caledonia, almost all species belonging to the major coral reef fish families of interest (e.g. Serranidae, Lutjanidae, Lethrinidae, Scaridae, Acanthuridae and Siganidae) are caught. In addition, several species belonging to the families Carangidae, Haemulidae and Labridae are also regularly targeted. All these species were therefore censused and considered as commercial for the purpose of our study. They were studied by underwater visual censuses using the line-transect method [5] in the 2–8-m depth range. This census method is derived from terrestrial procedures. Its precision and accuracy for underwater work has been previously demonstrated [11, 21] and utilized by several authors [20, 23, 32, 34]. On each station, two divers censused fishes along a 50-m transect, one on each side of the transect line. The observers counted all commercial fish, and recorded the estimated perpendicular distance between the fish and the transect line. Density and biomass estimates (see below) are based on the detectability functions of species. These parameters are usually better estimated for commercial fish species by the method we used than by fixed-width transects or fixed-radius point counts [21]. The size of fish (total length) was estimated using 1-cm classes for fish ranging from 1 to 10 cm, 2-cm classes for fish ranging from 10 to 30 cm, 5-cm classes for fish from 30 to 60 cm, and 10-cm classes for fish larger than 60 cm. Increasing size classes is recommended for increasing fish size [3]. If fishes were in a school or a group, their number was estimated and the perpendicular distance of the closest fish and the furthest fish was recorded. Despite usual bias of visual census, this method is particularly efficient in biotopes where human visits (diving, spearfishing, etc.) are rare, because the behaviour of fish remains natural [21].

2.3. Demographic structures

Each fish may be assigned to one demographic category, according to the main characteristics of the species to which it belongs. The knowledge of the biological and ecological characteristics for the species of New Caledonian reefal and lagoonal waters [24] allowed us to define three main demographic categories: species with a short life-span (characterized by fast growth, small size, high gonado-somatic index and early reproduction), species with a long life-span (characterized by slow growth, large size, low gonado-somatic index and late reproduction), and species with intermediate characteristics [24]. The demographic structure, expressed in terms of density and biomass, is a useful parameter for understanding differences in fish community patterns, even when

restricted to only commercial species. Indeed, this allows prediction of the major descriptors of the response of fish communities to potential disturbances which might affect them [26, 31].

2.4. Data analyses

Data of the two observers cannot be used as replicates because the environment within a station may be heterogeneous (for example, when the census was carried out 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. Among the many density estimators that may be chosen [6], the most robust for this type of data is [51]:

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

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

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

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

The weight of fish was calculated from length/weight relationships as previously defined [33]. Biomass can be calculated in a similar way to density:

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

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

A principal component analysis (PCA) was applied for the 904 stations to the three 'global' fish descriptors (i.e. species richness, density and biomass) which were normalized due to their different natures. The heterogeneity of dispersion was tested with random permutations of stations between the nine areas (e.g. 3 zones × 3 reef types) [42]. The data met the Levene's test criteria (homogeneity of variances) [48], and two-way ANOVAs (zone × reef type) were then performed on the different types of data (species richness, density and biomass). Reef types were considered as nested within the zones. A posteriori differences among zones were tested by Scheffé tests. If a significant nested effect is detected, it is not possible to use post hoc tests to assess the global reef type effect (e.g. for all zones pooled together). However, in this case it is possible to test the reef type effect within each zone, using a posteriori SNK tests. The surface areas of the studied sites (i.e. the slopes of the three reef types and the three zones) were obtained with both marine maps from the Mission Océanographique du Pacifique and aerial

photographs from the Institut Géographique National. The stocks were estimated by:

$$S_i = A_i \times B_i$$

where S_i is the stock for zone or reef type i (tonne), A_i is the surface area of zone or reef type i (km^2), and B_i is the mean biomass in zone or reef type i (g·m^{-2}, which is equivalent to tonne·km^{-2}).

3. RESULTS

3.1. Spatial structure of the whole commercial ichthyofauna

The ANOVAs indicated that the factors 'zone' and 'reef type' were statistically significant on the patterns found (*table I*). The mean species richness and mean biomass per census were significantly higher in the north zone than in the two others (*table II*). The mean density was highest in the west zone, and lowest in the east zone (*table II*), but the difference between these values was not statistically significant (*table I*). The highest values of mean species richness, density and biomass were found on barrier reefs (*table II*), and patterns were significant except for densities between barrier and intermediate reef (*table I*). There were also significant interactive effects between zones and reef types (*table I*), mainly underlining that differences between reef types for the three descriptors tested (species richness, density and biomass) within each zone were, globally, similar to differences for all zones pooled together.

Table I. Summary of ANOVAs involving species richness, density and biomass of the total ichthyofauna. In each case, the first line indicates the result of the ANOVA and the second the post hoc planned comparison (Scheffé tests). For reef type effect within zone, SNK tests were used for pairwise comparisons among treatments. N, north zone; W, west zone; E, east zone; B, barrier reef; I, intermediate reef; F, fringing reef; Fr, Français' barrier reef; Co, Cook's barrier reef; and Li, lagoonal islands.

Source of variation	Species richness	Density	Biomass
Zone effect	$P < 0.0001$	ns	$P < 0.0001$
	N > E > W		N > W > E
Reef type effect	$P < 0.0001$	$P = 0.0051$	$P < 0.0001$
		B = I > F	
Reef type effect within zone			
North	ns		Fr = Co > Li[a]
West	B > I > F		B > F > I
East	B = I > F		B > I > F

[a] In the north zone, both the Français' and the Cook's reefs are barrier reefs. The term 'lagoonal islands' includes fringing reefs (Bélep Islands) and also a few intermediate ones (see *figure 1*).

Table II. Total species richness, mean species richness, mean density ($\times\ 10^{-4}$ indivuals$\cdot$m^{-2}) and mean biomass (g$\cdot$m^{-2}) per census on the different reef types of each major zone sampled. Values in parentheses are confidence intervals at $\alpha = 5\ \%$ level.

	No. of stations	Total no. of species	Mean species richness	Mean density	Mean biomass
North zone[a]					
Français' reef	60	143	28.2 (2.0)	491 (70)	447 (103)
Lagoonal islands	76	159	27.7 (2.1)	520 (89)	231 (43)
Cook's reef	38	131	30.4 (3.2)	693 (108)	390 (87)
Total	174	187	28.4 (1.4)	541 (61)	339 (68)
West zone					
Barrier reef	109	193	27.3 (1.6)	757 (55)	343 (35)
Intermediate reef	110	174	20.6 (1.8)	635 (37)	167 (20)
Fringing reef	68	144	17.2 (2.0)	436 (40)	270 (28)
Total	287	226	22.4 (1.1)	622 (36)	258 (21)
East zone					
Barrier reef	126	187	28.0 (1.6)	459 (66)	196 (33)
Intermediate reef	127	204	26.3 (1.8)	569 (97)	175 (23)
Fringing reef	190	210	20.7 (1.3)	445 (82)	115 (18)
Total	443	252	24.4 (1.0)	476 (58)	158 (16)
All zones					
Barrier reef	333	244	28.1 (0.9)	578 (82)	309 (68)
Intermediate reef	257	238	24.0 (1.3)	567 (94)	184 (36)
Fringing reef	314	220	21.1 (1.1)	438 (78)	152 (34)
Total	904	264	24.5 (0.7)	556 (65)	259 (63)

[a] In the north zone, both the Français' and the Cook's reefs are barrier reefs. The term 'lagoonal islands' includes fringing reefs (Bélep Islands) and also a few intermediate ones (see *figure 1*).

The PCA also revealed striking differences in communities (*figure 2*). The test of random permutations was highly significant ($P < 0.0005$), underlining that fish communities were significantly different between the nine areas studied.
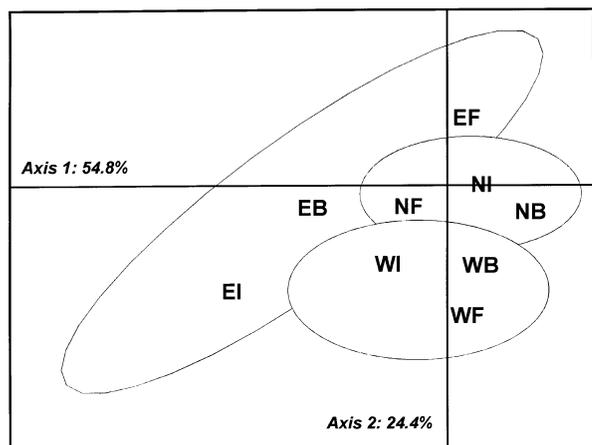
Figure 2. Plot of the first factorial plane of the PCA monitored on the normed data of species richness, density and biomass of the commercial fish from the 904 coral reef stations. Only the position of the centres of gravity are indicated as follows: EB, east zone barrier reefs; EI, east zone intermediate reefs; EF, east zone fringing reefs; NB, north zone barrier reefs; NI, north zone intermediate reefs; NF, north zone fringing reefs; WB, west zone barrier reefs; WI, west zone intermediate reefs; WF, west zone fringing reefs.

The short-lived species represented more than one quarter of the fish density in each zone, ranging from 26.4 % in the north zone to 36.7 % in the west zone (*table III*). Long-lived species were also abundant, mainly in the north zone where they constituted more than one third of the total density. The most abundant species in each zone belonged to the intermediate life-span categories, constituting up to 50.4 % of total density in the east zone (*table III*). A χ^2 test indicated that the demographic structures, expressed in terms of density, were significantly different between zones ($P < 0.05$). Patterns were different in terms of biomass, mainly because long-lived species represented a more important part of the fish communities of commercial interest than for densities (*table III*). These species represented about half of the total biomass in the east zone, but were as high as 77.1 % of the total biomass in the north zone. Patterns among zones, in terms of biomass, were significantly different (χ^2 test; $P < 0.001$).

3.2. Spatial distribution of fish families and species

Patterns of density displayed marked differences according to families and zones (*figure 3*). In the west zone, Lutjanidae (0.131 individuals$\cdot$m^{-2}) and Scaridae (0.195) were significantly more abundant (SNK test, $P < 0.05$) than in the two other zones. A similar pattern was found in the east zone for Lethrinidae (0.043 individuals$\cdot$m^{-2}) and Siganidae (0.055); whereas Acanthuridae were significantly (SNK test, $P < 0.01$)

Table III. Demographic structure of the commercial fish communities in the three main zones, expressed (A) in percentage of density and (B) in percentage of biomass (all reef types pooled).

	North	West	East
(A)			
Short life-span	26.4	36.7	28.3
Intermediate life-span	39.1	43.7	50.4
Long life-span	34.5	19.6	21.3
(B)			
Short life-span	4.9	14.0	10.9
Intermediate life-span	18.0	24.5	36.4
Long life-span	77.1	61.5	52.7

more abundant in the north zone (*figure 3*). Acanthuridae, Scaridae and Lethrinidae displayed increasing densities from fringing to barrier reefs. An opposite trend was found for Siganidae, whereas Lutjanidae were significantly more abundant (SNK test, $P < 0.01$) on intermediate reefs (*figure 3*). The total biomass was significantly lower in the east zone than in the two other zones (SNK test, $P < 0.05$), and the magnitude of the between zone differences was more marked than for densities (*figure 4*). This indicates that fish reached larger mean sizes in the north zone [32]. Similar trends were observed for most families, although differences between east and west zones were significant only for Lutjanidae and Acanthuridae ($P < 0.05$). Biomass was particularly high in the north zone for Acanthuridae (105 g·m^{-2}), Scaridae (103) and, to a lesser extent, Serranidae (25). As for density, total biomass increased from fringing reefs to barrier reefs (*figure 4*).

This pattern was also similar for most of the other families, except for Siganidae and Lutjanidae. Siganids displayed lower biomass on barrier reefs while lutjanids showed no significant pattern (SNK test, $P > 0.05$) among reef types.

Not surprisingly, most species displayed a pattern of distribution similar to the family to which they belong. In most cases, mean weight of individuals, density and/or biomass were significantly higher in the north zone than in the two others, the west zone displaying intermediate values, such as for *Plectropomus leopardus*, *Lutjanus bohar*, *Cheilinus undulatus*, *Scarus microrhinos* and *Naso unicornis* (*table IV*). Some other species displayed higher values for these descriptors in the west zone, such as *Siganus lineatus*. *Lethrinus nebulosus* was the only species to show higher density in the east zone, but this difference was not statistically significant ($P > 0.05$) (*table IV*).

Differences among reef types were also marked (*table IV*), thus highlighting an important land/ocean gradient for most species. Mean weight of individuals, density and biomass were higher on barrier reefs than on intermediate and coastal fringing reefs, for *L. bohar*, *C. undulatus* and *N. unicornis*. Some species had their highest descriptor values on fringing reefs, such as *Siganus lineatus* for density, and others on intermediate reefs, such as *P. leopardus* for biomass, whereas their mean weight was significantly higher ($P < 0.05$) on barrier reefs (*table IV*).

3.3. Standing stock estimates

The total standing stock on the inner coral reef slopes of the whole Northern Province could be
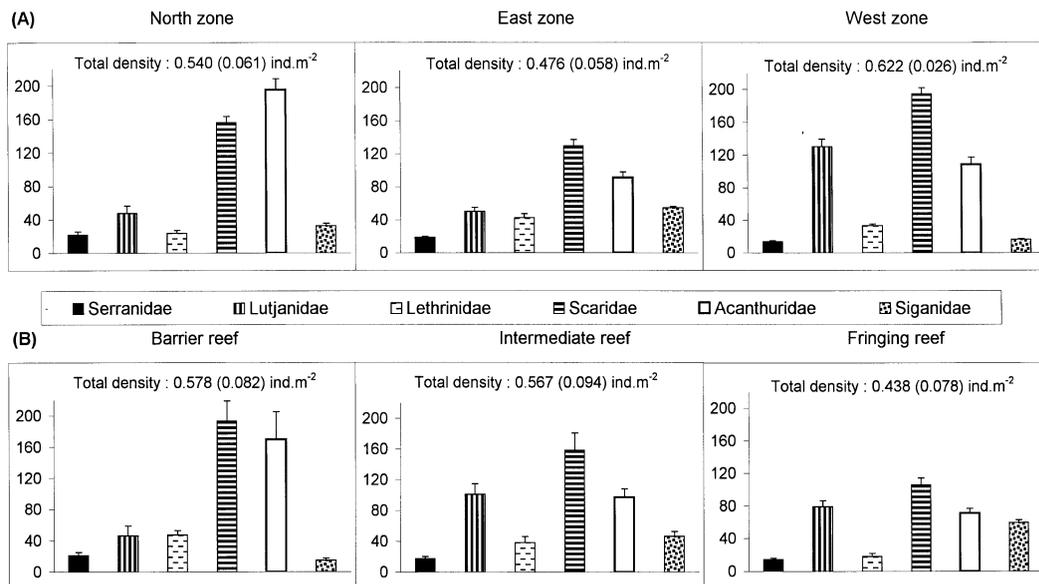
Figure 3. Mean densities of six major commercial fish families on (A) the three main zones, and (B) on the three main reef types. Vertical bars and values in parentheses are confidence intervals at α = 0.05.
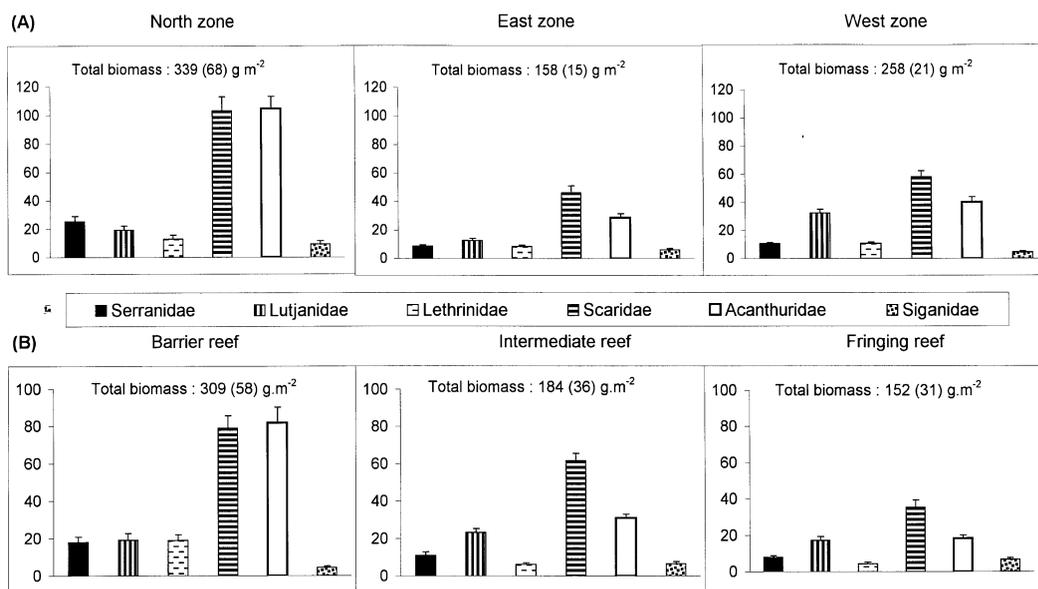
Figure 4. Mean biomass of six major commercial fish families on (A) the three main zones, and (B) on the three main reef types. Vertical bars and values in parentheses are confidence intervals at $\alpha = 0.05$.

estimated at 65 000 tonnes. The north zone is characterized by a very high total standing stock (43 000 tonnes), about six-fold higher than that of the east zone (7 500). The standing stock of Acanthuridae (10 640 tonnes), Scaridae (11 350) and, to a lesser extent, Serranidae (2 610) were particularly high in that zone (*table V*). Considerable differences appeared between standing stock of the three reef types. Total standing stocks were approximately eight-fold higher on barrier reefs than on both intermediate and fringing reefs (*table V*). Fringing and intermediate reefs have similar total stocks, as well as for the different families. Stocks were particularly high on barrier reefs for Acanthuridae (14 000 tonnes) and Scaridae (12 400).

4. DISCUSSION

4.1. Between-zone patterns

Several factors may be associated with the observed patterns, with possible combinations among them. Terrigeneous influence may be considered as a first factor. Several workers have mentioned terrigeneous impact as a factor influencing the structure of fish communities, but without any quantification/correlation of this phenomenon [2, 51, 52]. A previous study has clearly shown, however, that species richness, density and biomass of most fish families and/or species were correlated to a terrigeneous runoff gradient, the highest values being found in areas far from the coasts, although some particular species displayed higher affinities for coastal fringing reefs [32]. The present work strongly supports this view. The north

zone in particular experiences little terrigeneous runoff, which is in contrast with both the east and west zones where numerous rivers and large mangrove areas exist. In addition, the east coast is subjected to higher and more regular rainfall when compared to the west coast [34].

This observed pattern could also be the result of differential availability of recruits across the lagoons, habitat selection by recruits and differential survivorship after settlement, in combination with lagoonal currents. These factors are likely to occur in combination, as mentioned in works in various geographical areas [10, 30, 45]. However, as recruitment and settlement processes, and lagoonal currents in the studied areas are as yet unknown, it is presently impossible to estimate the contribution to overall variability from each of these factors, either singularly or in combination.

Reef morphology, in particular the length of reefs, may be another important factor for interpreting the high biomass values in the north. Longer and/or larger coral reefs usually provide a larger number of habitats and microhabitats for fish [12, 13, 30, 46]. Indeed, the barrier reefs in the north zone (both Cook's and Français' reefs, *figure 1*), are very extensive and reticulated with numerous coral heads and pinnacles, interrupted by few passes [32]. Conversely, barrier reefs in both east and west zones are not as reticulated and are interrupted by numerous passes.

However, the most important factor explaining the observed patterns is likely to be linked to fishing pressure. The whole Northern Province is characterized by very low human densities: about 41 500

Table IV. Mean weight (kg), density ($10^{-4} \times$ indivuals·m^{-2}) and biomass (g·m^{-2}) of some fish species in (A) the three zones and (B) three reef types. Values in parentheses are confidence intervals at $\alpha = 0.05$ ('+' indicates a value < 0.1). Statistical significance was tested with SNK tests for all pairwise comparisons among treatments ($\alpha = 0.05$).

Fish species		(A) Zones			
		North	West	East	Significance
Plectropomus leopardus	weight	1.51 (0.14)	1.06 (0.12)	0.89 (0.07)	N > W = E
	density	76 (12)	45 (4)	42 (7)	N > W = E
	biomass	11.5 (2.2)	4.6 (0.6)	3.8 (0.3)	N > W = E
Lutjanus bohar	weight	2.31 (0.24)	1.73 (0.22)	1.37 (0.18)	N > W > E
	density	38 (11)	17 (5)	15 (5)	N > W = E
	biomass	8.7 (2.4)	2.8 (0.3)	2.1 (+)	N > W > E
Lethrinus nebulosus	weight	1.42 (0.23)	0.68 (0.11)	0.44 (0.09)	N > W > E
	density	13 (7)	18 (9)	25 (15)	E = W = N
	biomass	1.9 (0.2)	1.3 (+)	1.1 (0.1)	N > W = E
Cheilinus undulatus	weight	15.03 (3.37)	8.93 (1.87)	9.01 (2.11)	N > E = W
	density	11 (4)	4 (1)	3 (1)	N > E = W
	biomass	16.8 (2.9)	3.3 (0.2)	2.7 (+)	N > W > E
Scarus microrhinos	weight	1.56 (0.18)	1.37 (0.15)	0.99 (0.06)	N = W > E
	density	89 (24)	50 (11)	49 (17)	N > W = E
	biomass	13.9 (2.5)	7.3 (1.0)	4.8 (0.7)	N > W > E
Naso unicornis	weight	1.36 (0.12)	1.13 (0.10)	0.72 (0.06)	N > W > E
	density	129 (17)	46 (7)	53 (14)	N > E = W
	biomass	17.5 (2.0)	5.7 (+)	3.9 (0.5)	N > W > E
Siganus lineatus	weight	0.45 (0.05)	0.73 (0.07)	0.21 (0.05)	W > N > E
	density	7 (4)	31 (5)	15 (5)	W > E > N
	biomass	0.3 (+)	2.2 (0.1)	0.9 (+)	W > E > N

Fish species		(B) Reef types			
		Barrier	Intermediate	Fringing	Significance
Plectropomus leopardus	weight	1.60 (0.33)	0.99 (0.26)	0.84 (0.23)	B > I = F
	density	36 (20)	66 (28)	47 (19)	I = F = B
	biomass	5.8 (0.3)	6.5 (0.3)	3.9 (0.1)	I = B > F
Lutjanus bohar	weight	1.95 (0.36)	1.76 (0.38)	0.52 (0.13)	B = I > F
	density	40 (23)	9 (5)	7 (3)	B > I = F
	biomass	7.8 (0.6)	1.6 (+)	0.4 (+)	B > I > F
Lethrinus nebulosus	weight	0.94 (0.16)	0.42 (0.10)	0.35 (0.09)	B > I > F
	density	23 (11)	25 (9)	30 (12)	F = I = B
	biomass	2.2 (0.2)	1.1 (0.1)	0.8 (+)	B > I > F
Cheilinus undulatus	weight	13.41 (2.79)	4.91 (1.33)	0.79 (0.15)	B > I > F
	density	11 (6)	2 (1)	1 (1)	B > I > F
	biomass	14.1 (0.8)	0.9 (+)	0.1 (+)	B > I > F
Scarus microrhinos	weight	1.71 (0.18)	0.96 (0.06)	0.99 (0.07)	B > F = I
	density	62 (21)	69 (19)	35 (11)	I = B > F
	biomass	10.6 (1.1)	6.7 (0.7)	3.5 (0.3)	B > I > F
Naso unicornis	weight	1.25 (0.12)	0.86 (0.06)	0.58 (0.04)	B > I > F
	density	108 (23)	48 (11)	35 (10)	B > I = F
	biomass	13.5 (1.1)	4.1 (0.4)	2.0 (0.2)	B > I > F
Siganus lineatus	weight	0.08 (+)	0.56 (0.06)	0.68 (0.06)	F > I > B
	density	2 (2)	20 (6)	40 (7)	F > I > B
	biomass	0.1 (+)	1.1 (0.1)	2.7 (0.2)	F > I > B

inhabitants in total, including only 900 persons in the Bélep Islands (north zone, see *figure 1*). In the north zone, only 28 tonnes of fish are caught each year, which is negligible compared to the standing stocks found, even though the commercialized part of these catches (e.g. 2 tonnes versus 26 tonnes of subsistence fishing) must be considered with caution [27]. One can thus estimate that fish stocks in the north zone are almost non-exploited. The high percentage of long-lived species in this zone largely supports this view, in particular because these types of species are usually those targeted in tropical artisanal fisheries [21, 40]. Conversely, both the west and east zones are subjected to a higher fishing pressure [27].

4.2. Between-reef type patterns

The possible causes of differences between reef types are likely to be similar in nature to those explaining between-zone patterns, only the particulari-

Table V. Total standing stocks (in tonnes) and stocks of six fish families (A) in the three geographical zones and (B) in the three reef types. Values in parentheses are confidence intervals at $\alpha = 0.05$.

	(A) Zones			(B) Reef types		
	North	West	East	Barrier	Interm.	Fringing
Total	43 000 (7 500)	14 500 (1 000)	7 500 (1 000)	51 700 (1 550)	6750 (550)	6 550 (580)
Serranidae	2 610 (460)	600 (65)	420 (45)	3030 (510)	340 (50)	260 (40)
Lutjanidae	2 040 (400)	1 870 (180)	690 (60)	2 810 (500)	1 160 (165)	630 (75)
Lethrinidae	1 350 (260)	580 (60)	490 (40)	2 050 (350)	220 (25)	160 (30)
Scaridae	10 640 (1 800)	3 280 (215)	2 110 (210)	12 410 (1 950)	2 170 (200)	1 450 (100)
Acanthuridae	11 350 (2 000)	2 640 (320)	1 690 (135)	14 000 (2 840)	970 (70)	610 (75)
Siganidae	970 (200)	260 (25)	300 (35)	980 (155)	260 (70)	290 (35)

ties of the reef types are evoked here. The large surfaces of barrier reefs in the north zone, in combination with the high biomass in this zone, obviously contribute significantly to the large standing stocks found on barrier reefs. Conversely, fringing and intermediate reefs have a more patchy distribution, and their areas are consequently smaller. In addition, the barrier reefs are much more extensive and reticulated than both fringing and intermediate reefs, thus likely providing a larger number of microhabitats for fish [12, 13, 30, 46].

As previously mentioned, there are known links between terrestrial runoffs and the structure of fish communities. In particular, densities and biomass of species of commercial interest are higher on barrier reefs subjected to low terrestrial inputs [32]. In coastal areas, reefs located near mangroves have low fish biomass, in relation with high turbidity [49]. However, terrigeneous influence is not a simple factor. Indeed, within coastal reefs, it was found that reefs subjected to land erosion, mainly as a consequence of open fit mining, tended to support higher densities and biomass than reefs subjected to low terrigeneous inputs, possibly due to an increase in productivity through nutrient enrichment [34, 39].

The observed patterns may also be linked to the differential accessibility of the various reef types to fishermen. Although approximately 95 % of the artisanal fishing fleet is motorized, many fishermen do not like to fish on barrier reefs far from the coasts. This is particularly true for the fishermen in the north zone, where the Français' and Cook's reefs are far away from the land, and in any case fish are sufficiently abundant in areas closer. Although not frequently observed, this fear of fishing away from the land has also been observed in some barrier reef areas not very far offshore (both on west and east zones) which have numerous coral heads representing navigation hazards.

4.3. Fish stocks

When comparing fish stocks, one should remember that the values are a function of the biomass and surface area for which they are estimated. A survey of the literature indicates that our findings are among the highest biomass values known to date for coral reef

fish (*table VI*). The biomass found in the north zone and on the barrier reefs was particularly high, because of the unusually large size of most fish in these areas [32]. As the present study was concerned only with commercial species, the total biomass must be even higher. Several mechanisms may explain the observed high biomass. The possible role of the zones sampled on overestimated findings has been discussed elsewhere [32]: it was argued that, in New Caledonia, the inner reef slopes (areas where most reef sampling took place) usually support higher densities and biomass than reef flats or deeper reef areas [24]. It has also been demonstrated that several species may be attracted to the diver in places where human disturbance is very low, possibly inducing overestimates of densities and/or biomass [21]. However, high biomass values are probably explained essentially by the low fishing pressure in the Northern Province ($\approx$ 1 330 tonnes, [27, 32]), as found in this study. Indeed, the densities found were not exceptionally high (*table VI*), and the high biomass was mainly due to the unusually large sizes of individuals resulting in higher mean weights of most species, particularly those with a long life-span.

5. CONCLUSION

Although the nature of the structure of fish communities was not really surprising, the patterns found here are interesting in a context of an expected development of artisanal fishing activities [9, 26]. This allows some degree of prediction of what may be found in different zones and reef types, and consequently what may be fished and how much [26]. Our estimates of commercial fish standing stocks for the whole Northern Province (remember that only the inner coral reef slopes are considered here) seem sufficiently high to allow the development of fishing activities, in particular because the current fishing pressure, with a catch of about 1 330 tonnes·year^{-1}, is very low (but see the second companion paper [27]). This is especially true for the north zone which may be considered as non-exploited. The standing stocks are strongly dominated by herbivorous fish, mainly Acanthuridae and Scaridae. As these two families are currently subjected

Table VI. Biomass (g·m^{-2}) and densities (individuals·m^{-2}) obtained on some reefs in the Indo-Pacific area (values with * considered all fish species, including the non-commercial ones).

Area or island	Type of biotope	Biomass	Density	Source
New Caledonia (north)	inner reef slopes	339	0.54	this study
New Caledonia (east)	inner reef slopes	258	0.48	this study
New Caledonia (west)	inner reef slopes	158	0.62	this study
Hawaii	patch reef	106*	3.10*	[4]
Chesterfield Islands	fringing reef	140*	2.60*	[24]
Great Barrier Reef	outer reef	156*	3.2*	[52]
Great Barrier Reef	mid-shelf reef	237*	8.4*	[52]
Great Barrier Reef	fringing reef	92*	7.0*	[52]
Mayotte	barrier reef (reserve)	202	7.51*	[29]
Mayotte	barrier reef (fished)	79	9.05*	[29]
Ouvéa	barrier reef	187	0.7	[24]
Ouvéa	barrier reef	260*	3.7*	[24]
New Caledonia	barrier reef (reserve)	182	0.9	[25]
(SW lagoons)	barrier reef (reserve)	262*	3.6*	[25]
(SW lagoons)	intermediate reef	301*		[25]
Réunion	rocky slope	161*	3.02*	[31]
Réunion	isolated rocks	34*	1.05*	[31]

to low fishing pressure, one can thus imagine a relatively easy redirection of the fishing effort towards these fish. At the moment the fishing pressure is mainly focused on carnivorous 'line-fish' species, such as Lethrinidae, Serranidae and some non-ciguatoxic species of Lutjanidae. As most of these fish, mainly Lethrinidae, are not restricted to coral reefs and occur in neighbouring areas, such as near-reef and lagoon bottom zones [22], it is necessary to have a more precise estimate of their total stocks. Particularly from the perspective of local management, the only way to allow a sustainable development of fishing activities is to have the best possible knowledge of fish community structure and stocks in the various biotopes forming the lagoon (this study, [22]). This information, combined with an exhaustive analysis of the socio-economics of the artisanal fisheries [27], should help to prevent inappropriate management options. In this context, our whole study (e.g. this work, in combination with those presented in the two companion articles) may have implications for estimating fish stocks, for improving the management of artisanal fisheries as well as for understanding community ecology for reef sites elsewhere in the South Pacific, a region where these types of data sets are unfortunately seldom simultaneously available.

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