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PATTERNS IN THE TROPHIC STRUCTURE OF FISH POPULATIONS ACROSS THE SW LAGOON OF NEW CALEDONIA

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ABSTRACT

The cross shelf distribution of coral reef fishes according to their trophic structure is examined for 123 visual transects in the SW lagoon of New Caledonia. Abundance is maximum nearshore whereas biomass is evenly distributed across shelf. Piscivores (4-19 % of biomass) are dominated by serranids, with increasing numbers of lutjanids and carangids near the barrier reef. Invertebrate feeders (15-40 % of biomass) increase from the coast to the barrier reef, the latter being characterized by mullids and lethrinids. Small, abundant species are differentially distributed, pomacentrids, dominating nearshore, are gradually replaced by apogonids and Anthias spp. near the barrier reef. Grazers are the main group in biomass but their importance decreases from 65 % on the coast to 28 % on the barrier reef. Scarids, the main component of grazers (> 50 % of biomass) show an even cross shelf distribution, whereas acanthurids increase in biomass from 19 % on the coast to 46 % on the barrier reef, siganids showing the opposite trend. Comparison with the neighbouring Great Barrier Reef indicates some analogies such as close species pool, similar biomass distribution of large grazers, of several families of invertebrate feeders and planktivores. However, there are some major differences such as overall biomass and abundance cross shelf distribution, average size, distribution of apogonids, labrids, caesios and small grazers. These discrepancies may be partly explained by geomorphological differences between the two regions.

INTRODUCTION

The lagoonal fisheries of New Caledonia (NC) are largely unexplored. One of the programmes of ORSTOM is to quantify the potential of this resource. One of the major method used is visual surveys. NC is surrounded by a large lagoon (20 000 km2) which width varies from 1 to 80 km. There are large differences in biotope characteristics across this shelf. In the same manner local fish populations are likely to be influenced by coastal/oceanic gradients in a similar way to that demonstrated for the neighbouring Great Barrier Reef (GBR) of Australia (Russ, 1984; Williams, 1982; Williams & Hatcher, 1983). These workers showed that the species composition and trophic structure of reef assemblages varied greatly over short distances (< 100 km) across shelf. By comparison, latitudinal influences were weak even among reefs separated by over 1000 km. Given the potential of such patterns to affect the results of our surveys, we made a visual assessment of cross shelf influences on community structure in a near pristine area where the shelf is approximatively 50 km wide. We are reporting the preliminary results in the present paper.

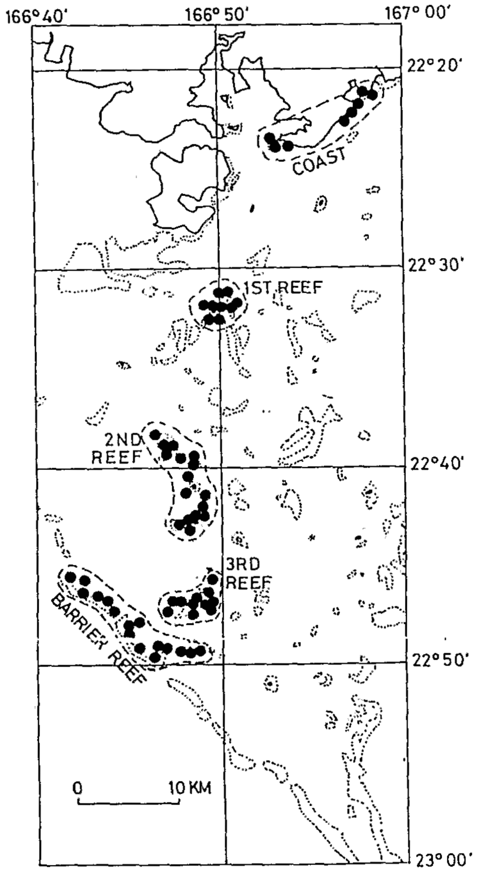


Figure 1. Location of stations. Each point represents at least two transects.

METHODS

All fish were recorded by visual transects. Each transect is 100m long. On each site, two transects were laid along depth contours. A total of 123 transects, being distributed into five geographical zones (Figure 1), were performed on a coast-barrier reef axis. Depth ranged from 1 to 12m. In each zone, as many different types of habitat as possible were sampled (sheltered, exposed, gentle slope, cliffs...). Two divers, one on each side of the transect line, recorded visually conspicuous fish within 5m of the line. Fish size was estimated in 3 cm class for small fish (< 20 cm) and 5 cm class for larger fish. Fish were recorded to the species level when possible, otherwise at the genus or family level. Biomass was estimated by converting visually estimated length to weight from length - weight relationships available from earlier studies in the lagoon (Kulbicki, unpublished data). Fish were grouped into six major trophic categories : piscivores, carnivores 1 (macro invertebrate feeders), carnivores 2 (micro invertebrate feeders), grazers, plankton feeders and omnivores. This classification is based partly on our data base and to a great extent on literature (Hiatt & Strasburg, 1960; Hobson, 1974; Parrish et al., 1985; Parrish et al., 1986; Parrish, 1987).

RESULTS

Species composition

Fish are classified into 370 species or groups, since a number of fish could not be identified to the species level. A total of 47 families were recorded, of which 19 had 5 species or more (Table 1).

Table 1. Cross shelf distribution of the major families (> 5 species).

Families	coast	1st reef	2nd reef	3nd reef	barrier reef	Total
POMACENTRIDAE	33	25	37	18	28	50
LABRIDAE	27	21	31	26	32	43
CHAETODONTIDAE	25	24	23	20	20	32
SERRANIDAE	16	20	20	14	18	27
ACANTHURIDAE	15	15	15	17	17	22
SCARIDAE	15	14	13	14	14	17
MULLIDAE	9	3	11	7	11	14
LETHRINIDAE	4	2	11	7	9	13
BALISTIDAE	4	5	5	4	9	11
LUTJANIDAE	3	3	6	7	9	11
POMACANTHIDAE	7	8	9	5	4	10
TETRODONTIDAE	2	1	6	4	6	10
APOGONIDAE	2	3	1	6	4	9
CARANGIDAE	1	0	6	3	2	9
HOLOCENTRIDAE	3	2	4	5	7	9
SIGANIDAE	8	6	8	2	5	9
HAEMULIDAE	3	3	3	2	3	5
NEMIPTERIDAE	1	1	5	2	3	5
OTHERS (29 FAMILIES)	13	9	35	19	27	56
TOTAL SPECIES	191	165	249	180	228	362
No OF TRANSECTS	16	18	32	24	33	123

Fifty percent of all species are represented by only 6 families. Due to unequal sampling effort in each zone, comparison of species between zones should be interpreted with caution. However, some trends seem obvious. Scaridae, Serranidae and Acanthuridae have approximatively the same number of species across shelf, whereas Pomacentridae, Chaetodontidae, Pomacanthidae and Siganidae tend to have more species near the coast. By contrast, Lethrinidae, Lutjanidae, Balistidae and Tetrodontidae have more species near the barrier reef. Species were grouped by major trophic categories (Table 2). Despite the coarse classification we used, some groups were difficult to categorize. For instance, the non piscivore apogonids can be either considered as carnivore 2 or as zooplanktivores depending on species and size. Similarly, Abudebduf spp. may feed on algae, small invertebrates or zooplankton depending on species or size. Since it is often difficult to separate underwater youngs from our five species of Abudebduf, they were grouped as omnivores. A multinomial χ^2 test indicates that there is no significant difference ($\alpha > 0.05$) between reefs in trophic distribution. Piscivorous and carnivorous species represent 62 % of all species, their importance increasing significantly ($\alpha < 0.05$; comparison of means) from 50 % nearshore to 60 % beyond the 2nd reef. By contrast, nearshore have significantly higher proportions ($\alpha < 0.01$) of grazers species than beyond the 2nd reef. No difference between reefs could be detected for the other trophic categories.

Table 2. Number of species per trophic category across shelf.

trophic groups	coast		1st reef		2nd reef		3rd reef		barrier reef		total	
	nb.	%	nb.	%	nb.	%	nb.	%	nb.	%	nb.	%
piscivores	18	9.3	20	12.0	37	14.3	21	11.4	25	10.7	50	15.7
carnivores 1	29	14.9	24	14.5	51	19.8	37	20.0	50	21.4	74	20.2
carnivores 2	50	25.8	38	22.9	67	26.0	51	27.6	66	28.3	104	28.4
grazers	55	28.3	48	28.9	55	21.3	46	24.9	51	21.9	69	18.9
plankton feeders	20	10.3	22	13.2	26	10.1	16	8.6	23	9.9	41	11.2
omnivores	22	11.3	14	8.4	22	8.5	14	7.6	18	7.7	28	7.7

Table 3. Abundance of the various trophic groups across shelf. In each case, the top number represents numbers, the second is the number of fish/transect and the last number is percentage.

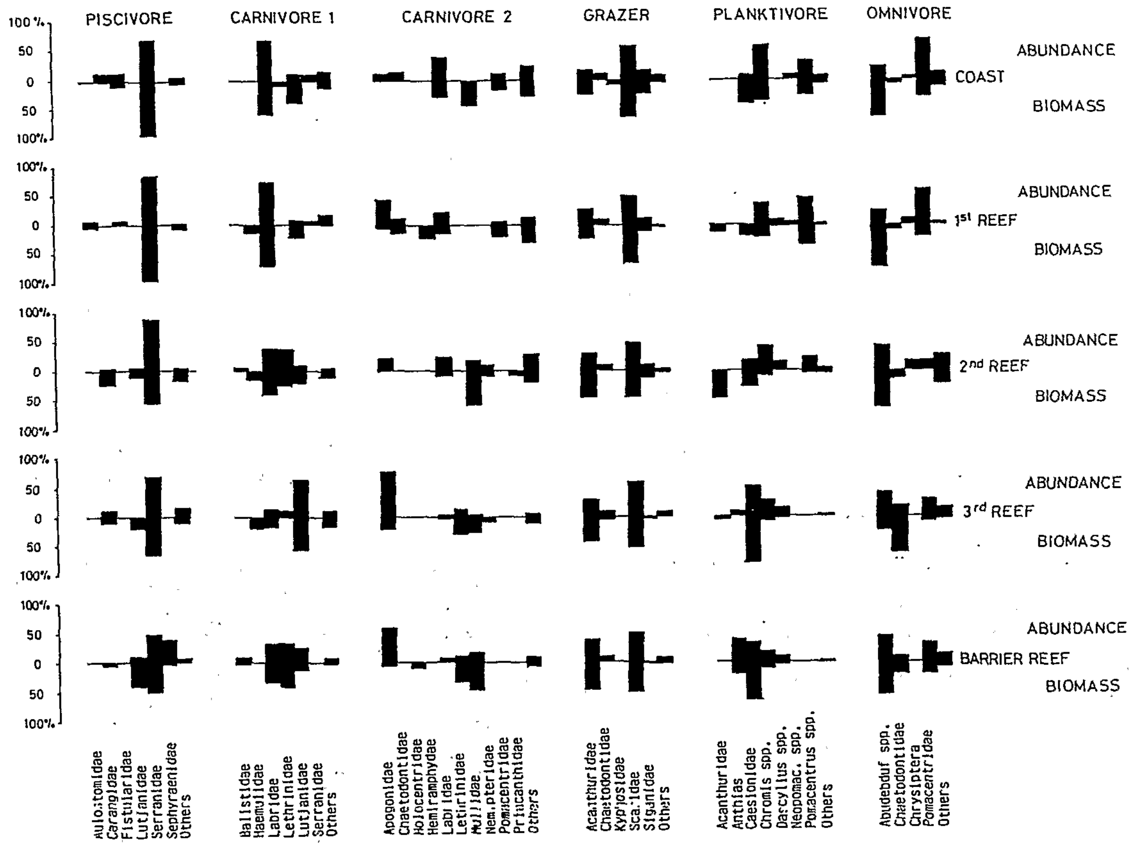
	coast	1st reef	2nd reef	3nd reef	barrier reef	total
piscivores	235 14.7 0.7	209 11.6 0.5	540 16.9 2.0	142 5.9 0.4	524 15.9 1.4	1650 13.3 1.0
carnivores 1	510 31.9 1.5	550 30.6 1.4	1054 32.9 3.8	1104 46.0 3.3	706 21.4 1.9	3929 31.9 2.3
carnivores 2	1852 116 5.4	1403 78 3.6	2261 71 8.3	8852 369 26.7	14435 437 38.5	28804 234 16.8
grazers	4462 279 13.0	2940 163 7.5	4071 127 14.9	2240 93 6.7	4202 127 11.2	17915 146 10.4
plankton feeders	20279 1267 58.9	21258 1181 54.1	16829 526 61.4	20588 858 62.0	16149 489 43.0	95103 773 55.3
omnivores	7072 442 20.6	12961 720 33.0	2649 83 9.7	273 11 0.8	1510 46 4.0	24465 198 14.2
total	34410 2150 100	39321 2184 100	27404 856 100	33199 1383 100	37526 1137 100	171860 1397 100

Abundance

Abundance for the various trophic groups is indicated on table 3. Fish are significantly more abundant ($\alpha < 0.05$) near the coast (2150-2180 fish/transect) than in the middle lagoon (856) or the barrier reef (1137 to 1383 fish/transect). This difference is mainly due to larger numbers of plankton feeders and omnivores near the coast. Plankton feeders are the main trophic group, averageing 55 % of the total abundance. Piscivores and large carnivores make only 3.3 % of the abundance. The third reef excepted (5.9 fish/transect), piscivores are in fairly stable numbers along the coast-barrier reef axis (11.6-16.9 fish/transect). The low piscivore numbers on the third reef are compensated by larger numbers of carnivores 1. The significant ($\alpha < 0.05$) increase in small carnivores near the barrier reef is mainly due to the presence of Apogonidae and Gnathodentex aurolineatus. By contrast, omnivores were more abundant near the coast.

Figure 2 indicates the main families or genera in terms of relative abundance. Piscivores are dominated by Serranidae. The importance of this family is the greatest in the middle lagoon where it is dominated by one species, Plectropomus leopardus, which represents 50-75 % of all piscivores on the 2nd and 3rd reefs. Large carnivores are dominated by Labridae in the nearshore-middle lagoon areas, the main species being Choerodon graphicus.

Figure 2. Contribution across shelf of the main families (> 5 %) to abundance and biomass.



Lutjanidae and Lethrinidae tend to replace the Labridae towards the barrier reef, whilst small Serranidae are limited to the coastal zone. Small carnivores are also dominated nearshore by Labridae, Thalassoma spp. being the major component. Apogonidae increase in considerable proportions towards the barrier reef and are the main reason for a three fold increase of small carnivores between the coast and the barrier reef. Mullidae are also an important component of this trophic group on the barrier reef, mainly because of Mulloidichtys flavolineatus. Grazers are dominated by the Scaridae (48-58 %), Scarus sordidus being characteristic of the near-shore zones, whilst Scarus schlegeli is found preferentially near the barrier reef. Acanthuridae tend to increase in abundance from the coast (16 %) to the barrier reef (38 %) whereas Siganidae, dominated by Siganus argenteus are mainly found near-shore. The species composition of Acanthuridae changes drastically on the coast-barrier reef axis, A. mata is found near-shore, Zebrasoma spp. are more characteristic of the middle lagoon, whereas Naso brevirostris and A. triostegus are found mainly on the barrier reef. However, the most abundant Acanthuridae is A. nigrofuscus which is ubiquitous. Plankton feeders are dominated numerically by the Pomacentridae, which are presented according to their main genera on Figure 2. Pomacentrus spp. are found mainly nearshore areas with Chromis spp. and Neopomacentrus spp. Chromis spp. have however a wider range, being still important on the barrier reef. The middle lagoon is a transition zone where Dascyllus spp. are at their maximum abundance. Anthias spp. and Caesionidae dominate the barrier reef area. Omnivores are abundant essentially nearshore. Abudebduf spp. is the dominating genus except nearshore where Pomacentrus spp. dominates. Chrysiptera spp. are more characteristic of the middle lagoon reefs and omnivorous Chaetodontidae are found preferentially near the Barrier Reef.

Biomass

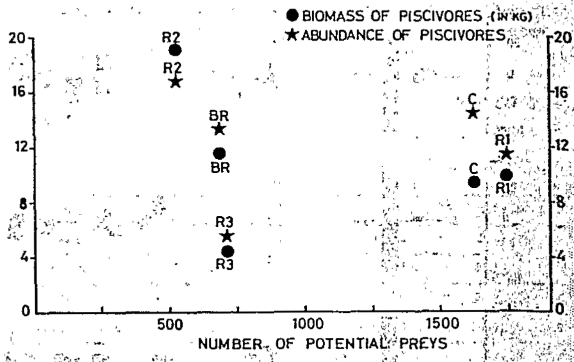
Table 4 indicates the distribution of biomass by trophic groups. With the exception of the third reef, all areas have approximatively the same biomass/transect (92-110 kg). The most important component is grazers (39.5 % of total biomass), however, there are noticeable changes in trophic structure depending on zones. Thus, piscivores represent 20.3 % of the fish biomass on the 2nd reef, when elsewhere this group varies from 5.4 to 12.7 %. This is mainly due to the presence of a few very large fish (5 sharks and 2 Epinephelus cylindricus, totaling 140 kg). Serranidae are the dominant family, essentially nearshore (over 90 %), faster fish (Carangidae, Lutjanidae) becoming more important towards the barrier reef

Table 4. Biomass distribution of the various trophic groups across shelf.
Top number : biomass (kg)
2nd number : biomass/transect (kg)
3rd number : % per zone
4th number : average weight (g)

	coast	biomass (kg) - average weight (g) 1st reef	2nd reef	3rd reef	barrier reef	total
piscivores	153.7 9.6 8.7 654	183.4 10.2 10.6 878	618.0 19.3 20.3 1144	100.5 4.2 5.4 742	385.0 11.7 12.7 734	1440.6 11.7 12.5 873
carnivores 1	180.8 11.3 10.3 354	223.3 12.4 13.0 406	431.2 13.5 14.2 409	334.8 13.9 17.9 303	404.3 12.3 13.3 573	1574.4 12.8 13.7 401
carnivores 2	98.5 6.2 5.6 53	62.2 3.5 3.6 44	167.1 5.2 5.5 74	170.8 7.2 9.2 19	825.2 25.0 27.2 57	1323.8 10.8 11.5 46
grazers	1035.6 64.7 58.8 232	792.0 44 46 269	1054 32.9 34.7 259	718.4 29.9 38.5 321	935.2 28.3 30.8 222	4535.2 36.9 39.5 253
plankton feeders	156.4 9.8 8.9 7.7	164.8 9.2 9.6 7.8	769.2 24.0 25.3 46	526.1 21.9 28.2 26	424.4 12.9 14.0 26	2040.9 16.6 17.8 21
omnivores	135.8 8.5 7.7 19	297.7 16.5 17.2 23	65.6 2.0 2.1 25	14.9 0.6 0.8 55	62.7 1.9 2.1 42	576.7 4.7 5.0 24
total	1760.9 110.0 100 51	1723.4 95.7 100 44	3039.5 95.0 100 111.0	1865.5 77.7 100 56	3036.8 92.0 100 80	11491.6 93.4 100 67

(Figure 2). Large carnivores have a rather homogeneous biomass distribution across the lagoon (Table 4), Labridae being dominant nearshore then replaced by Lutjanidae and Lethrinidae towards the barrier reef (Figure 2). Haemulidae are typically found in the middle lagoon. Small carnivores represent 3.6-9.2 % of the biomass except on the barrier reef where they make up to 27 % of the biomass. This sudden increase is due to a mullid, Mulloidichtys flavolineatus and a lethrinid, Gnathodentex aurolineatus. The small carnivore group is very diverse, Labridae and Mullidae being the main families. Apogonidae, despite their abundance represent only 5-19 % of small carnivore biomass. Grazers decrease in biomass from the coast to the barrier reef (58.8 to 30.8 %). The main family, Scaridae (43-65 % of biomass), change little in importance across the reef, whilst Acanthuridae increase from 19 % to 46 % towards the barrier reef. Siganidae are essentially restricted to coastal areas. A characteristic of the grazers is that very few species make over 10 % of the grazers biomass. This indicates an even distribution of the biomass between species, except for A. dussumieri and Naso unicornis which make respectively 11 - 25 % and 17 % of the grazers biomass in the barrier reef area. Plankton feeders are better represented in biomass in the middle reef and barrier reef than on the coastal areas, which is the inverse of that observed for abundance (Figure 2). This is due to the importance of large species in the middle lagoon (A. bleekeri, Naso vomer, N. hexacanthus) which feed mainly on gelatinous zooplankton. On the barrier reef, plankton feeder biomass increase is due to Caesionidae. By contrast, omnivores are concentrated near the coast, making up to 16.5 % of the biomass on the first reef. Pomacentrus philippinus and Abudebdug spp. make the bulk of this trophic group.

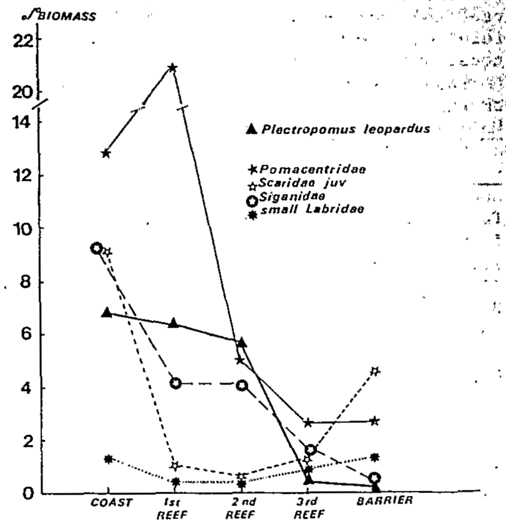
Figure 3. Relationship between potential prey abundance and predator abundance or biomass.



Predator-prey

Figure 3 indicates that there is no correlation between potential prey abundance and piscivore abundance (r = 0.02) or piscivore biomass (r = - 0.30). Potential prey are defined as fish of less than 10 cm. However, piscivores are selective on their preys (Parrish et al., 1986). The major piscivore species in the coastal zone, 1st and 2nd reefs is Plectropomus leopardus. Goeden (1978) indicates as major prey items of this species : Atherinidae (30 % of prey occurence), Pomacentridae (17 %), Scaridae (14 %), Labridae (7 %) and Siganidae (3 %). Atherinidae being pelagic were not sampled in the present survey, but one notices that Pomacentridae, juvenile Scaridae and Siganidae do all decrease from the coast towards the barrier reef (figure 4), small Labridae are the only exception, but they have the lowest contribution to total biomass. If all prey species are pooled, a Spearman's rank test indicates that Plectropomus leopardus and its prey follow the same pattern between reefs (rs = 0.90, α = 0.05).

Figure 4. Cross shelf distribution of Plectropomus leopardus and its preferred preys.



Size distribution

Average weight are indicated by table 4. Fish in the coastal zone have significantly lower size ($\alpha < 0.05$) than average, whilst the second reef supports fish having size significantly larger than average ($\alpha = 0.01$), no difference being detected for the other reefs. A total of 75 species were recorded on all stations across the reef. Eleven of these species (Cephalopholis miniatus, Epinephelus cyanopodus, E. maculatus, Lethrinus nebulosus, Scarus gibbus, Acanthurus dussumieri, Zebrasoma velliferum, Naso brevirostris, N. unicornis, Siganus punctatus and S. corallinus) show an increase in size from the coast to the barrier reef (Rank test, $\alpha = 0.05$), whilst only three species (Parupeneus multifasciatus, Siganus argenteus and Lo vulpinus) present the opposite trend. Abundance (fish/transect) and average weight show an inverse trend ($\alpha < 0.05$, $N = 5$, $s = 117$ for Kendall coefficient of concordance) if one excepts piscivores for which there is no pattern of variation.

DISCUSSION

The choice of method (i.e. visual censuses) introduced a level of sampling error that limits the detection of pattern to one of relatively gross change. This method, however, is more easy to replicate than any of the more accurate alternatives (eg dynamite sampling of Williams & Hatcher, 1983) and is non destructive. Also, it was important to use the same method as that used for surveying other parts of the lagoon of NC.
Visual censuses are known to favor conspicuous and large species (Harmelin-Vivien et al.,1985). In the present study, which is derived from resource assessment data, particular attention was drawn towards the species which make the bulk of the biomass. Small species such as Gobiidae or Blennidae and cryptic species such as most Holocentridae and Muraenidae are certainly well underestimated. However, from rotenone poisonings, we know that in the present study areas such species account for less than 15 % of the total biomass.

Biomass estimates are based on visual size estimates. This method tends to underestimate size by 10 - 20 % depending on species and size (Harmelin-Vivien et al., 1985). For comparisons between reefs, the bias being similar for all stations this bears little consequence. However, when comparing to other studies this underestimate should be kept in mind.

The main biases stem from the trophic classification. Most fish have a diversified diet and thus belong to several trophic groups at a time. The contribution of the various food items for a given species vary also with size, seasons and food availability. Concerning piscivores, Parrish et al. (1986) indicate that such a gross classification may hide a rather important contribution of occasional piscivorous species.

The overall structure observed in the present study presents major differences with other fish distributions in the Pacific such as Hawaii (Brock et al., 1979; Parrish et al., 1986), French Polynesia (Galzin, 1985) or Guam (Jones & Chase, 1975; Molina 1981). The region presenting the most analogies with ours is the GBR (Williams & Hatcher, 1983; Russ, 1984). However, even for this neighbouring zone there are some major differences.

Two main physical features differ between the GBR and our study site. The distance between inshore and outershelf in Williams & Hatcher (1983) was of 65 miles, being only of 25 miles in the present case. Secondly, the reefs studied on the GBR are separated by wide and deep channels (> 70 m), whereas in our lagoon average depth between reefs is 20 m. These geomorphological differences may explain that only 6.8 % of Williams & Hatcher's species were ubiquitous, this proportion being of 20 % in our study. Similarly, 60 % of the species were restricted to one reef on the GBR, whereas species found on only one reef or two adjacent reefs represented merely 25 % of all species in our case. Looking at number of species per family, these factors may also explain an increase from inshore to the outershelf of acanthurids on the GBR, this family presenting no such variation across shelf in NC. However, other differences in species distribution need other explanations.
For instance, chaetodons show opposite cross shelf trends on the GBR and NC. Similarly, pomacentrids have more species nearshore in NC, whereas they are more diverse on the mid-shelf of the GBR. These differences could be related to coral distributions and water quality. On our shelf transect, nearshore areas have dense coral cover and low turbidity.

In the tropical Indo-Pacific, Parrish et al. (1986) indicate that piscivores range from 5.7-54 % in biomass, 1-6 % in abundance and 8-41 % in species numbers according to 8 studies. Our values fall well within the ranges of this review, however they differ specifically from any of the data presented there. Williams & Hatcher's data (1983) for instance show piscivore abundance similar to ours, but lower biomass and lower species numbers. Another trait of piscivores in our study is the low cross shelf variability, whereas on the GBR, Hawaii and East Africa (Parrish et al., 1986) the piscivore component shows considerable local variations. The main piscivore families in NC are serranids and large lutjanids which is similar to most areas except Hawaii and French Polynesia.

Invertebrate feeders present analogous trends across both the GBR and NC shelfs. Thus, total carnivore (1+2) biomass shows a significant increase ($\alpha < 0.05$, $r = 0.91$) from the coast to the barrier reef in the present study. Similarly on the GBR Williams & Hatcher (1983) show that the outershelf supports a greater biomass of carnivores than the inner reefs. At the family level, if Balistidae, Haemulidae, Holocentridae and Lethrinidae have analogous cross shelf distributions in both regions, Apogonidae and Labridae present entirely opposite patterns.

The cross shelf distributions of large grazers show analogies between the GBR (Russ, 1984; Williams & Hatcher, 1983) and NC. Thus, in both regions acanthurids increase in biomass from shore to the barrier reef and siganids show the opposite trend. By contrast, small grazers such as pomacentrids and chaetodons are very poorly represented in NC compared to the GBR.

The cross shelf distribution of planktivores shows marked differences with the GBR. Thus, Williams & Hatcher (1983) found that caesios were the major biomass contributors of this group and that they favored the mid-shelf, whereas in NC they are found essentially near the barrier reef. By contrast, large acanthurids such as *Naso hexacanthus* or *N. vomer* also gelatinous plankton feeders, are the most important biomass contributors in our middle lagoon, whereas these species favor the outershelf on the GBR.

This inter regional comparison could be continued for small planktivores and omnivores and show that a few genera such as Neopomacentrus or Chromis have similar trends, whereas other genera such as Pomacentrus follow different cross shelf distribution patterns. The problem is to know why some species show similarities and others not. Both regions have a very similar species pool. Thus, there is over 60 % overlap between the GBR checklist of Russell (1983) and our collections. This percentage is even higher if one considers "large" species (> 10 cm average length). Therefore, it is likely that the larval pools show great analogies, if considered at the regional level, but that larval dispersal follow very different trends. As mentioned earlier, these two regions show marked geomorphological differences. In the lagoon of NC a number of large species may move from one reef to another and therefore select their habitat, whereas on the GBR distances and depth may greatly impede these movements. The data presented on the similar distributions of *Plectropomus leopardus* and its favored preys may be an indication of such a selection of habitat by large predators. Another example might be the parallel increase of fast moving piscivores (Lutjanids and carangids) and of schooling preys such as apogonids, caesios and *Anthias* spp. near the barrier reef. Some species are locally known to migrate seasonally. Thus, *Siganus argenteus* recruits and spawns on the barrier reef, but adults are found mainly nearshore. By contrast, longline catch data (Kulbicki et al., 1987) indicate that most carnivores are larger as distance to the coast and depth increase. This suggests that either these fish migrate with age or that they grow better offshore or both. If such habitat selection exists, it is likely to be related to food availability or quality. Food could be at times a limiting factor on coral reefs. Were this the case, one would expect decreased size with increasing abundance. This latter trend was found by Williams & Hatcher (1983) and by the present study, but only when considering all species. At the intraspecific level such a correlation could not be demonstrated.

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