Effects of marine reserves on coral reef fish communities from five islands in New Caledonia

L. Wantiez[1], P. Thollot[2], M. Kulbicki[3]

[1] Consultant in Environment and Marine Resources, BP 219, 98845 Nouméa Cedex, New Caledonia Tel/Fax: (687) 27 14 47
[2] Consultant in Environment and Marine Resources, BP 9239, 98807 Nouméa Cedex, New Caledonia
[3] ORSTOM, Centre de Nouméa, BP A5 Nouméa Cedex, New Caledonia

Abstract. The effect of marine reserve protection on coral reef fish communities was studied on five islands located in the southwest lagoon of New Caledonia. Commercial fish communities and Chaetodontidae, sampled before fishing prohibition and after five years of protection, were compared. Reference stations were also sampled to assess variability in unprotected communities on the same time scale. The hypothesis that marine reserves protect and develop fish stocks was confirmed. Species richness, density and biomass of fish on the protected reefs increased respectively by 67%, 160% and 246%. This increase was statistically significant, whereas the reference stations showed only a small increase in density. There were significant increases in the species richness, density and biomass of the major exploited fish families (Serranidae, Lutjanidae, Lethrinidae, Mullidae, Labridae, Scaridae, Siganidae and Acanthuridae) and also of the Chaetodontidae. No significant increase in the mean lengths of fishes was noted among the main species, with the exception of one species of Siganid. Size structure changed for most of the main species, as the proportion of small individuals increased after five years of protection. Detrended correspondance analysis indicated that marine reserve protection was the most important determinant of the fish community structure. The second determinant was the position along an inshore-offshore gradient. Marine reserve protection resulted in an increase in the relative abundance and species richness of large edible species within the assemblages.

Introduction

Reef fishes are particularly sensitive to overfishing (Russ 1991). Classical fishery management, based upon the control of catch rate or fishing effort, requires large amounts of information, is complicated and expensive to enforce, and is difficult to adapt to multispecies stocks (Roberts and Polunin 1991). Marine reserves have often been considered as a less expensive and better alternative to classical management practices (Plan Development Team 1990; Roberts and Polunin 1991, 1992; Munro and Fakahau 1993). Marine reserves are thought to protect spawning stock biomass and intraspecific genetic diversity, maintain population age structure, and ensure sufficient recruitment supply (Plan Development Team 1990). Marine reserves are also supposed to provide sources of recruitment for surrounding areas, and to enhance adjacent unprotected areas through emigration of adult fish (Plan Development Team 1990). There have been a number of studies on the effect of marine reserves in the Indo-Pacific (see Roberts and Polunin 1991 for review). Most of them are limited to the effect of marine reserves on the densities and size of fish in the absence of fishing. Significant differences are usually found between protected and unprotected areas, fish being more abundant and larger in protected areas (Roberts and Polunin 1991, 1992). In the tropical Indo-Pacific zone, these studies concern Australia (Ayling and Ayling 1986; Bienssen 1989), the Philippines (Russ 1985; Alcala 1988), Kenya (Watson and Ormond 1994), and the Red Sea (Roberts and Polunin 1992). However, few data are available on protected zones, before they become reserves to prove that the differences are really due to protection policy, rather than spatial differences between communities (Russ and Alcala 1989, 1994 ; Roberts and Polunin 1991, 1992).

The aim of the present study was to assess the effects of marine reserves on coral reef fish communities by comparing fish populations on five islands from the southwest lagoon of New Caledonia, before and after fishing prohibition. Species richness, density and biomass were compared and size distribution and community structure were studied. These islands supported substantial amounts of recreation fishing (spearfishing, hand line and gillnets), before the South Lagoon Marine Park was created by the South Province of New Caledonia.
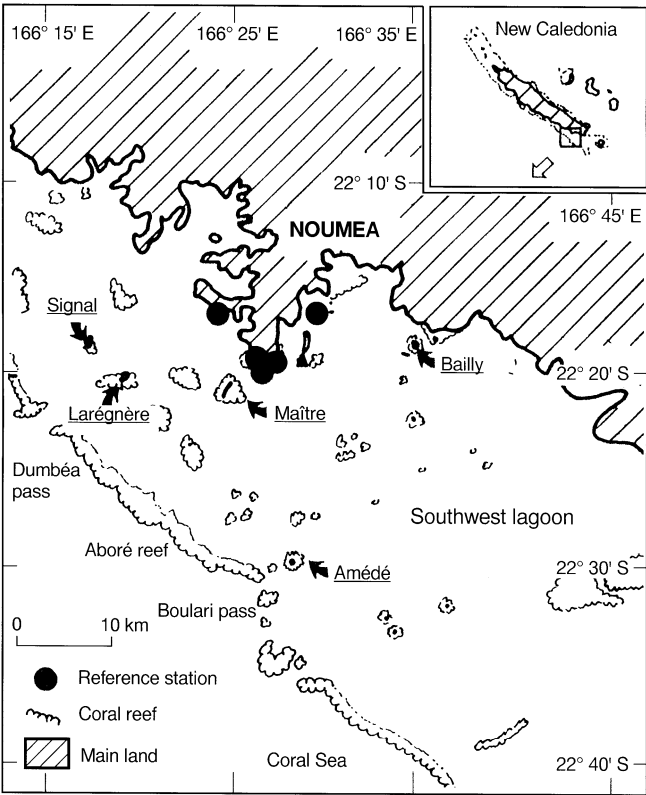

Correspondence to: L. Wantiez

Fig. 1. Location of the study area. *Arrows* indicate the location of the five protected islands

Table 1. Major characteristics of the studied marine reserves. Sampling dates before fishing was prohibited are given in parenthesis in the first column

Name of reserve	Island type	Area (km²)	Distance to coast (km)	Distance to barrier reef (km)
Amédée (1985)	Coralline	2.8	18.0	4.0
Signal (1990)	Coralline	4.3	11.1	6.8
Larégnère (1985, 1990)	Coralline	8.5	10.5	7.4
Maitre (1986, 1990)	Coralline	9.0	4.3	13.9
Bailly (1990)	Continental	2.4	1.5	26.5

Materials and methods

Study location and sampling

In 1989, five islands of the Southwest lagoon of New Caledonia were declared permanent marine reserves by the South Province of New Caledonia (Fig. 1, Table 1): Amédée, located near the barrier reef, Signal, Larégnère and Maître located in the middle of the lagoon, and Bailly located near the coast. All are coralline islands except Bailly which is a high island. Fishing and collecting have been prohibited on these islands, with active enforcement of park regulations begining in 1990.

The fish communities around the five islands were sampled by visual census between 1985 and 1990 (Kulbicki, unpublished data). This set of data (28 stations) is used to characterize the fish populations before fishing was prohibited. In 1994, the fish communities of the protected islands were re-sampled (16 stations), after five years of protection (Wantiez and Thollot 1994). Six other stations, distributed in the lagoon and sampled in 1990 (Kulbicki unpublished data) and in 1994 (Wantiez and Thollot 1994), have been used as references (Fig. 1).

Visual censuses

All surveys followed the same procedures. Among the 950 lagoon fish species of New Caledonia (Rivaton et al. 1990), only 205 commercially important species and characteristic species were censused. The families censused are shown in Table 2 and the complete list of the species is given in Wantiez and Thollot (1994).

For each station, two 50 m line transects were laid on the bottom. One transect was set along the reef front, the other was set perpendicularly, from the reef flat to the outer part of the reef, in order to obtain the most realistic description of the station. Along each transect a diver counted all fish, estimating their length and the perpendicular distance of the fish to the transect. Length was given in 2 cm size classes for fish smaller than 30 cm, 5 cm size classes for fish between 30 and 50 cm, and 10 cm size classes for fish larger than 50 cm. Only fish less than 1.5 m above the bottom were counted. The distance from the fish to the transect was recorded in 1 m classes up to 5 m, and in 2 m classes beyond 5 m. Fish were not recorded beyond 10 m from the transect. Data from Kulbicki (1988), Kulbicki and Wantiez (1990) and Kulbicki et al. (1994) indicate that for most species, the difference between observed and real length is less than 15%. A comparison between experienced and inexperienced divers using the same method during a survey on Abore reef (SW lagoon of New Caledonia) indicates that differences in density and biomass do not exceed 15% between divers (Kulbicki et al. 1996). The divers involved in the present study had a good knowledge of the fish fauna and previous training in visual censuses. Consequently, differences in length, distance and number estimates between divers were likely to be minor.

Data analysis

There are many techniques available for estimating density (Burnham et al. 1980). Among these, Kulbicki and Duflo (unpublished data) showed that the most robust descriptor is:

$$De = (2L)^{-1} \sum_{i=1}^{p} n_i d_i^{-1},$$

where De: density (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); p: number of species. Average distance for species i to the transect is calculated as follow,

$$d_i = \frac{1}{n_i} \sum_{j=1}^{o_i} n_j d_j$$

Table 2. List of the fish families censused. The number in parenthesis indicates the number of species

Chanidae (1)	Lutjanidae (18)	Mullidae (14)	Labridae (10)
Serranidae (25)	Haemulidae (9)	Kyphosidae (1)	Scaridae (22)
Priacanthidae (1)	Sparidae (1)	Chaetodontidae (31)	Acanthuridae (24)
Sillaginidae (2)	Lethrinidae (18)	Mugilidae (2)	Siganidae (9)
Carangidae (11)	Nemipteridae (1)	Sphyraenidae (4)	Scombridae (1)

where o_i: number of occurrences of species i; n_j: number of fish of species i observed at occurrence j; d_j: distance of fishes of species i to the transect at occurrence j.

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

$$Bi = (2L)^{-1} \sum_{i=1}^{p} w_i d_i^{-1}$$

where Bi: biomass (g m^{-2}); w_i: weight of species i (g).

Wilcoxon-Mann-Whitney tests (Siegel and Castellan 1988) were used to compare species richness, density and biomass of the fish community before and after the islands were protected. The characteristics of the reference stations were also compared before and after to estimate the importance of the temporal effect, using paired comparison tests (Sokal and Rohlf 1981). The size structure of the major species was analyzed using χ^2 test (Siegel and Castellan 1988). A detrended correspondence analysis (DCA) (Hill and Gauch 1980) was used to study the community structure. The analysis was performed on the data matrix of the mean densities of species on each island before and after the marine reserves were created. A transformation log ($De + 1$), recommended by Legendre and Legendre (1984) for Poisson distributed data, was applied to clarify the projections of the objects (samples) and the descriptors (species) on the factor axis. The species found in only one sample were removed in order to clarify the projections on the principle axes (Hill 1979).

Results

Reference stations

Species richness per station, total biomass of the reef fish communities and of each of the major fish families were similar in 1990 and 1994 at the reference stations (Fig. 2, Table 3A). A significant increase in density occurred between 1990 and 1994 (Table 3A). The density of Chaetodontidae (mainly *Chaetodon plebeius* and to a lesser extent *Chaetodon trifasciatus*) and Labridae (mainly *Choerodon graphicus* and to a lesser extent *Hemigymnus melapterus*) increased significantly, but biomass did not change (Fig. 2). Other families showed no change.

Protected islands

The characteristics of the reef fish communities in the marine reserves on the five islands changed drastically after five years of fishing prohibition (Table 3B). The number of species per station increased by 67%, the density by 160% and the biomass by 246%. Species richness, density and biomass increased significantly on Amédé, Larégnère and Maître (Fig. 3). On Signal, only biomass increased significantly (Fig. 3). The species richness per station, density and biomass of the nine major families increased significantly, with the exception of species richness and density of Lutjanidae and species richness of Acanthuridae (Fig. 4). Species richness per station was the least variable index and biomass the most variable. The changes in density and biomass of the nine major families reflected the increase in density and biomass of the most abundant species censused: *Plectropomus leopardus* (Serranidae), *Lutjanus fulviflamma* (Lutjanidae), *Lethrinus atkinsoni* (Lethrinidae), *Parupeneus ciliatus* (Mullidae), *Choerodon graphicus* and *Hemigymnus melap-*
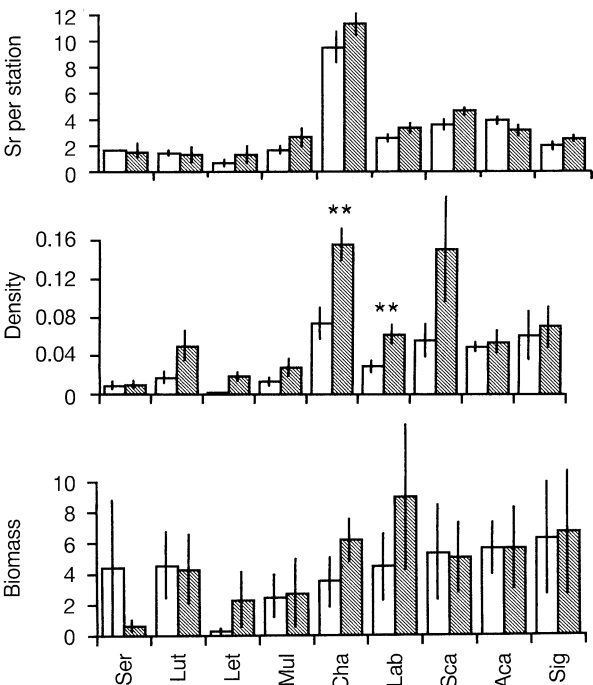

Fig. 2. Species richness per station (*Sr* per station), density (fish m^{-2}) and biomass (g m^{-2}) of Serranidae (*Ser*), Lutjanidae (*Lut*), Lethrinidae (*Let*), Mullidae (*Mul*), Chaetodontidae (*Cha*), Labridae (*Lab*), Scaridae (*Sca*), Acanthuridae (*Aca*) and Siganidae (*Sig*) at the reference stations between 1990 (*white*) and 1994 (*grey*). A paired comparison test (Sokal and Rohlf 1981) was used to test the differences; **, significant at $P < 0.01$; bars indicate $\pm$ standard error of mean

Table 3. Average species richness per station density and biomass of fish on (A) the reference stations in 1990 and 1994, and on (B) marine reserves (Amédée, Signal, Larégnère, Maître and Bailly) before and after marine reserves were created

A Reference stations	Species richness per station	Density (fish m^{-2})	Biomass (g m^{-2})
1990	29.83 $\pm$ 8.08	0.322 $\pm$ 0.142	42.98 $\pm$ 25.98
1994	31.67 $\pm$ 6.18	0.608 $\pm$ 0.159	42.78 $\pm$ 15.08
Difference	NS	**	NS

B Marine reserves	Species richness per station	Density (fish m^{-2})	Biomass (g m^{-2})
Before	29.97	0.408	50.94
After	49.94	1.062	176.06
Difference	***	***	***

A paired comparison test (reference stations) and a Wilcoxon-Mann-Whitney test (marine reserves) were used to test the differences over time (Sokal and Rohlf 1981, Siegel and Castellan 1988); NS, not significant ($P > 0.05$); **, significant at $P < 0.01$; ***, significant at $P < 0.001$; 95% confidence of means are given

terus (Labridae), *Scarus schlegeli* and *Scarus sordidus* (Scaridae), *Naso unicornis* (Acanthuridae), and *Siganus doliatus* (Siganidae) (Table 4). It should be noticed that *L. fulviflamma, P. ciliatus, H. melapterus* and *S. doliatus* are not target species in New Caledonia. Density and biomass
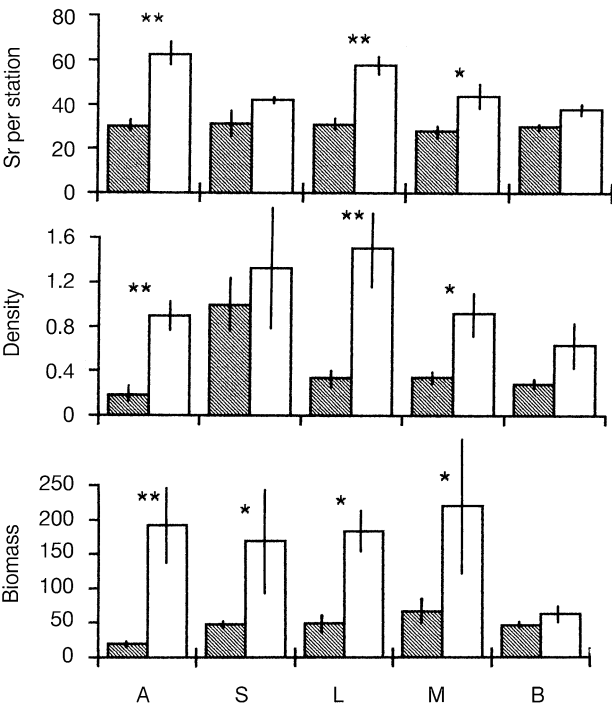
Fig. 3. Species richness per station (Sr per station), density (fish m^{-2}) and biomass (g m^{-2}) of fish on Amédée (*A*), Signal (*S*), Larégnère (*L*), Maître (*M*) and Bailly (*B*) before (*grey*) and after (*white*) marine reserves were created. Wilcoxon-Mann-Whitney test (Siegel and Castellan 1988) was used to test the differences; *, significant at $P < 0.05$; **, significant at $P < 0.01$; bars indicate $\pm$ standard error of mean
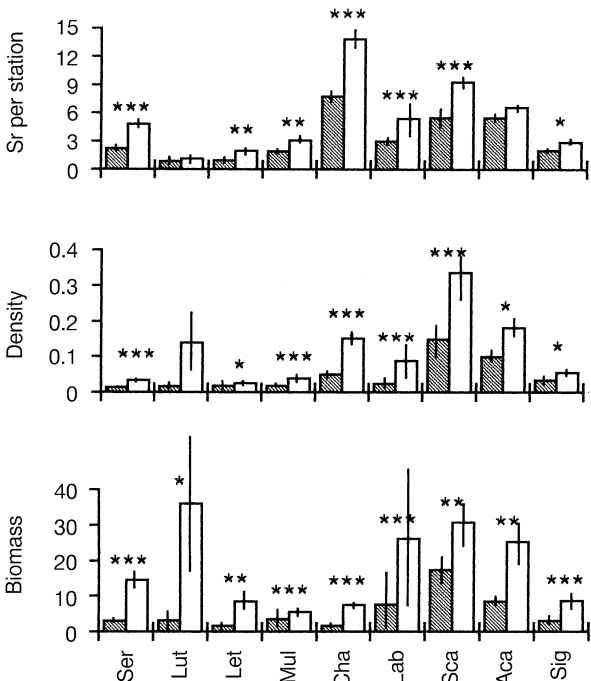
Fig. 4. Average species richness per station (Sr per station), density (fish m^{-2}) and biomass (g m^{-2}) of Serranidae (*Ser*), Lutjanidae (*Lut*), Lethrinidae (*Let*), Mullidae (*Mul*), Chaetodontidae (*Cha*), Labridae (*Lab*), Scaridae (*Sca*), Acanthuridae (*Aca*) and Siganidae (*Sig*) on Amédée, Signal, Larégnère, Maître and Bailly before (*grey*) and after (*white*) marine reserves were created. Wilcoxon-Mann-Whitney test (Siegel and Castellan 1988) was used to test the differences; *, significant at $P < 0.05$; **, significant at $P < 0.01$; ***, significant at $P < 0.001$; bars indicate $\pm$ standard error of mean

did not change significantly for one of the most important species *Acanthurus blochii* (Acanthuridae) (Table 4).

The mean size of the major species showed different patterns over time (Table 4). The average size of *Plectropomus leopardus*, *Hemigymnus melapterus* and *Acanthurus blochii* did not change after five years of fishing prohibition. In contrast, the mean size of six other species

significantly decreased (*Lethrinus atkinsoni*, *Parupeneus ciliatus*, *Choerodon graphicus*, *Scarus schlegeli*, *Scarus sordidus* and *Naso unicornis*). *Lutjanus fulviflamma* and *Siganus doliatus* are the only dominant species whose mean size increased. However, the differences were close to the resolution of the length-estimations, with the exception of *L. atkinsoni*, *P. ciliatus* and *S. sordidus*.

Table 4. Average density, biomass and mean length of the major species of the main fish species censused on Amédée, Signal, Larégnère, Maître and Bailly, before and after marine reserves were created

Species	Density (10^{-2} fish m^{-2})			Biomass (g m^{-2})			Mean size (cm)		
	Before	After	D	Before	After	D	Before	After	D
Plectropomus leopardus	0.24 (0.08)	1.64 (0.20)	***	1.42 (0.67)	10.02 (1.92)	***	32.8 (1.66)	31.0 (0.96)	NS
Lutjanus fulviflamma	1.23 (1.22)	2.52 (1.47)	*	2.41 (2.37)	16.24 (11.87)	*	22.0 (0.03)	24.2 (0.12)	***
Lethrinus atkinsoni	0.03 (0.03)	1.18 (0.54)	**	0.15 (0.15)	3.77 (1.51)	**	30.0 (0.00)	23.1 (0.40)	***
Parupeneus ciliatus	0.14 (0.05)	1.31 (0.46)	***	0.59 (0.24)	3.04 (0.94)	***	26.2 (0.84)	19.4 (0.43)	***
Choerodon graphicus	0.95 (0.24)	4.73 (1.27)	***	5.39 (1.51)	17.21 (4.40)	***	29.7 (0.60)	25.7 (0.27)	***
Hemigymnus melapterus	0.55 (0.12)	2.19 (0.27)	***	1.09 (0.31)	4.32 (0.86)	***	19.8 (0.61)	20.0 (0.41)	NS
Scarus schlegeli	0.56 (0.17)	1.74 (0.40)	**	1.67 (0.48)	3.46 (0.65)	*	22.7 (0.43)	19.6 (0.46)	***
Scarus sordidus	1.05 (0.32)	7.29 (2.10)	***	2.24 (0.60)	3.12 (0.64)	NS	20.4 (0.51)	11.2 (0.20)	***
Acanthurus blochii	1.26 (0.50)	1.36 (0.39)	NS	1.65 (0.33)	2.21 (0.65)	NS	18.5 (0.33)	18.8 (0.26)	NS
Naso unicornis	0.18 (0.07)	2.08 (0.66)	***	1.35 (0.65)	8.94 (3.67)	**	30.5 (1.37)	25.6 (0.55)	***
Siganus doliatus	1.09 (0.25)	2.69 (0.51)	**	1.32 (0.27)	3.90 (0.77)	**	17.1 (1.10)	19.0 (0.20)	***

Wilcoxon-Mann-Whitney test (Siegel and Castellan 1988) was used to test the differences (D);
NS, not significant ($P > 0.05$); *, significant at $P < 0.05$; **, significant at $P < 0.01$; ***, significant at $P < 0.001$; standard error of mean is given between brackets

The patterns of size distribution of the major species significantly changed over time, with the exception of *Plectropomus leopardus* (Fig. 5). Density and biomass of *P. leopardus* increased (Table 4) but no significant modification occurred within the size distribution. The other dominant species showed different patterns (Fig. 5). Small individuals were proportionally more numerous in 1994 for *Lethrinus atkinsoni*, *Parupeneus ciliatus*, *Scarus schlegeli*, *Scarus sordidus* and *Naso unicornis*. Conversely, larger individuals were proportionally more numerous in 1994 for *Hemigymnus melapterus* and *Siganus doliatus* (Fig. 5). Temporal changes in size distribution of *Lutjanus fulviflamma*, *Choerodon graphicus* and *Acanthurus blochii* were more difficult to analyze (Fig. 5). The size distribution of the fish was generally more regular following the creation of the marine reserves (Fig. 5).

According to the DCA, the fish community structure had noticeably changed after marine reserves were created (Fig. 6). The first axis determined by the DCA reflected the marine reserve effect, the protected samples being projected on the left part of the axis for all islands. The characteristic species of these assemblages are revealed by the projection of the species on the first two axes of the DCA (Fig. 7, Table 5). Marine reserves were characterized by numerous species: Serranidae (e.g. *Plectropomus leopardus*), Lutjanidae (e.g. *Aprion virescens*), Lethrinidae (e.g. *Lethrinus atkinsoni*), Chaetodontidae (*Chaetodon* spp.), Labridae (e.g. *Bodianus perditio*, *Hemigymnus melapterus* and *Choerodon graphicus*), Scaridae (*Scarus* spp.) and Acanthuridae (*Acanthurus* spp. and *Naso* spp.). These are generally large and edible species with the exception of the Chaetodontidae. A few species characterized the fish community of the islands before fishing prohibition, including several schooling species (Fig. 7, Table 5): *Lutjanus gibbus*, *Gnathodentex aurolineatus*, *Lethrinus* spp., *Kyphosus vaigiensis* and *Siganus corallinus*. Consequently, it seems that the effect of marine reserves on fish community structure was to increase the relative importance of species which were rare or absent before the marine reserves were created. The second axis reflects an inshore-offshore pattern (Fig. 6) in the relative importance of fish species (Table 5).

Discussion

Validity of methods

Two major questions arise from the data set: the precision of length estimates and the position of the reference stations. Previous studies (Kulbicki 1988; Kulbicki and Wantiez 1990; Kulbicki et al. 1994) have indicated that the precision of length estimates is usually within 15%. Some variation occurs between species (elongate species being usually not as well estimated as round species). However, there should be little or no bias in size distribution comparisons in the present study since only one species is considered at a time. For biomass estimates, it is difficult to appreciate the influence of size precision, but it should be noted that for commercial species (Serranidae, Lutjanidae, Lethrinidae), data from Kulbicki et al. (1994, 1995a, 1995b) indicate that weight estimates from visual censuses are on average less than 15% different from weight of fish caught in the same area by hook and line.

Reference stations are all located nearshore. Therefore, only Bailly is truly comparable to these reference stations. However, a comparison of data from the entire southwest lagoon of New Caledonia collected by Kulbicki (1991) indicates that density had not significantly changed and species richness and biomass had decreased between 1985–1988 and 1989–1991 (Table 6). Consequently, if an increase in commercial species is observed after protective measures were enforced, it is likely that this difference can be attributed to a reserve effect.

Temporal variation

Species richness and biomass of fish did not change significantly at reference stations between 1990 and 1994, but fish density increased significantly (by 89%). The increase in Chaetodontidae, a family generally associated with living corals (Hourigan et al. 1988; Russ 1991; Williams 1991), and Labridae could be explained by interannual variation, replenishment of living corals and copious fish recruitment between 1990 and 1994. The occurrence of numerous juveniles of Scaridae in 1994 is consistent with these hypotheses. No major hurricane had directly affected the southwest lagoon between 1991 and 1994, though New Caledonia is usually hit by hurricanes during the summer months (Anonymous 1981). In the tropical Indo-Pacific, recruitment of fish is at its peak during the summer months (Williams and Sale 1981; Munro and Williams 1985; Walsh 1987). Hurricanes have negative effects on coral reefs and their communities (e.g. Letourneur et al. 1993), reducing species richness and abundance of fish. The absence of major meteorological disturbances between 1991 and 1994 on the sampled sites may have induced better conditions for coral reef development and fish recruitment in 1994. Conversely, in 1990 most sampling took place after hurricane Lili (April 1989), Delilah (January 1989), Nancy (January 1990) and Hilda (March 1990). A few schools of Lethrinidae and Lutjanidae were also observed in 1994 and contributed noticeably to the increase in fish density. Sampling these species is difficult because of their schooling behaviour and such schools could have been present but not observed in 1990.

Marine reserve effects

Species richness per station, density and biomass of fish on the five islands studied changed significantly after five years of fishing prohibition. The increase in these characteristics (67% for species richness, 160% for density and 246% for biomass) was in marked contrast to unprotected reference stations where only an increase in density was observed. Consequently, it is likely that the changes observed on the protected islands during this study can be directly attributed to a marine reserve effect. The major edible and exploited fish families (Serranidae, Lutjanidae, Lethrinidae, Mullidae, Labridae, Scaridae, Acanthuridae and Siganidae) had increased. This increase is probably linked to fishing prohibition and decrease of habitat

destruction. Populations of Chaetodontidae, a non-target family considered as an index of the reef health, increased both in reserve and non-reserve areas. Therefore, there could be a combination of both marine reserve effect and changes in recruitment patterns over time.

The marine reserve effect was most marked on Amédée and least pronounced on Signal. This can be explained by a more effective enforcement on Amédée than on the other islands, namely a ranger living permanently on the island. Furthermore, Amédée is located offshore and is under the
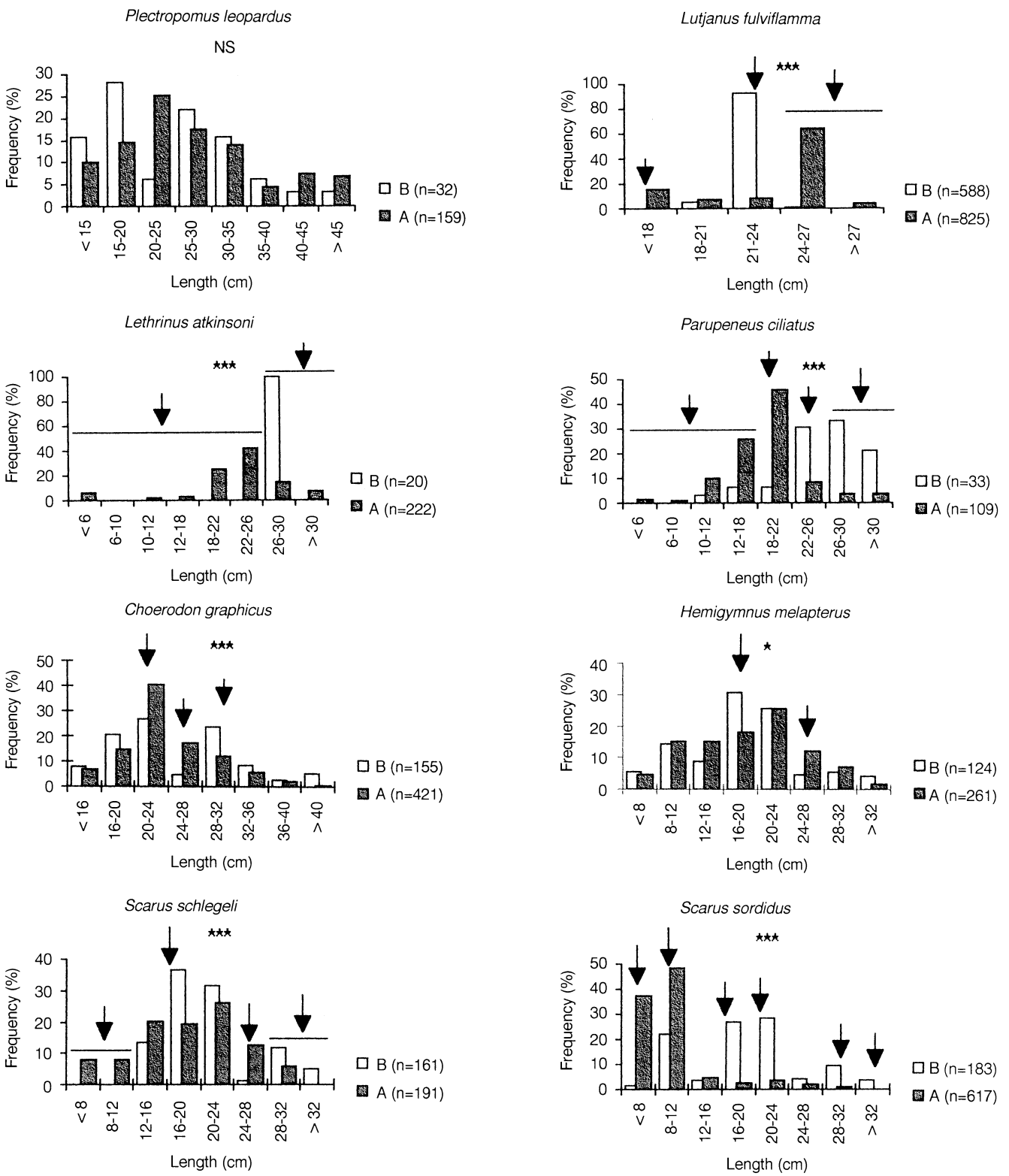

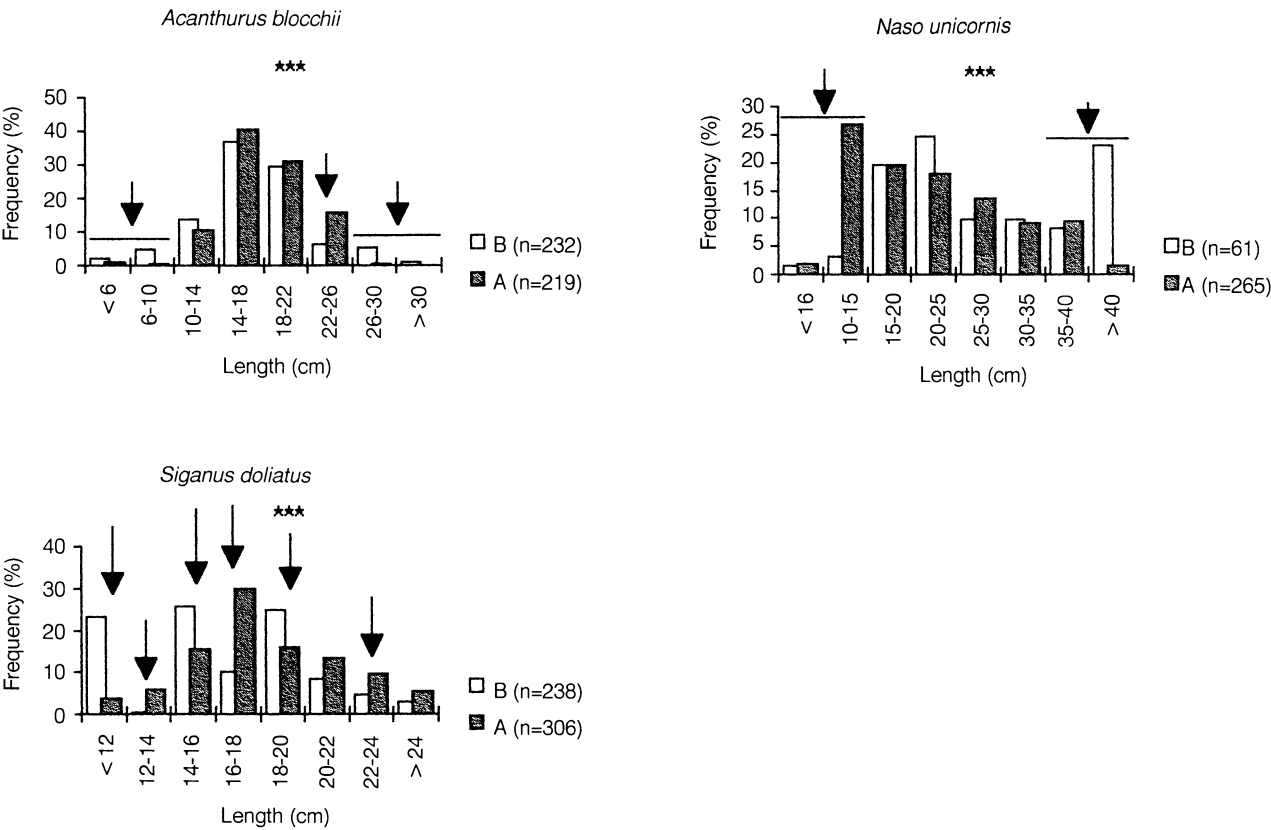**Fig. 5.** (for legend see next page)

Acanthurus blocchii

Naso unicornis

Siganus doliatus

Fig. 5. Length distribution of the major fish species on Amédée, Signal, Larégnère, Maître and Bailly, before (*B*) and after (*A*) marine reserves were created. Chi-square test was used to compare the length distributions (pooled classes are represented by *horizontal lines*); NS, not significant ($P > 0.05$); *, significant at $P < 0.05$; ***, significant at $P < 0.001$. Significant differences ($P < 0.05$) within length classes are marked by an *arrow*

influence of the nearby barrier reef. Terrigenous influence and pollution is limited there, and the reef is well developed with a high diversity of habitats (Holthus personal communicaton). Such reefs can be colonized by a high diversity and abundance of fish (Carpenter et al. 1981; Williams and Hatcher 1983; Roberts and Ormond 1987). On the other hand, surveillance was least effective

on Bailly, which is not patrolled regularly by coast guards. In addition, Bailly is located very close to the city of Mont Dore and can be easily reached by canoe. Consequently, fishing activities were still observed after the reserve was designated. Habitat diversity and reef area are low in the surroundings of Bailly. Therefore, migration and possibly recruitment could be lower on average at Bailly than at the offshore stations. On Signal, only biomass increased significantly; density did not change, possibly because schools of Lethrinidae (*Lethrinus harak*) and Lutjanidae
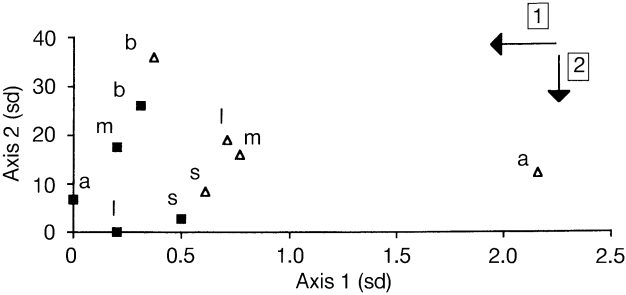

Fig. 6. Projection of the samples on the first two axes determined by the DCA. Δ, before marine reserves were created; ■, after marine reserves were created; *a*, Amédée; *s*, Signal; *l*, Larégnère; *m*, Maître; *b*, Bailly; axis 1, reserve effect; axis 2, inshore-offshore distribution; *sd*: standard deviation
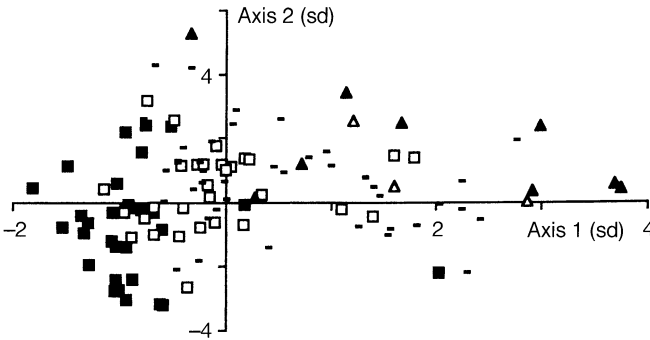

Fig. 7. Projection of the species on the first two axes determined by the DCA. Species names are listed in Table 5; ▲, species whose density was more than 10 times greater before marine reserves were created; Δ, species whose density was 3 to 10 times greater before marine reserves were created; ■, species whose density was more than 10 times greater after the marine reserves were created, □, species whose density was 3 to 10 times greater after the marine reserves were created; -, species which are not part of any group; *sd*: standard deviation

Table 5. Characteristic species of the fish assemblages of Amédée, Signal, Larégnère, Maître and Bailly before and after marine reserves were created, determined by the DCA

Species	Group		Species	Group	
Before			*Scarus chameleon*	■	
Epinephelus merra	Δ		*Scarus ghobban*	□	
Lutjanus gibbus	▲		*Scarus frenatus*	■	O
Lutjanus quinquelineatus	▲		*Scarus psittacus*	■	O
Lutjanus russeli	▲	I	*Scarus rivulatus*	■	I
Gnathodentex aurolineatus	▲	O	*Scarus rubrioviolaceus*	□	
Lethrinus genivittatus	Δ		*Acanthurus albipectoralis*	■	
Lethrinus nebulosus	▲	O	*Acanthurus mata*	□	O
Lethrinus obsoletus	▲		*Naso annulatus*	■	
Lethrinus rubrioperculatus	▲	O	*Naso brachycentron*	■	
Upeneus tragula	▲	I	*Naso brevirostris*	■	O
Kyphosus vaigiensis	Δ	I	*Naso litturatus*	■	
Heniochus singularis	▲		*Naso unicornis*	□	O
Siganus corallinus	▲	I	*Zebrasoma velliferum*	□	I
After			*Siganus puellus*	□	I
Cephalopholis argus	■		*Scomberomorus commerson*	□	O
Epinephelus caeruleopunctatus	□		**Not characteristic**		
Epinephelus fasciatus	□	O	*Cephalopholis boenack*	-	I
Epinephelus maculatus	■		*Cephalopholis urodeta*	-	O
Plectropomus laevis	■	I	*Epinephelus cyanopodus*	-	O
Plectropomus leopardus	□		*Epinephelus macrospilos*	-	
Variola louti	■	O	*Epinephelus polyphekadion*	-	I
Priacanthus hamrur	■	O	*Epinephelus ongus*	-	O
Caranx ignobilis	■		*Carangoides ferdau*	-	
Caranx melampygus	■		*Plectorhinchus goldmani*	-	
Aprion virescens	■	O	*Mulloides flavolineatus*	-	
Lutjanus bohar	■	O	*Parupeneus barberinus*	-	
Lutjanus fulviflamma	□		*Parupeneus cyclostomus*	-	
Lutjanus kasmira	■		*Parupeneus indicus*	-	I
Diagramma pictum	■		*Parupeneus pleurostigma*	-	
Gymnocranius sp.	■	O	*Parupeneus spilurus*	-	
Lethrinus atkinsoni	■	O	*Chaetodon auriga*	-	
Lethrinus harak	□		*Chaetodon benetti*	-	I
Lethrinus lentjan	■		*Chaetodon citrinellus*	-	
Lethrinus xanthochilus	■	O	*Chaetodon flavirostris*	-	
Monotaxis grandoculis	□	O	*Chaetodon kleinii*	-	I
Parupeneus ciliatus	□		*Chaetodon mertensii*	-	O
Parupeneus trifasciatus	□		*Chaetodon trifasciatus*	-	
Chaetodon baronessa	□		*Chaetodon ulietensis*	-	I
Chaetodon ephippium	□	I	*Chaetodon vagabundus*	-	
Chaetodon lineolatus	■		*Heniochus chrysostomus*	-	
Chaetodon melanotus	□		*Heniochus monoceros*	-	
Chaetodon ornatissimus	■	O	*Cheilinus chlorourus*	-	
Chaetodon pelewensis	□	O	*Scarus* spp.	-	
Chaetodon plebeius	□	I	*Scarus altipinis*	-	
Chaetodon speculum	□	I	*Scarus microrhinos*	-	O
Chaetodon trifascialis	□		*Scarus niger*	-	I
Chaetodon unimaculatus	□		*Scarus oviceps*	-	
Coradion altivelis	□	I	*Scarus schlegeli*	-	
Forcipiger flavissimus	■	O	*Acanthurus blochii*	-	I
Heniochus acuminatus	■		*Acanthurus dussumieri*	-	I
Heniochus varius	□	O	*Acanthurus nigricauda*	-	
Bodianus loxozonus	■	O	*Ctenochaetus striatus*	-	
Bodianus perditio	□		*Zebrasoma scopas*	-	
Cheilinus trilobatus	□	O	*Siganus argenteus*	-	
Choerodon graphicus	□	I	*Siganus doliatus*	-	
Coris aygula	■	O	*Siganus punctatus*	-	O
Hemigymnus melapterus	□		*Siganus spinus*	-	
Cetoscarus bicolor	■	O	*Siganus vulpinus*	-	
Hipposcarus longiceps	■	O			

Symbols refer to Fig. 7; Before, fish species characterizing the assemblages before marine reserves were created; After, fish species characterizing the assemblages after marine reserves were created; Not characteristic, fish species which do not characterize the marine reserve effect; ▲, species whose density was more than 10 times greater before marine reserves were created; Δ, species whose density was 3 to 10 times greater before marine reserves were created; ■, species whose density was more than 10 times greater after the marine reserves were created, □, species whose density was 3 to 10 times greater after the marine reserves were created; -, species not characteristic of the marine reserve effect; I, species characteristic of the inshore assemblages; O, species characteristic of the offshore assemblages

Table 6. Species richness per station, density and biomass of fish in the southwest lagoon of New Caledonia in 1985–1987 and 1988–1991 (data from Kulbicki 1991)

Southwest lagoon	Species richness per station	Density (fish m^{-2})	Biomass (g m^{-2})	Number of stations
1985–1988	29.1 ± 2.2	0.431 ± 0.056	97.1 ± 14.7	174
1989–1991	32.7 ± 2.0	0.696 ± 0.387	70.8 ± 10.3	133
Difference	*	NS	**	

A Student test was used to test the differences; NS, not significant ($P > 0.05$); *, significant at $P < 0.05$; **, significant at $P < 0.01$; 95% confidence of means are given

(*Lutjanus quinquelineatus*) were observed before protection was effective, but not in 1994. As stated for the reference stations, the sampling of these schooling species was inadequate. It is possible that schools of these species were present in 1994 but not censused.

Our results support the hypothesis that the creation of marine reserves develops fish stocks. Similar results were reported in the Philippines, where total fish abundance increased in three reserves over a one year period of protection (White 1986). Unfortunately, no data were given on the temporal variability of the fish communities. Comparison between fished and unfished areas from elsewhere support our results (Russ 1985; Alcala 1988; Russ and Alcala 1989; Polunin and Roberts 1993; Roberts and Polunin 1992), but the differences might be attributed to spatial variability. Another effect usually attributed to marine reserve is an increase of the average size of target species (Russ 1985; McClanahan and Muthiga 1988; Roberts and Polunin 1991). In the present study, there has been an influx of small fish (i.e. by recruitment). Habitat protection and low disturbance in marine reserves may have enhanced settlement rates (Roberts and Polunin 1991) and recruitment may have been more effective after the islands were protected. Larger specimens may be located in deeper water, e.g. Lutjanidae, Lethrinidae and to a lower extent Serranidae that venture over soft bottoms, but this is unlikely for the other reef fish families censused (Wantiez 1992, 1993). However, large specimens of *Plectropomus leopardus*, *Lutjanus fulviflamma*, *Lethrinus atkinsoni* and *Siganus doliatus* have been observed in the protected areas.

According to the present analysis, marine reserves modified the community structure of the fish fauna. After protective measures were taken, the relative importance of numerous species (large carnivorous, Scaridae and Acanthuridae) increased in the community because of fishing prohibition and a likely modification of behaviour over time (Russ 1991), with fish becoming less cautious. Protection of spawning stock biomass, development of fish populations, protection of population age structure, improvement of the habitat are confirmed by our results. Further studies need to be conducted to confirm whether marine reserves ensure recruitment for adjacent sites and export adult fish.

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