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Considering multiple-species attributes to understand better the effects of successive changes in protection status on a coral reef fish assemblage

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Abstract:

The response of fish assemblages to changes in protection status is a major issue for both biodiversity conservation and fishery management. In New Caledonia, the Aboré reef marine reserve harbours more than 500 fish species, and has been subjected to changes in protection status since 1988. The present study investigates the impact of these changes on a wide subset of species (213), based on underwater visual counts collected before the opening and after the closure to fishing of this marine protected area (MPA). We analysed the spatial and temporal variability in fish assemblage attributable to protection status, explicitly considering habitat. To understand the successive responses of fish assemblage to fishing and protection, the assessment models included four criteria defining species groups that partition the fish assemblage: trophic regime, adult size, mobility, and interest for fishing. We could therefore identify the negative impact of opening the MPA to fishing on piscivores and highly mobile species. Surprisingly, target species were not affected more than non-target species. Model results were used to identify species groups that respond to fishing and protection. These results utilize fisheries-related criteria to provide new insight into the response of fish assemblages to protection from the perspective of MPA monitoring.

Keywords: assessment model, coral reef ecosystem, fish assemblage, fishing effect, MPA effect

1. Introduction

A key issue in tropical areas is the impact of the huge diversity found on tropical reefs on the effect of management measures. In particular one may question the relative impact of such measures on the species composition of fish assemblages and their capacity of adaptation and their resilience knowing that these highly diverse assemblages are subject to a number of anthropogenic and natural disturbances (Hughes, 1994; Connell, 1997; Nyström and Folke, 2001). In New Caledonia, recreational and subsistence fishing activities, mining and industrial activities, growing population and the development of tourism have all had a negative impact on the reef systems (Labrosse *et al.*, 2000).
MPAs are acknowledged as a major tool for biodiversity conservation and fisheries management (Agardy*,* 1994; Sumaila *et al.,* 2000) but they can also be seen as an instrument for an experimental approach aimed at improving our understanding of how communities respond to fishing. In this respect, MPAs are a tool for actively adaptive management in the sense of Walters and Hilborn (1976).
Many studies have focused particularly on marine reserves and assessed their effects on fish assemblages and on marine organisms (see reviews by Roberts and Polunin, 1991; Russ, 2002; Halpern, 2003; Pelletier *et al.*, 2005). In most existing papers, the impact of reserve or fishing experiments was assessed on a taxonomic basis (usually families) (e.g. Alcala, 1988; Jennings *et al.*, 1996; McClanahan and Kaunda-Arara, 1996; Russ and Alcala, 1998) or for species bearing particular importance in the context of the study (e.g. García-Rubies and Zabala, 1990; Letourneur, 1996; Edgar and Barrett, 1999; Johnson *et al.*, 1999). Methods have classically tested differences in density, biomass and species richness between the reserve and a comparable zone. Few studies have evaluated reserve effects by grouping species other than at a taxonomic level; most have considered only a limited number of species or sometimes trophic groups (e.g. Russ and Alcala, 1996).
Assessment for a given species or species group does not provide a synoptic view of the impact of the reserve. Assessing the impact of a reserve at the fish assemblage level is more desirable in providing scientific elements for an ecosystem approach to management (Botsford *et al.*, 1997; Jennings and Kaiser, 1998). This is particularly true in coral ecosystem where diversity is particularly high (over 600 observable species in New Caledonia according to Kulbicki et al., 2007). The structure of the assemblage can be analyzed based on taxonomic, ecological or economic grouping of species. This approach has been at the heart of several studies on the effects of MPAs on the reef fish assemblages of New Caledonia (Ferraris *et al.*, 2005; Amand *et al.,* 2004; Kulbicki et al., 2007). These first studies have demonstrated the advantage of multi-species groups over single species approaches in these highly diversified systems.
The objective of this study is to assess the effects of successive changes in protection status on the fish assemblage of the Aboré reef reserve. Located in the South Lagoon of New Caledonia, SW Pacific Ocean, this MPA had been in place for three years, when part of it was open to fishing. Two years later, it was closed to fishing again. Fish assemblages were surveyed before and after the opening and the closure. We anticipated that changes in the fish assemblage would vary according to environmental factors and hypothesized that species attributes such as diet, species size, home range or interest for fishing would be important factors in this variation. For instance, highly targeted species may be more impacted by fishing than less valued ones, and mobile species may be less affected than sedentary ones.

2. Material and methods

The Aboré reef reserve MPA has been studied by Amand et al. (2004), Ferraris et al. (2005) and Kulbicki et al. (2007) and this present study contributes distinct data sets and time frames. Earlier studies used data from censuses where all fish species were recorded, resulting in more than four hundred species observed, but it could only be performed by highly trained divers and the number of replicates was necessarily low (69) as these censuses were time consuming. Data used in the present study pertain to a restricted list of species (213), but correspond to a much larger number of transects (212) and could thus be performed by less trained divers.

Several factors that might explain the variations of observed fish counts independently of protection status were investigated. Then, the impacts of opening the area to fishing and the second closure of the area were tested using a range of biological responses such as species richness, abundance, biomass and mean individual size. The fish assemblage was partitioned based on mobility, trophic regime, adult size and interest for fishing, and each response was calculated according to the different partitions. By crossing variables and partitions of fish assemblage the metrics per species group could be analyzed and the effects of changes in protection status at the fish assemblage level were assessed simultaneously. We were able to demonstrate the benefits of our approach, by comparing these results with an overall approach considering responses averaged over all species. The partitioning provided insights to better understand the effects of such changes on the fish assemblage.

2.1. Study area

The Nouméa lagoon, located in New Caledonia, SW Pacific Ocean (Figure 1), is a large lagoon seascape including coral reefs where several marine reserves (no take zones) were established in the 1980s to protect the coral reef ecosystem from the impacts of fishing. The present study took place in the Aboré reef reserve, located on a 25 km-long barrier reef, 20 km off Nouméa, and representing about 15 000 ha. The area was closed to fishing from 1988 to 1993, and then two-thirds of the reef (area B) were again opened to fishing from August 1993 until July 1995 for a fishing experiment. The opening of the reserve immediately resulted in an intense fishing pressure; in the first two weeks, eight hundred boats were observed and the fish yield was 8.7 tons as estimated from a sampling of 57% of these boats (Sarramégna, 2000). These levels more or less corresponded to what had previously been observed over an entire year (Sarramégna, 2000). The whole reef has been closed to fishing since August 1995 (Figure 2; Table 1).

2.2. Sampling protocol

The impact of allowing fishing in the reserve and the restoration effect after the final closure on fish assemblage was monitored from 3 surveys. In July 1993, a survey was performed using 60 transects in 5 locations spaced along the reef (Figure 2), just before resumption of fishing on two-thirds of the Aboré reef (area B, Figure 2), while one third remained closed (area A). In July 1995, a second survey of 110 transects was conducted on both the area A closed to fishing and the area B open to fishing. Area B was closed again to fishing in September 1995, resulting in the entire closure of the Aboré reef for the second time. Six years later, in 2001, a third survey of 42 transects was conducted on the Aboré reef MPA (Table 1). The experimental design stratified the reef into 2 geomorphological zones: the inner reef flat and the inner reef slope (Figure 2). The reef flat is a very shallow area ranging from 0.7 to 1.5 m, whereas the inner reef slope is an intermediate zone between the reef flat and the sandy bottom lagoon, with inner spurs and grooves (Battistini *et al.*, 1975). For each of the 3 years surveyed, the 5 sampling locations regularly spaced along the reef were selected to ensure a good longitudinal coverage where both geomorphological zones were present (Figure 2). At each location for each geomorphological zone, at least 2 transects, 500 m apart, were sampled (see Table 2 for sampling design by year, area and geomorphological zone).

Our study is based on so-called commercial transects during which 213 species corresponding to 32 families from a restricted list were counted, including all fished species plus a number of species of scientific interest. Quantitative estimates of abundance of coral reef fishes using the 'distance sampling' method (Buckland *et al.*, 2001) were made using underwater visual census (UVC) (Kulbicki and Sarramégna, 1999). Fifty m transects were marked by lines set on the bottom. A diver swam along the transect line and recorded fishes of the species list mentioned above. For each observation, the diver recorded the species and the size of the fish. Biomass of each fish was calculated through available length-weight relationships (Kulbicki *et al.*, 2005; Kulbicki, 2006).

2.3. Partitioning the fish assemblage

Choosing criteria for constructing species groups raised the question of defining partitions of the fish assemblage that would be relevant to the impact of protection status. Four criteria were used: mobility, interest for fishing, trophic guild (feeding habits) and adult size. Following Grimaud and Kulbicki (1998), four mobility groups were defined: (1) territorial species with a very restricted range (usually <10 m²), (2) sedentary species with a restricted range (10 to several 100 m²), (3) weakly mobile species often distributed over the entire reef area (up to several 1000 m²) and (4) highly mobile species usually foraging over very large areas. Species groups corresponding to distinct interests for fishing were defined based on Jollit *et al.* (unpublished): (1) highly targeted by spear fishing, (2) moderately targeted by spear fishing, (3) incidentally targeted by spear fishing, (4) highly targeted by line fishing, (5) moderately targeted by line fishing, (6) bycatch of line fishing, and (7) not fished. The trophic groupings were based on diet composition following the results of Ferraris et al. (2005): (1) piscivores, (2) macrocarnivores, (3) microcarnivores, (4) coral feeders, (5) herbivores, (6) microalgae feeders and detritivores, and (7) zooplankton feeders. Six size classes were defined based on adult sizes (Kulbicki, 2006): (1) 0-7 cm, (2) 8-15 cm, (3) 16-30 cm, (4) 31-50 cm, (6) larger than 50 cm.

2.4. Data analysis

We aimed at testing the impact on the whole fish assemblage of both the fishing effect after removal of reserve status and the definitive closure of the B area. Thus, we assessed these effects at two levels: i) overall variables per transect, namely species richness, abundance, and biomass summed over all species; and ii) metrics computed per species group, namely species richness, abundance, biomass, and mean size per species group. Both the criteria to group the species and the variables define a set of metrics.

The methods used to assess the effects of changes in protection status upon the fish assemblage, involved both exploratory and inferential techniques. Exploratory techniques relied on the use of non-metric multidimensional scaling (MDS) to graphically display similarities between transects measured by the Bray-Curtis coefficient. The representativeness of the plots was evaluated by the stress value (Clarke and Warwick, 2001). Using the PRIMER software, we could visualize the influence of a factor of interest (like year or habitat) to explain differences among transects.

Inferential techniques include one-way ANalysis Of SIMilarities (ANOSIM) which rests on a permutation procedure to test whether a factor significantly explains differences between groups of transects (Clarke and Warwick, 2001). To perform this test (using the PRIMER software), similarities between transects were calculated using the Bray-Curtis coefficient. ANOSIM tests were based on 999 permutations of the transects between factor levels. Aside from ANOSIM, Generalized Linear Models (GLM) (McCullagh and Nelder, 1989) were performed using R software, with suitable data distribution depending on the variable modelled to test and assess the effects of both removal and closure of area B in 1995, while accounting for other factors that were relevant to explain the variability of the fish assemblage.

As the UVCs were performed by several divers, we first explored potential diver effects on variations in visual counts, using MDS plots, and ANOSIM applied to abundance, biomass and mean size data. Significant diver effects were detected, and thus an observer term was included as a factor in subsequent analyses in the way to consider the variability of counts brought by diversity of divers.

In addition to the four factors considered for models of overall metrics (year, area, habitat and diver), models of metrics per species group also included the species group factor, with levels depending on the species grouping criterion as described earlier in this section i.e. mobility (4 levels), interest for fishing (7 levels), trophic regime (7 levels), and size class (6 levels). These models included first-order interactions between factors (except for the diver factor), and in addition second-order interactions between year, area and species group, in order to assess possible species-group-specific effects of protection status. For overall metrics, one model was fitted for each variable, while for metrics per species group, one model was fitted for each combination of variable and species grouping criterion.

All metrics per species group were modelled in two steps: a binomial model for presence/absence and a lognormal model on non-zero values of corresponding metrics following the procedure proposed by Stefánsson (1996). This method is suited for quantitative data with large proportions of zero values that makes them unable to meet the assumptions of regular GLMs. Modelling non-zero values led to sixteen model fits, crossing four metrics (abundance, biomass, mean size and species richness per species group) with four grouping criteria. The goodness-of-fit of each model was assessed through adjusted R^2 and global Fisher tests, and the conformity of model residuals to linear model assumptions was checked from standard residual plots and tests (Venables and Ripley, 1997). Once validated, models were selected to eliminate non-significant terms, based on the Akaike Information Criterion (AIC) (Akaike, 1974). The significance of each effect was evaluated through the analysis of variance table based on the Type III sums of squares.

Regarding protection status, we were interested in both the fishing effect after removal of reserve status, and the definitive closure of B area. The effects of these changes in protection status were assessed and tested through the interaction between the year and the area (A/B) factors (year*area) for overall metrics, and in addition through the interaction between the year, area and species group factors (year*area*species group) for metrics per species group. When only the first order interaction between area and year was significant, all species groups responded in the same way to changes of protection status. The magnitude and direction of the effect was quantified by computing adjusted means per area, year and species group. Adjusted means correspond to predictions of the modelled metric based on the significant effects of the model, thus leaving aside residual variations. In the analysis, adjusted means were computed for the year, area and species group factors, while controlling for the diver effect. Multiple comparisons were performed using the Bonferroni correction for the following differences in adjusted means: (1) spatial difference between areas A and B in 1993, i.e. prior to the removal of reserve status; (2) temporal variation in area A and B between 1993, 1995 and 2001; (3) spatial difference between areas A and B in 1995 and 2001. When the second-order interaction between area, year and species group was significant, simultaneous confidence intervals were constructed per species group.

3. Results

3.1. Assessment of changes in protection status on overall metrics per transects.

Variations in species richness, abundance and biomass per transect depended on the area (Figure 3, Table 3). Mean species richness increased between 1993 and 1995 in area A then decreased in 2001, while in area B, it increased over the whole time period. Overall abundance per transect consistently decreased in both areas over the same period with a stronger decrease between 1993 and 1995 in area B and a stronger decrease between 1995 and 2001 in area A. Similarly, mean biomass decreased in both areas with a much more important decline in area A between 1993 and 1995.

The observed trends were validated by significant models for overall metrics and for metrics per species group. In all models, residuals (not reported) conformed well to linear model assumptions, the global *F*-test was highly significant, although the variance explained by these models was quite low (Table 4). For these overall metrics, the diver effect was significant and well accounted for by the models (Table 4). There was no significant interaction between area and year, meaning that no effect of the 1993 fishing event, nor the 1995 closure could be detected from the species richness, abundance, or biomass data. In contrast, both abundance (p=0.0003) and biomass (p=0.0027) decreased over the years surveyed as observed previously (Table 4). Species richness varied by area (p=0.0003) (Table 4) and both biomass and species richness were significantly lower in the inner reel flat zone (p=0.0003 and p<0.0001, respectively).

3.2. Changes in protection status and species attributes

The probability of occurrence of all adult size groups that was lower in area A than in area B in 1993 while the difference was the other way around in 1995, showing a significant effect of protection status (p<0.02) (Table 5). In all presence/absence models, the species group factor was highly significant (p<0.01), illustrating differences in average occurrence between species groups irrespective of how they were defined.

Variations in abundance and species richness were the metrics which were best described by the models in all species groups (Table 6). In order to rank factors according to their influence, we used the number of significant effects in the 16 models fitted (Table 7). Diver identity and species group effects were significant in all models, and thus explained more variance than spatial or temporal effects. First-order interactions involving the species group factor were also highly significant, pointing out the differences in response between groups to the effects of year, area and habitat.

The change in protection status significantly affected mean size in the groups defined by fishing interest (p<0.01). Protection status also significantly affected abundance in the different mobility grouping (p<0.01), as well as biomass in the different trophic groupings (0.05<p<0.01). The adjusted means (Figures 4-6) based on year, area and species group effects (see Methods section) illustrate the species group effects and the additive diver effect (Table 5).

Regarding the mobility criterion, between 1993 and 1995 (fishing period in area B), the abundance of sedentary species rose in area B and declined in area A, while the abundance of all other groups declined, particularly between 1995 and 2001 (Figure 4), but the only significant variation over time was the decline of highly mobile fishes in area B between 1993 and 1995, which can be explained

by the fishing impact. The abundance of this group remained stable after 1995, corroborating a relative protection effect.
Considering trophic groups (Figure 5), a decline in biomass between 1993 and 1995 was observed for all groups in both areas but zooplankton feeders. Yet, this decline was only significant for piscivores in area B in relation with the opening to fishing (note that 43% of piscivores were species highly or moderately targeted by both spear and line fishing). Macrocarnivores showed a global decline of biomass in both areas, with a biomass significantly lower in area B (fished) than in area A (no-take) in 1995. Between 1995 and 2001, all trophic groups tended to decline, except piscivores whose biomass increased slightly. Similar trends in abundance were observed also in area A. Zooplankton feeders display an inverse pattern in area B. Yet, almost half of the species in this group are highly or moderately targeted by spear fishing.
Finally, mean size in the different fishing interest groups showed a variety of patterns over time in areas A and B (Figure 6). Between 1993 and 1995, mean size decreased for most groups in both areas, except for species moderately targeted by line fishing, bycatch of line fishing, and for unfished species. As expected, unfished species were not affected by the opening to fishing, and species moderately targeted by line fishing and bycatch of line fishing declined in B while remaining stable in A between 1993 and 1995. After the final closure of area B, between 1995 and 2001, the mean size of several groups further declined in both areas. The decline was mitigated in both areas for species highly targeted by line fishing, and in area B for bycatch and moderate targets of line fishing. For these two groups, the decline in mean size was larger in area A. The mean size of species caught by spear fishing declined but not significantly and over the three years in both areas.
Note that no species group-specific protection status effect was found for the adult size criterion (Table 6).

4. Discussion

4.1. Spatio-temporal variations of the fish assemblage

First order interaction of year, area, and habitat with species groupings demonstrate that the complexity of variations in the measured abundance, species richness and biomass of the fish assemblage. The factors that determined significant single effects in the models were the year, habitat and diver factors. The significance level of the diver factor required the explicit inclusion of this factor in our models to control for observer variability. This aspect is often ignored or omitted in the literature.
Regarding temporal variations, a significant effect involving at least the year factor was found in 18 out of the 23 fitted models in the whole study. Such variations corresponded to decreases over time of the studied metrics, a result that was also pointed by Kulbicki *et al.* (2007), although from distinct approaches. The causes of such temporal variations remain poorly understood and are obviously linked to factors that cannot be accounted for in such models. Undoubtedly, environmental fluctuations and events explain some of these variations and mask the effects of changes in protection status. For example, large scale oceanographic and climatic features such as El Niño Southern Oscillation (ENSO) events are known to largely influence water conditions (temperatures for example) and may seriously affect habitats and disrupt benthic populations and their reproductive success (Allison *et al.*, 2003). Cyclonic events are also likely to occur in the studied area, and while no critical event took place during the period under study, consequences of such events may be observed on longer time scales. Other events like the strong winds that prevailed during the 1995 survey could also explain part of the variations under study. But without sampling outside of the MPA and over a long temporal series, it is difficult to detect effects of long term phenomena.
Based on inferential models, we could assess the effects of changes of protection status through the interaction between year and area factors for a range of metrics. Overall abundance, biomass and species richness proved not be sensitive to changes in protection status. Regarding metrics per species group, a few metrics, namely piscivore biomass, the abundance of highly mobile species and the mean size of line fishing bycatch, displayed significant variations that were consistent with the changes in protection status endured by the fish assemblage. Several other metrics showed non-significant variations which tended to be consistent with these changes, e.g. the biomass of herbivores, the mean size of species moderately targeted by line fishing and species highly targeted by line fishing. Other variations could not be easily related to changes in

protection status and overall there were few significant year*area interactions. In a number of cases, declining patterns observed in both A and B suggest a strong connection between these two adjoining areas. Such exchanges would inevitably reduce spatial differences in fish assemblage between A and B and therefore contribute to the lack of significant protection effects. The spillover of individuals from A to B would mitigate the decrease in B and/or the regeneration in A. Larval dispersion and larval settling depend on hydrodynamics that operate at scales larger than the MPA and may also contribute but are poorly known in this area. Fish movements may be particularly important in such coral reef formations consisting of linear barrier and multiple islands and coral patches. This point is confirmed by Chateau and Wantiez (2009) who recently showed that fish mobility in the Caledonian lagoon is more important than previously considered.
Habitat was a determining factor for explaining variations of the fish assemblage, even approximated at the scale of the geomorphological zone (significant factor in 14 models out of the 23 fitted). Geomorphological zones indeed correspond to distinct depth and coral type (Ferraris *et al.*, 2005). Therefore environmental variations affecting coral cover and reef structure may ultimately be reflected in spatio-temporal variations of fish assemblages. Fine scale changes in habitat structure may help to improve the explanatory power of the models (Ferraris *et al.*, 2005), but such data were not available for inclusion in our analysis. Ferraris et al. (2005) showed that while accounting for fine-scale habitat data improved model fits, the degree of significance of the effects was only improved marginally. In addition, poaching may occur in the MPA that will mitigate the effect of protection. Another hypothesis is that the general decline of fish populations in the whole SW lagoon is related to the increase in human population (that occurs in Nouméa region) and the evolution of fishing methods. Fishes of the reserve migrate to zones out of the MPA as these other areas become depopulated. The simultaneous decline in abundance of most of the groups, fished or not, argues against the direct impacts of fishing.

4.2. Partitioning the fish assemblage

One of our objectives was to utilize species attributes to better understand the consequences of changes in protection status on the fish assemblage. Partitioning the fish assemblage according to a range of criteria provided a variety of insights, and is a step toward an ecosystem-approach to MPA assessment. In fact, the models of overall metrics displayed few significant effects, and none in relation to changes in protection status. In contrast, metrics per species groups revealed a larger number of significant effects, most of which included the species group factor, which means that for a given species grouping criterion, the variation of the metric modelled differed across the species groups. Accordingly, corresponding models explained a much larger fraction of variance (up to 77%) compared to models of overall metrics (less than 30%). Therefore, including species attributes in the models improved the assessment. This method revealed that piscivores and highly mobile species were groups who react the most to opening to fishing (figures 4 and 5).
However, some of our results are not intuitive. Hence, significant effects of changes in protection status were detected for very mobile species, which a priori can move easily between areas A and B. This kind of effect is generally not expected. It is therefore important to note that 58% of the species of the highly mobile group are also species targeted or highly targeted by spear or line fishers. Yet, the abundance of these fishing groups was not significantly affected by changes in protection status. One could hypothesize that highly mobile species may have left area B after the opening to go to other reef areas with lower fishing pressure, including (but not exclusively) area A. Likewise, one could argue that partitioning species according to their interest for fishing gave few striking results, species strongly targeted by the main fishing gears showing little sensitivity to the opening of fishing. Beyond considerations about area connectivity, fish mobility and interest for fishing, these counter-intuitive results raise the question of defining species groups that are relevant to assess the effects of changes in protection status. One could thus contemplate to define groups based on the combination of two or more criteria.

4.3. Sampling considerations

Given the complexity of the data set, models appropriate to test the effects of changes in protection status had to include a relatively large number of explanatory factors: year, area, habitat, and diver. Although the number of observations was overall large (212 transects), it may not have been sufficient to unravel the variability attributable to these four factors.
In other studies of the Aboré reef fish assemblage, Ferraris *et al.* (2005), Amand *et al.* (2004) and Kulbicki *et al.* (2007) used a different set of observations based on the census of all observed

species for only two years, 1993 and 1995. The data set included only ca. 70 transects versus more than 200 (out of which 170 for both 1993 and 1995) in the present study. A larger number of significant interactions involving year and area were found in these two studies, including intuitive results. Although the data had been collected by several divers, subsequent variability was not problematic to evidence the effects at stake.

Note that the above works only dealt with the 1993-1995 variation, a fishing effect that was probably more conspicuous than a restoration effect. Yet, in the present study, this fishing effect was not so obviously detected. This lack of significance raises the question of additional sources of variability, such as the diver effect (between-diver variability in our data set and difference in divers between the other references and the present study). It may also be related to the issue of the species list retained for the visual counts. Note that the stratification of the sampling scheme and the geographical range of stations were the same in both data sets.

The present results lead us to conclude that additional sources of variation prevented us in this case from detecting the effects of changes in protection status (particularly the restoration effect), such as those mentioned hereabove in the discussion. When it comes to assessing restoration effects between 1995 and 2001, data is only available for 2001, with a lesser number of transects than the other two dates. Monitoring the restoration of the fish assemblage would require observations collected at several dates after the final closure.

Assessing the response of fish assemblages to changes in protection status is a major issue for fisheries management. This work sheds original insight into the issue of designing adequate protocols for monitoring MPA in terms of conservation of biodiversity and sustainable exploitation of resources. In this respect, considering species attributes was useful and the partitioning criteria considered provided a variety of insights to better understand the effects of such changes on the fish assemblage. Although based on a coral reef ecosystem case, our findings may be applied to other contexts.

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Tables

Table 1. Evolution of the protection status on the Aboré reef.

	Area A	Area B
1988 August	Closure to fishing	Closure to fishing
1993 July (first survey)	Closed	Closed
1993 September	Fishing closure maintained	Opened to fishing
1995 July (second survey)	Closed	Opened
1995 September	Fishing closure maintained	Closure to fishing
2001 August (third survey)	Closed	Closed

Table 2. Sampling scheme, reporting the number of transects per geomorphological zone, area (A and B) and year.

	A			B		
Geomorphological zone	1993	1995	2001	1993	1995	2001
Reef flat	12	16	10	18	24	8
Inner slope	12	32	8	18	38	16
Subtotal	24	48	18	36	62	24

Table 3. Means of overall variable by area and year.

	A			B		
	1993	1995	2001	1993	1995	2001
Species richness	22.8 ±7.5	24.2 ±6.9	21.0 ±4.4	19.2 ±6.1	20.6 ±6.55	21.2 ±5.6
Abundance	200.8 ±76.3	192.5 ±96.5	132.6 ±69.9	220.0 ±107.4	195.1 ±109.2	162.7 ±64.57
Biomass	45.3 ±48.8	23.6 ±19.8	13.4 ±12.6	26.6 ±19.5	21.8 ±17.0	15.2 ±11.9

Table 4. Model results for overall metrics per transect: significant effects and adjusted R^2. All effects are significant with $p < 0.01$.

Metric	Model	R^2
Species richness	**area** + **habitat** + **diver**	0.27
Abundance	**year** + **diver**	0.21
Biomass	**year** + **habitat** + **diver**	0.30

Table 5. Models of presence/absence per species group, with goodness-of-fit statistics. Significativity of factors is express by bold: highly significant effects ($p<0.01$); underlined: significant effects ($0.05>p>0.01$); italics: for non-significant effects ($p>0.05$).

Criterion	Effects retained	R^2
Mobility	**year + diver** + **mobility**	0.92
Trophic	year + **habitat** + **area** + **trophic**	0.49
Interest for fishing	*habitat* + *area* + **fishing** + diver + **habitat:fishing** + area:fishing	0.53
Adult size	**year** + **habitat** + *area* + **diver** + **adultsize** + **year:area** + **year:adultsize**	0.76

Table 6. Effects and goodness-of-fit (R^2) for models fit on non-zero values of metrics per species group. Bold: highly significant effects (p<0.01); underlined: significant effects (0.05>p>0.01); italics: for non-significant effects (p > 0.05).

Criterion	Metric	Effects retained	R^2
Mobility	Abundance	year + *habitat* + *area* + **diver** + **mobility** + **year:mobility** + **area:mobility** + **habitat:mobility** + **year:area:mobility**	0.58
	Biomass	*year* + **habitat** + *area* + **diver** + **mobility** + **year:mobility** + **habitat:mobility** + **area:mobility**	0.48
	Mean size	**year** + **habitat** + *area* + **diver** + **mobility** + year:mobility + **habitat:mobility**	0.34
	Species Richness	*year* **+** *habitat* **+** *area* **+ diver + mobility +** area:mobility	0.56
Trophic	Abundance	**year** + **habitat** + **area** + **diver** + **trophic** + *year:trophic* + **habitat:trophic** + **area:trophic**	0.77
	Biomass	**year** + **habitat** + *area* + **diver** + **trophic** + **year:trophic** + **habitat:trophic** + **area:trophic** + year:area:trophic	0.60
	Mean size	**year** + **habitat** + **diver** + **trophic** + **year:habitat** + **year:trophic**	0.44
	Species Richness	*year* + *habitat* + *area* + **diver** + **trophic** + **year:trophic** + **aire:trophic**	0.74
Interest for fishing	Abundance	**year** + *habitat* + *area* + **diver** + **fishing** + **year:fishing** + **habitat:fishing** + **area:fishing**	0.67
	Biomass	**year** + **habitat** + area + **diver** + **fishing** + **year:fishing** + **habitat:fishing** + **area: fishing**	0.54
	Mean size	**year + habitat +** *area* **+ diver + fishing +** year:area **+ year:fishing + year:area:fishing**	0.45
	Species Richness	**year + habitat + area + diver + fishing + year:fishing + habitat:fishing + area:fishing**	0.60
Adult size	Abundance	**year** + *habitat* + *area* + **diver** + **adultsize** + **year:adultsize** + **habitat:adultsize** + **area:adultsize**	0.77
	Biomass	**year** + **habitat** + *area* + **diver** + **adultsize** + **year:adultsize** + **habitat:adultsize** + **area:adultsize**	0.51

	Mean size	**year** + **habitat** + *area* + **diver** + **adultsize** + **year:adultsize** + **habitat:adultsize**	0.63
	Species Richness	**year** + *habitat* + *area* + **diver** + **adultsize** + **year:adultsize** + **habitat:adultsize + area:adultsize**	0.59

Table 7. Classification of models' factors by number of highly significant ($p<0.01$) and significant ($0.01<p<0.05$) occurrences in the 16 models of Table 6.

Factor	Number of highly significant occurrences	Number of significant occurrences
Diver	16**	
Group	16**	
Year:group	13**	1*
Year	12**	1*
Area:group	11**	1*
Habitat:group	11**	1*
Habitat	10**	
Area	2**	1*
Year:area:group	2**	1*
Year:habitat	1**	
Year:area	1*	

Figures

Figure 1. Geographic location of the studied area (Aboré reef) in the southern lagoon of New Caledonia, SW Pacific.

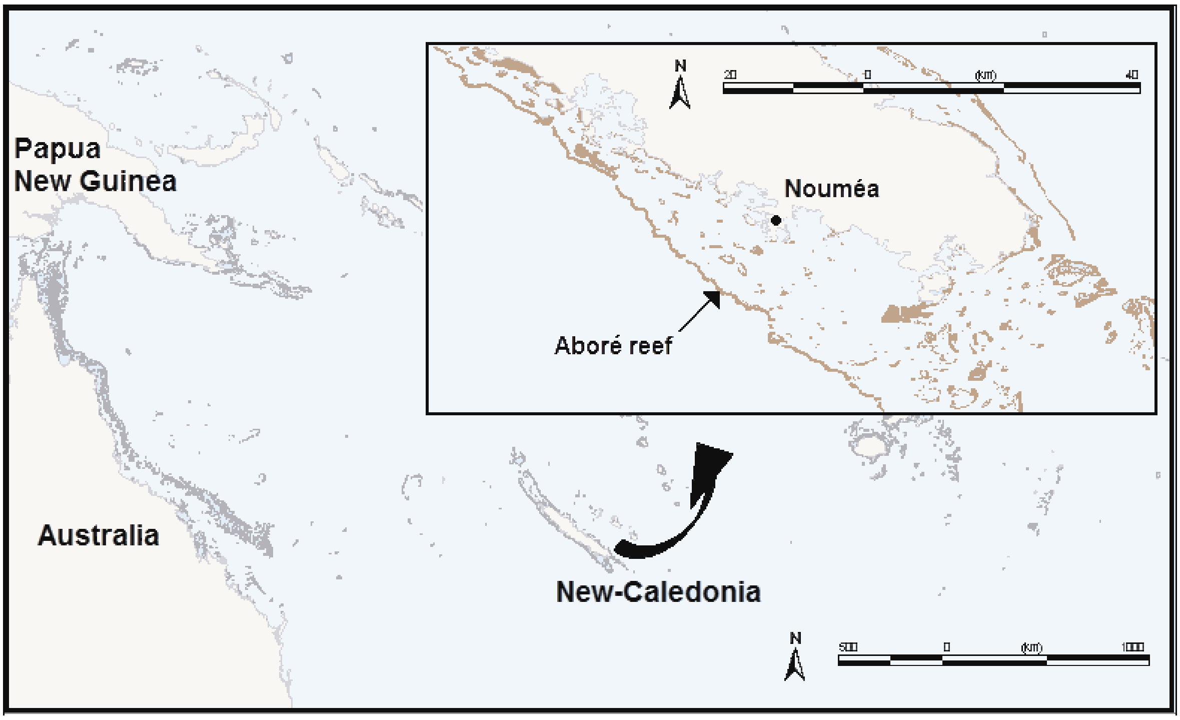

Figure 2. Sketch of the Aboré barrier reef, displaying i) the area A that has always been closed since 1990; ii) the area B that has been open to fishing between 1993 and 1995, and iii) the sampling locations crossing the two sampled habitats: inner reef flat and inner reef slope.

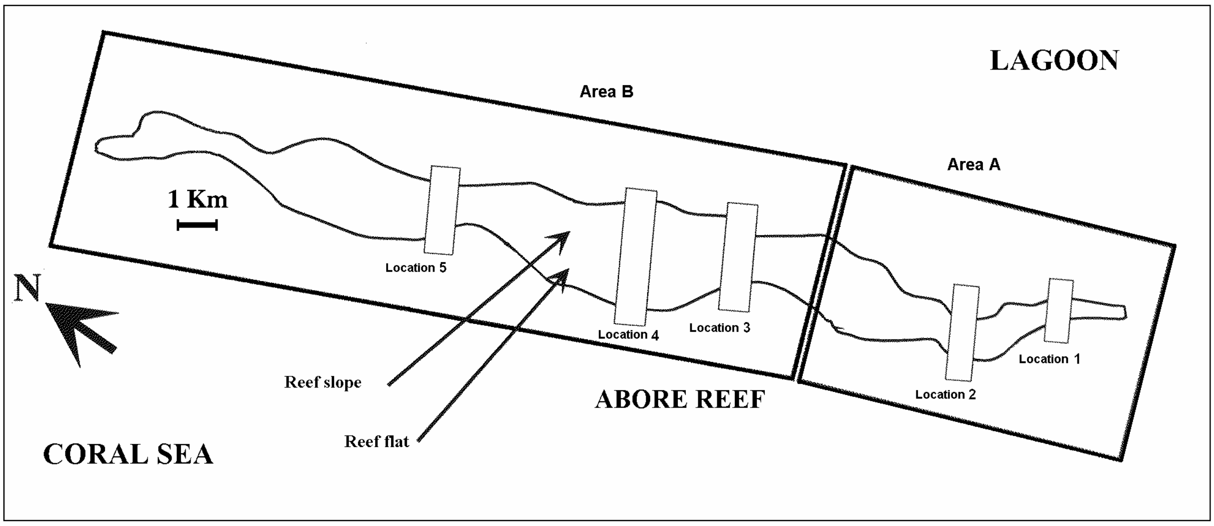

Figure 3. Boxplots of overall metrics per area (columns) and year (X-axis): species richness (top), abundance (middle), and biomass in grams (bottom). The horizontal bold line is the median, the lower and upper hinges correspond to the first and second quartiles, and the lower and upper whisker framed the third and fourth quartile. Points located outside the whiskers are outlying values.

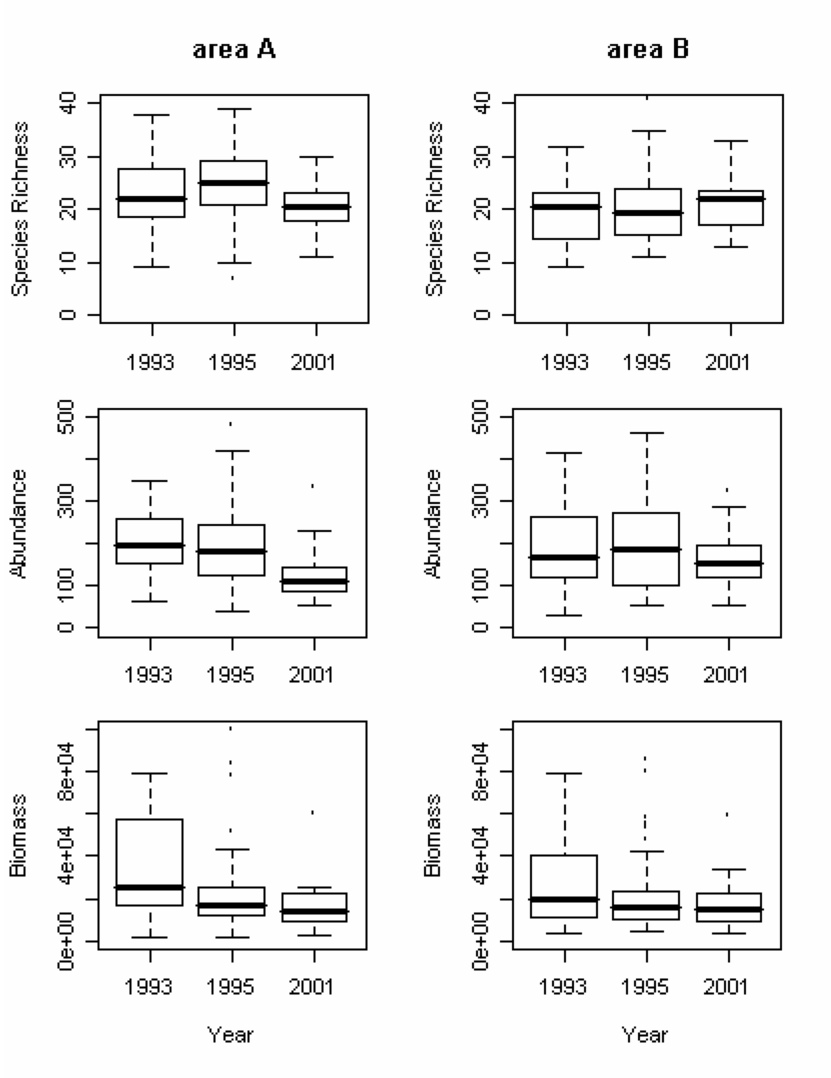

Figure 4. Adjusted means for the factors year, area, and species group factors in the model of log(abundance) per mobility group. “**” (resp. “*”) indicates a significant difference in adjusted mean at the p=0.01 (resp. p=0.05) level in multiple comparisons. Multiple comparisons were corrected using the Bonferroni method.

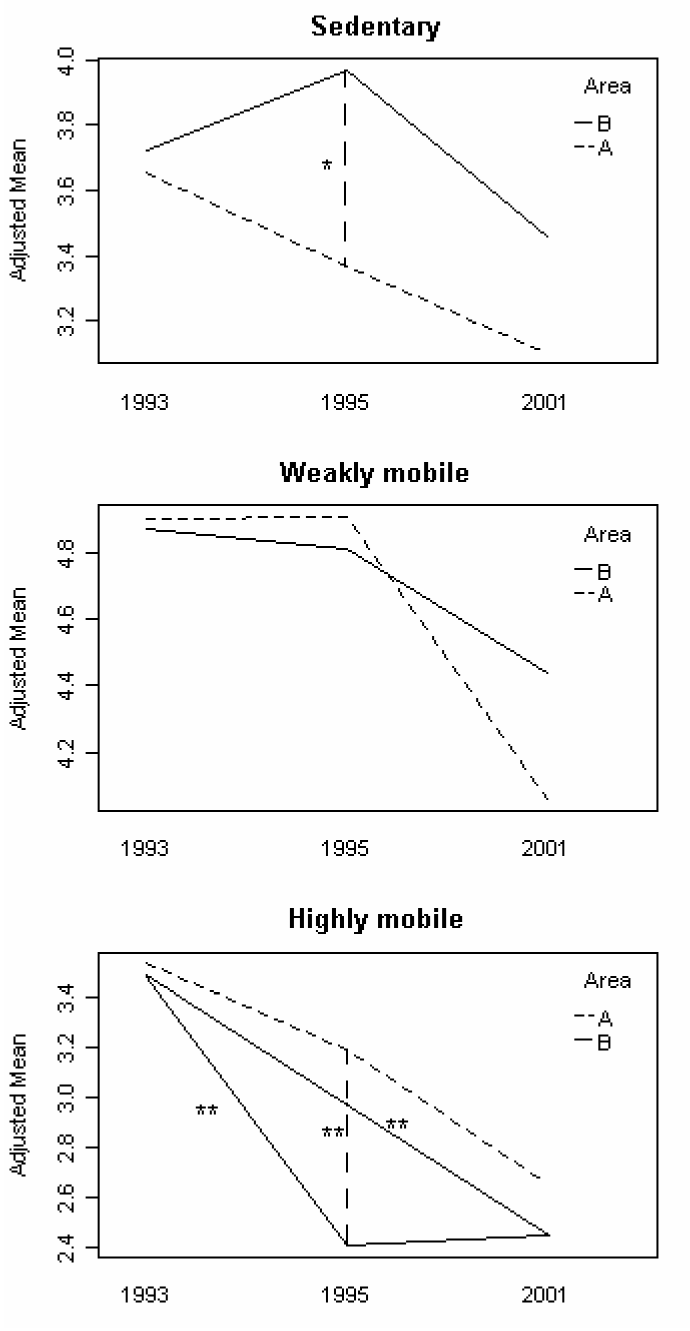

Figure 5. Adjusted means for the factors year, area, and species group factors in the model of log(biomass) per trophic group. "**" (resp. "*") indicates a significant difference in adjusted mean at the p=0.01 (resp. p=0.05) level in multiple comparisons. Multiple comparisons were corrected using the Bonferroni method. Coral feeder group constituted of only one species did not allowed statistical comparisons.

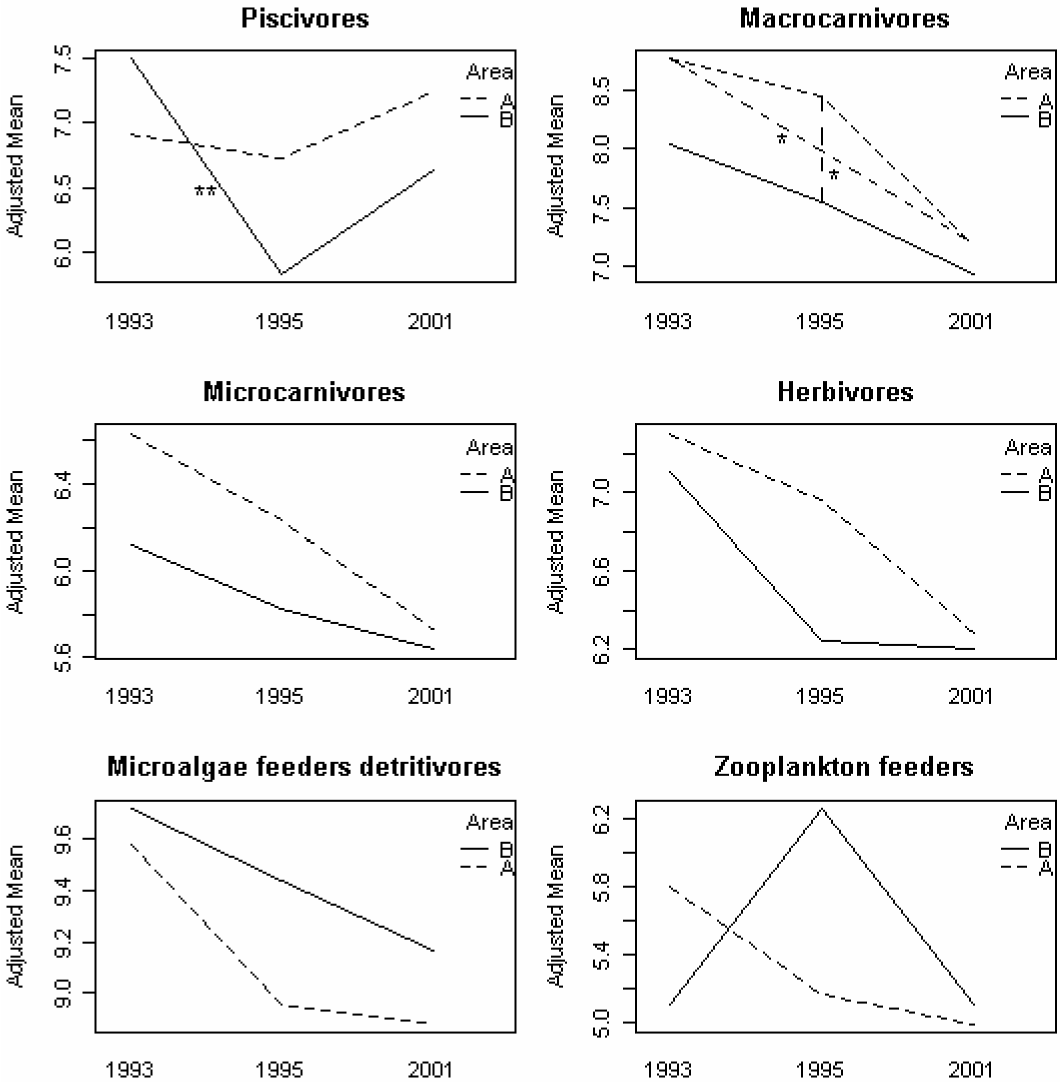

Figure 6. Adjusted means for the factors year, area, and species group factors in the model of mean size per fishing interest group. "**" (resp. "*") indicates a significant difference in adjusted mean at the p=0.01 (resp. p=0.05) level in multiple comparisons. Multiple comparisons were corrected using the Bonferroni method.