THE TROPHIC STRUCTURE OF CORAL REEF FISH ASSEMBLAGES:"TROPHIC SPECTRA" AS INDICATORS OF HUMAN DISTURBANCES

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Abstract: Ecosystem indicators were investigated through the study of the trophic structure of reef fish assemblages, in separate coral reef ecosystems of the south-west lagoon of New Caledonia. In a first step, a fractional trophic level was assigned for each fish species. Abundances profiles along trophic levels were subsequently plotted in order to search for trophic changes under various level of fishing pressure and urban influence. The comparison of these "trophic spectra" revealed that herbivores and predators of benthic invertebrates dominate the reef fish assemblages of the barrier reef, when omnivorous fishes and zooplankton feeders dominate on the fringing reefs of the bays. Trophic spectra also indicated changes in the trophic structure of reef fish assemblages following the embayment degree, and for various levels of fishing pressure. Such an approach seems to take advantage of detecting changes in the structure of fish assemblages in response to anthropogenic disturbances.

STRUCTURE TROPHIQUE DES ASSEMBLAGES DE POISSONS RECIFAUX : UTILISATION DES SPECTRES TROPHIQUES COMME INDICATEURS DE PERTURBATIONS ANTHROPIQUES

Mots-clés : *récifs coralliens, niveaux trophiques, eutrophisation, pêc*he

Résumé *: Des indicateurs écosystémiques ont été recherchés à travers l'étude de la structure trophique de l'ichtyofaune récifale dans différents systèmes coralliens du lagon sud-ouest de Nouvelle-Calédonie. Dans un premier temps, un niveau trophique fractionnel a été attribué à chaque espèce de poisson. Des profils d'abondance des poissons par niveau trophique ont ensuite été tracés dans le but de rechercher des modifications dans la structure trophique des peuplements soumis à une pression de pêche et une influence urbaine d'intensités différentes. La comparaison de ces "spectres trophiques" a fait apparaître une domination en abondance des poissons herbivores et des prédateurs d'invertébrés benthiques sur la barrière récifale, alors que le récif frangeant des baies se caractérise par une domination des poissons omnivores et zooplanctonophages. En faisant apparaître des singularités dans la structure trophique de l'ichtyofaune des baies selon le degré de confinement, et pour différentes pressions de pêche sur le récif barrière, ces "spectres trophiques" semblent capables de détecter des modifications de la structure des peuplements en réponse à des perturbations anthropiques.*

INTRODUCTION

Coral reefs are on of the most complex marine ecosystem in which fish assemblages reach their highest degree of diversity (Harmelin-Vivien, 1989). Coral reefs are affected by numerous disturbances, either natural or human related, calling for the development of ecosystem indicators. Unfortunately, ecological indicators on coral reefs are not as well developed as those for freshwater and temperate marine ecosystems. High diversity and biomass of life with heterogeneous spatial patterns discourage the search for indicator species of disturbances. Indeed, identify keystone principle at the community level seems to be of a major concern in order to develop ecosystem indicators on coral reefs.
The aim of the present study was to explore the trophic structure of coral reef fish assemblages in the south-west lagoon of New Caledonia. Our goal was to compare fish trophic spectra based on trophic levels for contrasted environmental conditions, either natural (different biota) or anthropogenic (pollution, eutrophication and fishing exploitation), in order to raise ecosystem indicators of coral reef communities.

MATERIAL AND METHODS

Study area and comparative design

During the past decade, several fish surveys were conducted in the south-west lagoon of New Caledonia (figure 1), in order to investigate effects of human disturbances on coral reef fish assemblages. For our comparative study, we used data sets from Nouméa bays and Aboré reef, a barrier reef located 20 km away from Nouméa (figure 1a). As the fringing reefs of the bays receive waste waters mainly in their bottom, we further considered a post-sampling design according to the embayment degree (figure 1b).

For our comparative purpose, we also divided Aboré reef into three zones : z1, z2, and z3. The entire reef was closed to fishing from 1990 to 1993. A first survey was conducted in 1993, right before the opening of z2 and z3 to fishing. As this resulted in a strong fishing pressure, the reef was definitely closed in 1995 (figure 1c). Before the final enclosure, another fish sampling was performed.

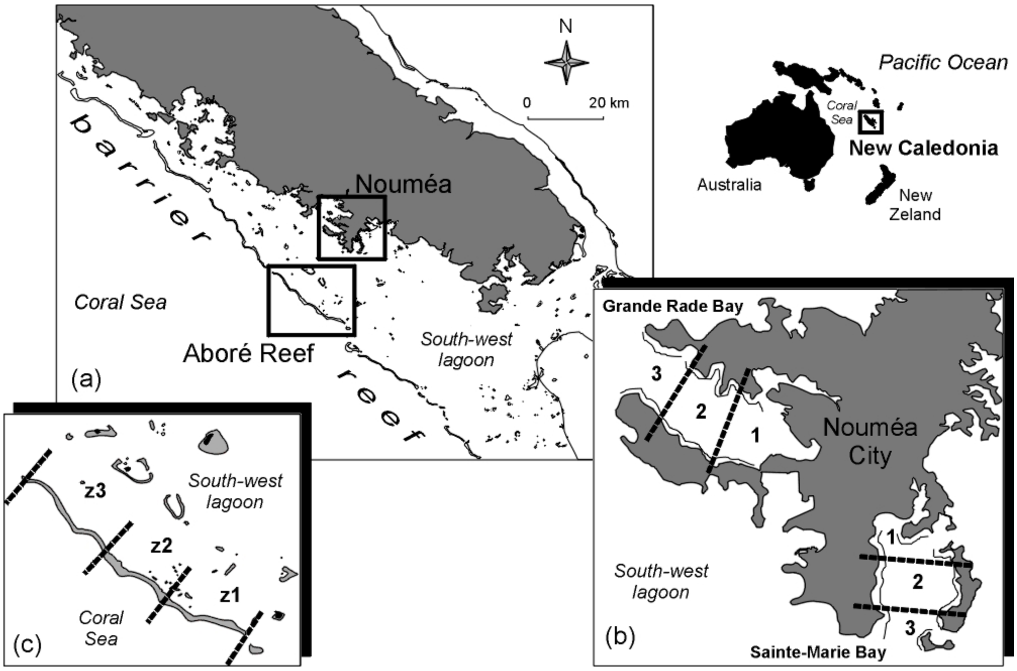

Figure 1. Studying area showing the location of the contrasted sites. (a) The Nouméa bays and Aboré reef in the south-west lagoon of New Caledonia; (b) post-sampling design in Nouméa bays in order to compare fringing reefs in the end (1), middle (2) and entrance (3) of the bays; (c) post-sampling design on Aboré reef.

Figure 1. Carte des différents sites de l'étude. (a) Les baies de Nouméa et le récif Aboré dans le lagon sud-ouest de Nouvelle-Calédonie; (b) les baies de Nouméa et les subdivisions fond (1), milieu (2) et sortie (3) de baie; (c) la division du récif Aboré en 3 zones.

Data sets

Fish were sampled by underwater visual census. For each sampling station, two experienced SCUBA divers counted simultaneously all fish species along a 50-m surveyor's tape. We used an estimate of fish abundance based on the weighted average distance of the fish to this transect line (see Wantiez *et al.* 1997). In total, data sets involved fish abundance for 646 species in 105 sampling stations. Following Froese & Pauly (2000), we estimated for 146 fish species their fractional trophic levels from stomach analyses previously conducted in the New Caledonian lagoons (Kulbicki, unpub. data). Assuming by convention a trophic level of 1 to primary producers and detritus (Froese & Pauly, 2000), the trophic level for an organism j ($Troph_j$) equals :

$$Troph_j = 1 + \sum_{i=1}^{G} DC_{ji} \times Troph_i$$

with G as the number of food items i in the diet of j, DC_{ji} the fraction of i in the diet of j, and $Troph_i$ as the trophic level of i. Trophic levels of food items (Table I) were found in the FishBase database (Froese & Pauly, 2000).

For the remaining fish species, we used the trophic level given in FishBase (300 species), or deduced trophic level according to con-generic analogies (200 species).

Prey	*Troph*
carcasses / detritus / debris	1
phytoplankton / benthic algae / weeds	1
sponges	2
sea cucumbers / sea urchins	2
worms / polychaetes	2.1
bivalves	2.1
zooplankton	2.1
hard corals / other polyps	2.3
gastropods	2.4
crabs	2.5
shrimps / prawns	2.6
jellyfish / hydroids / fish eggs / larvae	3
sea stars / brittle stars	3.1
lobsters	3.2
squids / cuttlefish / octopi / bony fish	3.5

Table I. Default *Troph* values of food items used for calculations of fish trophic levels (based on data from FishBase (Froese & Pauly, 2000)).
Table I. Valeurs des niveaux trophiques des proies utilisées pour calculer le niveau trophique des poissons (données issues de FishBase (Froese & Pauly, 2000)).

Data analysis

In a similar way to Froese *et al.* (2001), we plotted the total fish abundance along trophic levels for each sampling station. According to Gascuel (2002), we performed a *trophic spectrum* by smoothing each profile 3 times with a 3-point moving average technique. Therefore, as a first attempt to characterise the trophic structure of reef fish assemblages, we compared the shape of mean trophic spectra on a qualitative basis according to 1- the reef type (fringing reef of the bays *vs* barrier reef), 2- the embayment degree (end *vs* middle *vs* entrance of the two bays) and 3- fishing effects (the 3 zones of Aboré reef between 93 and 95).

RESULTS

Trophic structure of the fringing and the barrier reefs

Mean trophic spectra of the fringing reef and the barrier reef looked very different (figure 2). Total abundance was much higher in the bays. Trophic levels ranked from 2.5 (omnivores with mixed diet of benthic algae and sessile invertebrates) to 3.1 (zooplankton feeders) dominated in the bays. Oppositely, obligate herbivores (*Troph*=2) and predators of mobile invertebrates (trophic levels between 3.2 and 3.6) dominated the fish fauna on Aboré reef.

Trophic structure following embayment degree

Mean trophic spectra exhibited a conspicuous decrease in abundance of omnivorous fish (Troph=2.5-2.6) from the bottom to the entrance of the two bays, as for zooplankton feeders (Troph=3-3.1) from the bottom to the middle of the bays (figure 3).

Trophic structure following fishing pressure

From 1993 to 1995, the total fish abundance decreased in the 3 zones of Aboré reef (figure 4) except for predators of mobile invertebrates in the protected area (z1). This decrease was higher for herbivores on the entire reef, as well as for predators of mobile invertebrates in z3.

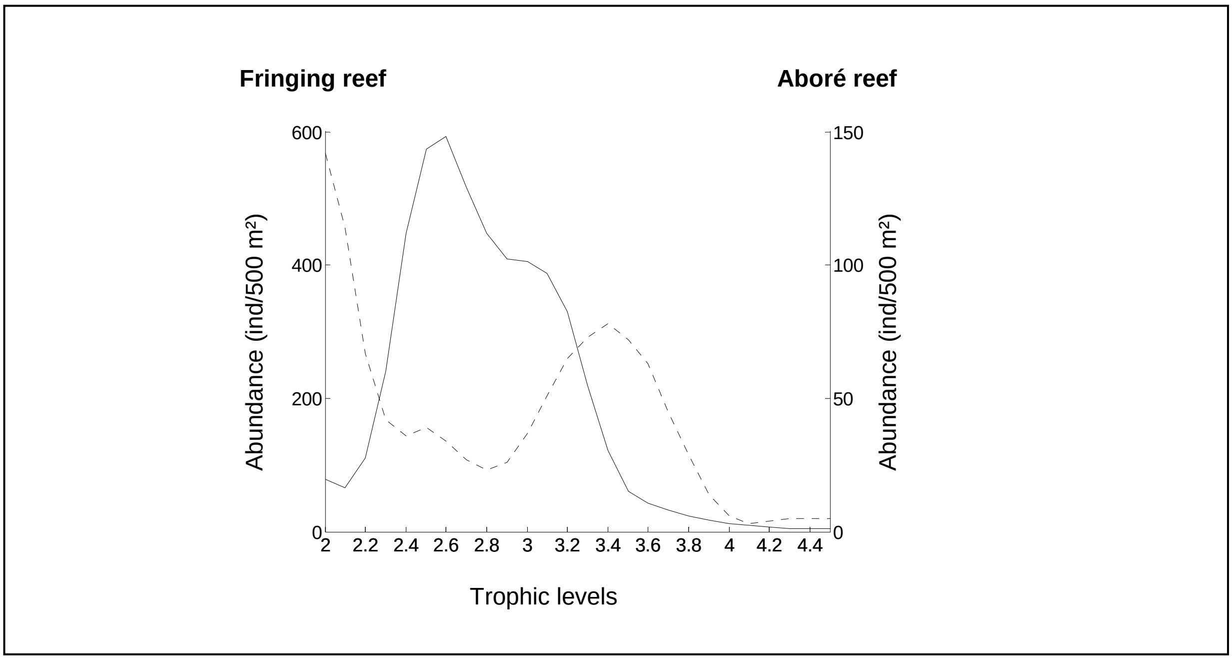

Figure 2. Mean trophic spectra of the fringing reef (solid line, n=38) and barrier reef (dotted line, n=67). Axes for abundance have been separated.
Figure 2. Spectres trophiques moyens du récif frangeant (courbe en trait plein, n=38) et du récif barrière (courbe en pointillés, n=67). Les axes des ordonnées ont été séparés.

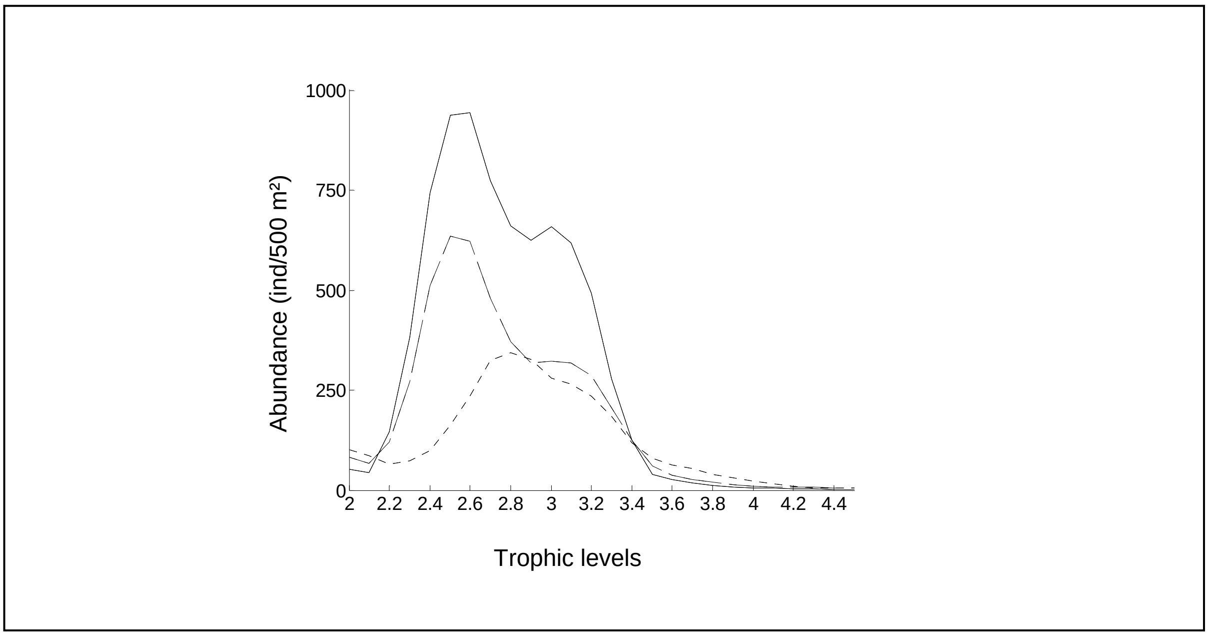

Figure 3. Mean trophic spectra of the bottom (solid line, n=11), the middle (dashed line, n=15) and the entrance of the two bays (dotted line, n=12).
Figure 3. Spectres trophiques moyens du fond (courbe en trait plein, n=11), du milieu (courbe en tiretés, n=15) et de l'entrée des deux baies (courbe en pointillés, n=12).

DISCUSSION

In the present study, we assumed that disturbances involve changes in the trophic structure of reef fish communities. Disturbances generally result in a decrease of live coral cover and its associated fine-scale topographic complexity (Jones & Syms, 1998). Consequently, competition for food and predator-prey interactions between reef organisms could be affected by this reduction of shelter availability. The trophic structure of the fish fauna is therefore expected to be affected, as coral reef fishes cover a wide range of trophic levels.
This study is a first attempt for using fractional trophic levels to simply describe the trophic structure of the reef fish fauna. Other studies have been put each fish species in a single trophic group (piscivores, herbivores, ...).

Fractional trophic levels allows to avoid such a decisive trophic partitioning, as most species have mixed diets. Plotting fish abundance by trophic levels enables to examine the trophic structure on a continuous trophic scale. In addition,

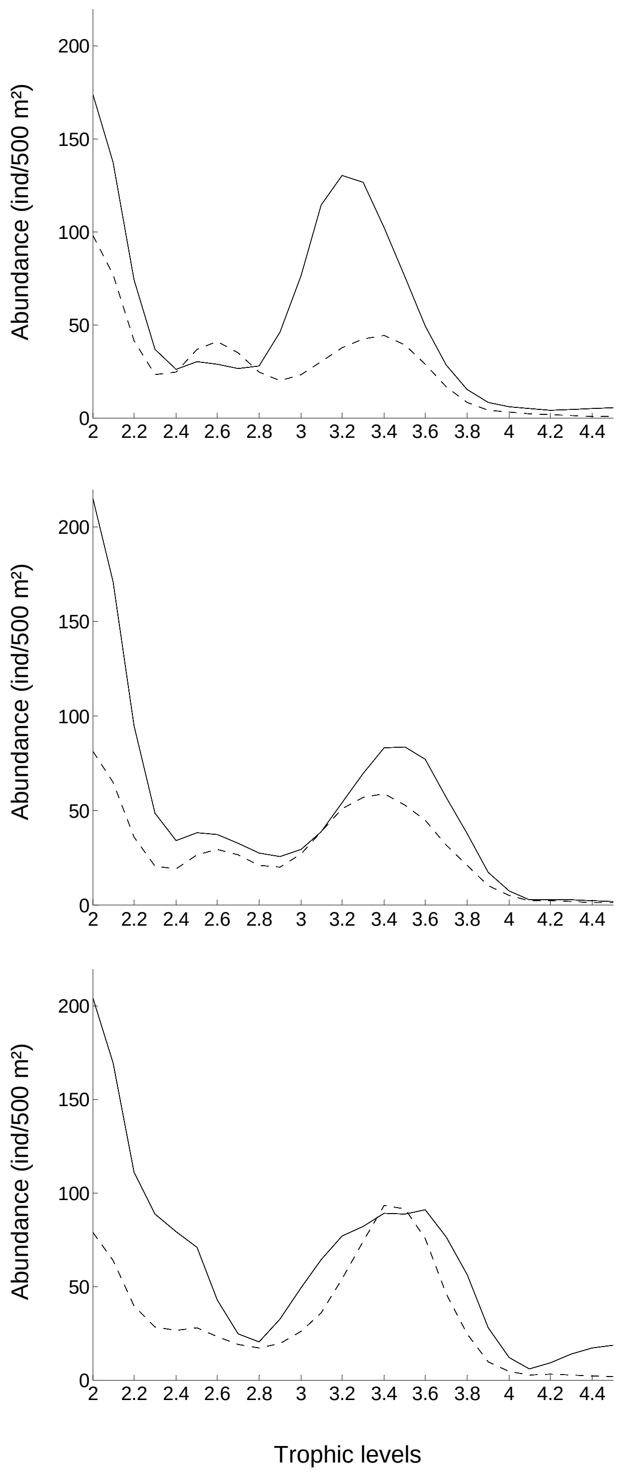

Figure 4**.** Mean trophic spectra of the three zones of Aboré reef in 1993 (solid line) and 1995 (dotted line) : z3 (n=8, 9) ; z2 (n=12, 14) ; z1 (n=13, 11) (first number of sampling station refers to 1993, second number to 1995).
Figure 4. Spectres trophiques moyens de chaque zone du récif Aboré en 1993 (courbe en trait plein) et 1995 (courbe en pointillés) : z3 (n=8, 9) ; z2 (n=12, 14) ; z1 (n=13, 11) (le premier nombre de stations se réfère à 1993, le second à 1995).

smoothing each trophic signature allows to spread abundance of a species on a range of trophic levels according to the intra-specific variability of diet composition. As a result, fishes are extremely opportunistic in their feeding, and each species should be better characterised by a range of trophic level values rather than a mean trophic level.

Our results follow those of a previous study (Kulbicki, 1988) conducted in the south-west lagoon of New Caledonia, where total fish abundance on fringing reefs was higher than barrier and lagoonal reefs. Using a different trophic partitioning, Kulbicki (1988) also observed that zooplankton feeders and omnivores dominated fish abundance on fringing reefs (respectively 50% and 30% of total fish abundance).

The bottom of the two Nouméa bays receive terrestrial runoffs and organic matter from domestic sewages. Primary production is high, and may promote the development of zooplankton and therefore zooplankton feeders. Such interpretation is supported by the decrease of abundance of zooplankton feeders along the embayment degree. Omnivores concentrated in sheltered part of the bays (bottom and middle), where topographic complexity is higher due to an extensive cover of large branching corals (Kulbicki, unpub. data). Similarly, Harmelin-Vivien (1992) found that zooplankton feeders and browsers of sessiles invertebrates were predominant in the harbour zone of Papeete (French Polynesia). Finally, obligate herbivores were less abundant in the bays than the protected area. The high fishing pressure suffered by herbivores such as Scaridae (parrotfish) and Acanthuridae (surgeonfish) may explain such patterns.

Using a different trophic partitioning on the Aboré reef data set, Ferraris *et al.* (in rev.) found that fish assemblages were dominated by "macro-carnivores" (i.e., large invertebrates feeders) and algal feeders (respectively 30% and 20 % of total fish fauna). They also showed a significant decrease in abundance of all trophic groups from 1993 to 1995 in all the three zones, except for "macro-carnivores". This may probably reflect a fishing effect, but recruitment fluctuations can lead to important variations in total fish abundance, as already observed in the south-west lagoon of New Caledonia (Wantiez *et al.*, 1997; Ferraris *et al.*, in rev.). Without statistical tests, trophic spectra anticipated this general decrease in fish abundance. In addition, as trophic levels provide a more accurate trophic partitioning, our results showed that some "macro-carnivores" decreased, and especially in z3, the further zone from the protected area z1.

The depicted differences between distinctive biota and stress levels in the south-west lagoon of New Caledonia have been already demonstrated in previous study. Even so, these preliminary results show that trophic spectra could provide easy understood and intuitive pictures of a trophic community structure at the ecosystem scale. Their ability to summarise the trophic structure of a highly diversified community whose species have very mixed diet and patchy spatial distributions make them potential candidates for community-based indicators. Nevertheless, combined effects of both habitat structure and human disturbances in the studied sites prevent a clear interpretation of the depicted differences. Even if trophic spectra seem to provide an easy tool to detect changes in the trophic structure of the reef fish fauna, the significance of such differences remain to be statistically tested.

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