

Trophic signature of coral reef fish assemblages: Towards a potential indicator of ecosystem disturbance

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Abstract – Face to the increasing anthropogenic disturbances that affect coral reef ecosystems, it becomes urgent to define appropriate ecological indicators for monitoring purposes. One useful approach is to search for a simplified description of the structure of biological communities that are highly diverse and complex on coral reefs. To this end, we propose to represent the trophic structure of coral reef fish assemblages by using fractional trophic levels assigned to each fish species. Fish abundance trophic spectra (i.e., the distributions of fish abundance per trophic level) were established for the fringing reefs of two bays located in the city of Nouméa (New Caledonia). The comparison of these trophic spectra revealed a similar trophic structure in the two bays, in spite of contrasted levels of fish abundance due to habitat damages. The embayment degree was characterized by changes in the fish trophic structure, reflecting a decreasing influence of urban and industrial wastes discharged in the bottom of the bays. This case of study shows the interest of using fractional trophic levels for the description of highly diverse biological communities. The trophic level-based approach offers new prospects in the search for ecological indicators, by characterizing the structure of biological communities by trophic signatures which testify to the disturbance level affecting their environment.

Key words: Fish community / Trophic level / Trophic structure / Ecological indicator / Anthropogenic disturbances

Résumé – **Signature trophique des peuplements de poissons des récifs coralliens : vers un indicateur potentiel de perturbation de l'écosystème.** Devant l'intensification des perturbations anthropiques affectant les récifs coralliens, il devient urgent de définir des indicateurs appropriés pour la mise en oeuvre de suivis écologiques. Une approche pratique est la recherche d'une représentation simplifiée de la structure des communautés biologiques, très complexes et diversifiées en milieu corallien. Dans ce but, nous proposons de représenter la structure trophique des peuplements de poissons récifaux à l'aide de niveaux trophiques fractionnels affectés à chaque espèce. Des spectres trophiques d'abondance des poissons (distributions d'abondance par niveau trophique) ont été établis sur les récifs frangeants de deux baies de la ville de Nouméa (Nouvelle-Calédonie). La comparaison de ces spectres trophiques fait apparaître une structure trophique identique dans les deux baies, malgré des niveaux d'abondances différents en raison de dégradations subies par l'habitat benthique. Le degré de confinement est caractérisé par des modifications de la structure trophique des peuplements de poissons qui traduisent une influence décroissante des rejets urbains et industriels déversés dans le fond des baies. Ce cas d'étude montre l'intérêt des niveaux trophiques fractionnels comme outil de représentation de communautés biologiques très diversifiées. Leur utilisation offre de nouvelles perspectives dans la recherche d'indicateurs écologiques, en caractérisant les schémas d'organisation des communautés par des signatures trophiques qui témoignent du niveau de perturbation de leur environnement.

1 Introduction

In an increasingly human-dominated environment, coral reef ecosystems are affected by various disturbances related to human activities, such as overfishing, destructive fishing practices, sediment loading and eutrophication (McClanahan et al. 2002; Hughes et al. 2003; Bellwood et al. 2004). These

disturbances affect coral reef community structure and function, mostly through the modification of ecological interactions between reef organisms (McClanahan et al. 2002; Dulvy et al. 2004). In such circumstances, there is an urgent need to define ecological indicators related to the structure of coral reef ecosystems. Ecosystem structure can be characterized by a food web that describes the organization of biological communities as networks of interacting species (Polis and Winemiller 1996). As trophic relationships are among the major forces structuring biological communities (Martinez 1995;

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Polunin and Pinnegar 2002; Cury et al. 2003), human-related disturbances are thought to impact to some extent the trophic structure of coral reef ecosystems. In this perspective, ecological indicators based on the trophic organization of coral reef fish assemblages may witness potential changes in the food web, since fishes cover a wide range of trophic levels from herbivores to top-predators.

A common way for studying the trophic structure of biological communities is to define trophic groups that include species having similar food sources (Raffaelli 2000; Luczkovich et al. 2002). Alternatively, describing community structure by the way of trophic levels is a promising approach (Bozec et al. 2003; Laurans et al. 2004; Gascuel et al. 2005). By feeding across several discrete trophic levels, organisms may have “effective trophic levels” that are fractional (Odum and Heald 1975; Levine 1980; Adams et al. 1983). Such trophic levels have been used to characterize food webs and compare ecosystem trophic structures (e.g. Christensen and Pauly 1993; Moloney et al. 2005). However, the full application of fractional trophic levels for the description of community structure has not yet been realised (Christian and Luczkovich 1999; Gascuel et al. 2005).

In the present paper, we address the ability of fractional trophic levels to describe the trophic structure of coral reef fish assemblages. In a preliminary study conducted on the fringing reefs of two urban bays of New Caledonia, Bozec et al. (2003) have investigated the distribution of fish abundance along fractional trophic levels assigned to each fish species. This resulted in “trophic spectra” (Gascuel et al. 2005) of fish abundance, which exhibited contrasted shapes according to the degree of embayment. Such changes were only depicted on a qualitative basis, reflecting modifications in the fish community through the relative contribution of some trophic levels to the whole trophic structure. In continuation of this approach, we propose to test the depicted effects on a more accurate statistical basis. Beyond the full analysis of this case-study, this paper also aims to put into perspective the use of trophic levels as indicators of disturbance impacts on coral reef ecosystems.

2 Material and methods

2.1 Data sets

The studied sites are located in the South-west lagoon of New Caledonia (Fig. 1) where urban and industrial influences are relatively low, except in the vicinity of the city of Nouméa (Labrosse et al. 2000; Bozec et al. 2005). Two bays were selected in the Nouméa peninsula, each undergoing distinctive anthropogenic disturbances, mainly in their bottom: 1- Sainte-Marie Bay which receives waste waters from the city; 2- Grande Rade Bay which is impacted by industry and port activities. A total of 38 sampling stations were performed on the fringing reefs of the two bays (Bozec et al. 2005). On each sampling station, fish were surveyed by underwater visual census within a 50 m × 10 m belt transect, set parallel to the shoreline.

A fractional trophic level was assigned to each of the 208 fish species censused. The FishBase database (Froese and Pauly 2000) provides trophic levels for a large number of coral

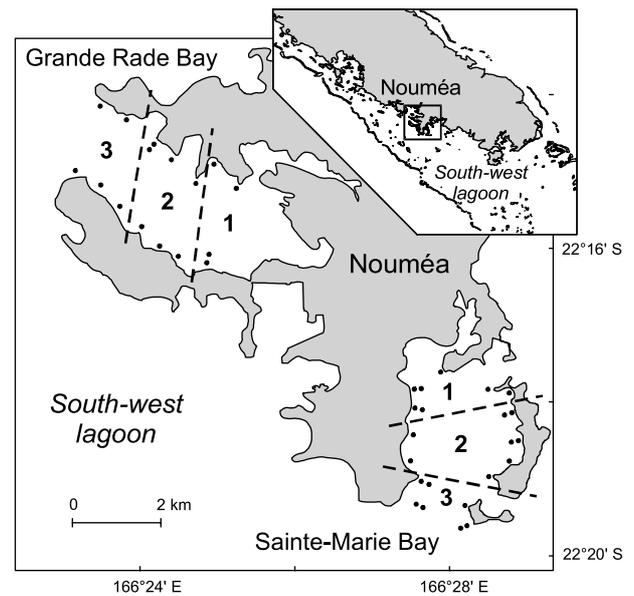


Fig. 1. Map showing the two bays in the Nouméa Peninsula, Sainte-Marie and Grande Rade. Dashed lines separate 3 portions of each bay according to the degree of embayment: (1) bottom, (2) middle, (3) mouth of the bays. Dark circles represent the positions of the 38 sampling stations.

reef fish species, calculated from dietary information gathered in the literature. According to Adams et al. (1983), the trophic level of a species j (TL_j) is calculated as follows:

$$TL_j = 1 + \sum_{i=1}^G DC_{ji} \times TL_i$$

with G as the total number of food items i in the diet of j , DC_{ji} the fraction (weight or volume contribution) of i in the diet of j , and TL_i as the trophic level of i . For 33 species, the trophic level was estimated using diet composition data from New Caledonia (Kulbicki, unpublished data) and standard prey trophic levels of FishBase. When no local dietary information was available, trophic levels were extracted from FishBase (129 species). Otherwise, the value of species from the same genus was assigned (46 species).

As correspondence between trophic levels and feeding habits is not always straightforward, we also classified all fish species into the following trophic groups: herbivores and detritivores (*Herbi*, 26 species), omnivores (*Omni*, 44 species), plankton-feeders (*Plank*, 14 species), sessile invertebrate-feeders (*Sessil*, 14 species), mobile invertebrate-feeders (*Mobil*, 89 species), facultative piscivores (*FPisci*, 10 species) and piscivores (*Pisci*, 11 species). The distribution of trophic level values by trophic group was examined using box-and-whisker plots in order to facilitate the interpretation of the subsequent analyses.

2.2 Data analyses

For each sampling unit, species abundances (numbers of individuals per 500 m²) were aggregated by trophic level,

from 2 to 4.5 by 0.1 step. The species-by-site array was then transformed into a trophic level-by-site array. The resulting table had 38 rows (sampling units) and 26 columns (trophic levels). In a second step, each row was smoothed 3 times with a 3-point moving average technique, defining a trophic spectrum (Gascuel et al. 2005) of fish abundance in the corresponding sampling station. In this manner, we roughly spread the abundance of a species into a range of contiguous trophic levels. Therefore, the trophic position of a species (i.e., its position within the food web) is thought to be better characterized by a range of fractional trophic levels rather than a single value, since trophic level generally changes during life-history (e.g., Jennings et al. 2002), and because most fish are extremely opportunistic in their feeding. The final array corresponded to a set of 38 trophic spectra of fish abundance.

Sampling stations were grouped into three categories of embayment (Fig. 1): bottom, middle and mouth of Sainte-Marie Bay ($n = 7, 8,$ and $7,$ respectively) and Grande Rade Bay ($n = 4, 7,$ and $5,$ respectively). For the three embayment degrees, a mean trophic spectrum was calculated by averaging the n trophic spectra for each embayment degree within each bay. To test the difference between the mean trophic spectra, we performed the following statistical approach. As a preliminary step, a logarithmic transformation was applied to the smoothed abundances in order to reduce the effects of dominant species (and therefore dominant trophic levels). We then performed a principal components analysis (PCA) centred by trophic levels on the log-transformed table to investigate the covariation between trophic levels. The bay and the embayment degree of each sampling station were used as supplementary variables for the characterization of the sites ordination on the factorial planes. In a second step, we used the site scores (i.e., scores of sampling stations) along the first two PCA axes as the dependent variables in the subsequent test. A two-way analysis of variance was then performed on the sites scores to test the differences in the trophic structure of fish assemblages between the two bays (term B, 2 levels) and the three embayment degrees (term E, 3 levels). The analysis of variance was conducted using the linear model procedure (LM) of the R software (R Development Core Team 2005) which is appropriate for unbalanced designs.

3 Results

3.1 Coral reef fish trophic levels

The fish species censused in the Nouméa bays cover a wide range of trophic levels (Fig. 2), from $TL = 2$ (herbivores and detritivores) to $TL = 4.5$ (strict piscivores). The highest number of species is found around 3.5. The omnivores and mobile invertebrate-feeders groups feed over a broad range of trophic levels. By contrast, herbivores and detritivores, and sessile invertebrate-feeders are characterized by a narrow distribution of trophic levels.

3.2 Trophic spectra

Sainte-Marie Bay displayed higher fish abundances than Grande Rade Bay (Fig. 3). Despite this contrast, the mean

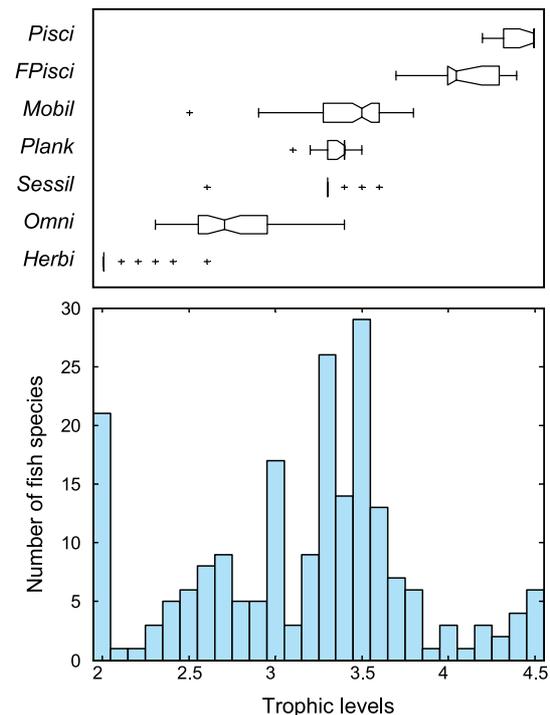


Fig. 2. Graphical display giving the correspondence between fish trophic levels and trophic groups. Box-and-whisker plots (top) show the distribution of the trophic level values of the species belonging to each trophic group. The boxes have lines at the lower quartile, median and upper quartile values, the whiskers give the extent of the rest of data, and outliers are displayed beyond the ends of the whiskers. The histogram (bottom) gives the frequency distribution of species along trophic levels ($n = 208$ species).

trophic spectra in the bottom and the middle of the two bays exhibited a similar shape. These trophic spectra were marked by two peaks, the first for TL around 2.6, and the second for TL around 3.3–3.4. Their magnitude decreased from the bottom to the middle in a similar manner in the two bays. At the bay mouths, abundance of these trophic levels is very low. The two peaks shifted back towards lower TL (2.4 and 3.2, respectively), whereas TL above 3.7 seemed to increase within the fish community. Abundance of fish at TL around 3.2 was markedly higher in the mouth of Sainte-Marie Bay compared to Grande Rade Bay.

3.3 PCA and analysis of variance

The first two PCA axes accounted for 67.8% of the total inertia of the trophic level-by-site abundance table. The first axis (Fig. 4a) is inversely linked to an increasing gradient in total abundance, as it takes into account the abundance of all trophic levels together. It underscores the contrast in total fish abundance between the two bays (Fig. 4b), especially in the abundance of TL around 2.6–2.7, and 3.3–3.4 in a lesser extent (Fig. 4a). These patterns recall the two peaks depicted on the mean trophic spectra (Fig. 3). The analysis of variance shows that the difference between the site scores of the two bays is significant along the first PCA axis (Table 1), indicating

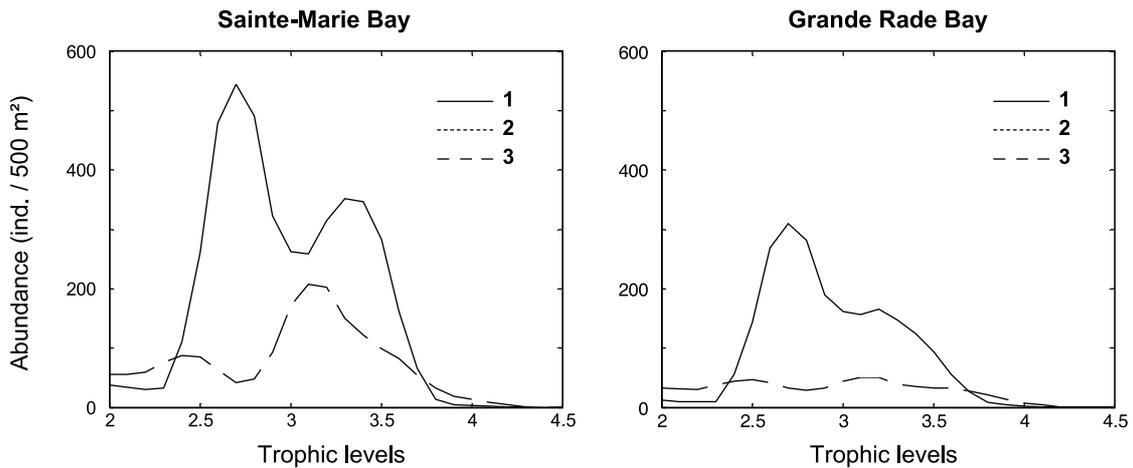


Fig. 3. Mean trophic spectra of fish abundance for the (1) bottom, (2) middle and (3) mouth of Sainte-Marie Bay and Grande Rade Bay.

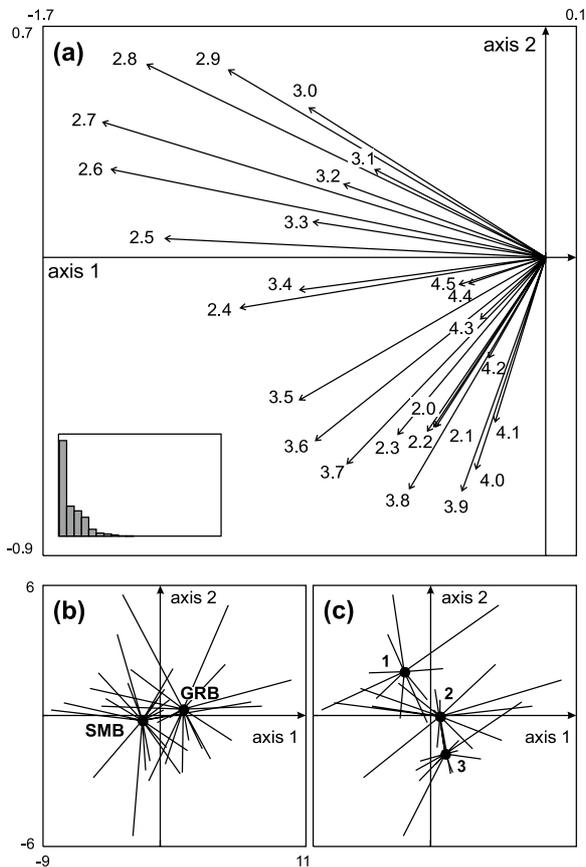


Fig. 4. First factorial plane of the PCA performed on the trophic level-by-sites abundance table. (a) ordination of trophic levels with histogram of eigenvalues; (b) and (c) ordination of sampling stations. The sampling stations have been scattered into categories of bay (SMB: Sainte-Marie Bay; GRB: Grande Rade Bay) and embayment degree (1: bottom; 2: middle; 3: mouth).

that fish abundance is significantly higher in Sainte-Marie Bay. Conversely, the embayment degree has no significant effect on the site scores along this axis. The second axis (Fig. 4a) depicts more subtle patterns in the abundance of trophic levels.

Table 1. Summary of results of the analysis of variance performed on the sites scores along the first two factorial axes. B: bay effect; E: embayment effect.

Response	Terms	Df	Sum	F	
Axis 1	B	1	94.23	6.90	*
	E	2	56.27	2.06	
	B × E	2	18.56	0.68	
	Residuals	32	437.31		
Axis 2	B	1	6.33	2.04	
	E	2	83.02	13.38	***
	B × E	2	3.27	0.53	
	Residuals	32	99.25		

Significance level is indicated by asterixes: * $p \leq 0.05$; *** $p \leq 0.001$.

TL around 3.8 (and TL around 2 in a lesser extent) are opposed to TL around 2.8, indicating that the formers increase when the latters decrease from the bottoms to the bay mouths (Fig. 4c). This shift in the fish trophic structure is confirmed by the analysis of variance that shows the significant effect of embayment degree on the site scores along the second axis (Table 1).

4 Discussion

4.1 Trophic structure of the fish assemblages in Nouméa bays

The trophic spectra described the trophic structure of fish assemblages in Nouméa bays. Fish abundance was significantly lower in Grande Rade Bay. One explanation is the poor coral cover observed in this bay compared to Sainte-Marie Bay (Bozec et al. 2005). Fringing reefs in the bottom of Sainte-Marie Bay are characterized by an extensive cover of branching corals that may provide refuge for small species. A reduction in coral cover and its associated topographic complexity limits refuge availability for the fish, and has been shown to reduce fish abundance (e.g.,

Sano et al. 1984; Friedlander and Parrish 1998). For example, *Pomacentridae* that are suspended-particle feeders (*TL* around 2.6) or plankton-feeders (*TL* around 3.4) occur in large schools that may contribute to the higher abundance in Sainte-Marie Bay.

Apart from these differences in total abundance, the embayment degree exhibited changes in the relative contribution of some trophic levels to the whole trophic structure. The abundance of omnivores (*TL* around 2.6), sessile invertebrates-feeders (*TL* around 3.3) and plankton-feeders (*TL* around 3.4) decreases from the bottom to the mouth of the bays, while abundance of herbivores (*TL* around 2) and carnivores (*TL* above 3.5) increases. These changes evolved in a similar way within the two bays. The bottom of the bays suffers from nutrient inputs and increased siltation (Fichez et al. 2005). It can be hypothesized that the enrichment of water may have favoured the production of fish. In Hawaii, Grigg (1994) found that fish abundance was significantly enhanced by sewage discharge, since enrichment may have provided a food subsidy to some fish, particularly for plankton and suspended-particle feeders. Other studies have shown that abundance of several trophic groups, such as herbivores, detritivores and plankton-feeders increased in some urban and industrial areas (Harmelin-Vivien 1992; Khalaf and Kochzius 2002). However, it is difficult to separate the respective share of disturbance effects from multiple sources. In the studying sites, as well as in the two Nouméa bays, the changes observed on fish assemblages may be the result of the synergetic effects of various disturbances, such as sedimentation, nutrient input, heavy metal load, and loss of habitat structure through coral destruction.

4.2 Trophic level as descriptors of fish trophic structure

Studying the trophic structure of biological communities involves species aggregation based on trophic similarities. Traditionally, reef fish ecologists used to lump species together into several trophic groups, on the basis of detailed gut content analyses (e.g., Hiatt and Strasburg 1960; Hobson 1974). However, the definition of such groups is difficult due to the high diversity of food habits (Sale 1991), the variability in the diet of some species (e.g., Beukers-Stewart and Jones 2004), and the lack of dietary information for many fishes. As a result, definitions of trophic groups vary amongst authors and the omnivorous category is often imprecise (Sale 1980; Parrish 1989). Problems then arise when attempting to compare fish trophic structure among studies.

Instead of using several pre-defined trophic categories, positioning species along a continuous scale of trophic levels allows to avoid a rigid trophic partitioning. As an alternative to the discrete trophic levels introduced by Lindeman (1942), various authors have proposed to use fractional trophic levels based on the relative contributions of the different food items to the total diet (Odum and Heald 1975; Levine 1980; Adams et al. 1983). Indeed, fractional values allow to rank organisms feeding on more than one trophic level (Vander Zanden and Rasmussen 1996; Williams and Martinez 2004). Fractional trophic levels can be directly estimated from dietary data as done in the present study (see also Pauly et al. 1998;

Stergiou and Karpouzi 2002), as output of mass balanced models such as ECOPATH (Pauly et al. 2000) and NETWRK (Ulanowicz 1987), and from the analysis of stable isotope ratios (review by Post 2002). These various estimates seem to be closely related (Vander Zanden et al. 1997; Kline and Pauly 1998), but dietary estimates require assumptions on the trophic level of prey items which introduces a supplementary source of bias. In addition, they do not account for the spatial and temporal variability of gut contents. As a result, isotope ratios may provide more accurate estimates of the trophic position in the food web (Vander Zanden and Rasmussen 1996; Pinnegar et al. 2002).

In the present study, trophic levels were estimated for all the species of a highly diverse biological community. In this case, the estimation of trophic levels is more readily completed from the compilation of diet information. At this stage, each trophic level must be considered as a rough estimate of the “mean trophic level” of a species which does not account for the inter-individual diet variability related to ontogenetic changes and food availability. Since the trophic position of a species should be better characterized by a range of trophic levels rather than a mean value, we applied an empirical smoothing according to Gascuel et al. (2005). In this manner, the abundance of a species was symmetrically distributed around its mean trophic level. Actually, this range extends for 7 contiguous increments of trophic levels for all species. We therefore presuppose a constant degree of diet variability at all trophic levels. Some authors have proposed to measure this variability with an “omnivory index” (Levine 1980; Pauly et al. 2000; Williams and Martinez 2004) based on the standard deviation around the mean trophic position. In the future, this index could assist in the choice of a particular weight for some trophic levels in the moving average. For the moment, we believe that this pragmatic approach is satisfactory regarding the huge lack of dietary data for coral reef fish populations.

4.3 Trophic levels as potential indicators of ecosystem disturbances

Trophic spectra only provided a snapshot of the trophic structure of fish assemblages in Nouméa bays. This should be considered as a potential picture of the community structure obtained with standard values of trophic levels. Ideally, these trophic levels should have been measured in situ, but this would require a sampling effort and laboratory analyses that are difficult to carry on for such a high number of species. Comprehensive studies on coral reefs involving ecosystem models such as ECOPATH (e.g., Arias-Gonzales et al. 1997; Bozec et al. 2004) allow to estimate fractional trophic levels under the constraint of equilibrium assumptions. By contrast, standard values of trophic levels may be useful for a convenient description of distribution patterns and structure of fish assemblages. Such descriptive studies do not require the development of a complete model of the food web.

Exploring the trophic structure of coral reef fish assemblages may provide relevant insights into the functioning of the entire reef ecosystem. In the two Nouméa bays, the trophic spectra displayed strong similarities despite differences in total abundance. Further investigations are desirable to test whether

the depicted patterns are recurrent on the fringing reefs of other bays submitted to similar disturbances. The detection of common patterns could define standard trophic spectra, i.e., trophic signatures that may be specific to fish community structure for particular environmental conditions. This was already shown in the South-west lagoon of New Caledonia, where trophic spectra exhibited a well-defined shape by habitat type in various locations (Gascuel et al. 2005). This clearly calls for an extension of such explorative studies, in order to raise generalizations on the trophic signature of coral reef fish assemblages related to environmental conditions. In addition, trophic spectra expressed in biomass rather than abundance may be used in complement for a better understanding of energetic pathways within coral reef food webs. Thus, trophic levels appear useful as ecological indicators in a management perspective. By promoting the comparison of fish trophic structure among coral reef ecosystems, they could provide a baseline for monitoring environmental conditions on disturbed and undisturbed coral reefs.

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