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Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific

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Abstract – This study examines the trophic status and relationships of coral reef fish in the lagoon of New Caledonia, southwest pacific. The feeding habits of 34 fish species collected at three contrasted sites were first described using a compilation of gut contents observations and data from the literature. The carbon and nitrogen isotope signatures of these fish and of some of their potential ultimate food sources were also determined at each site. Despite some spatial variations in the isotopic signatures of most food sources and fish trophic groups, the overall trophic structures of fish assemblages were similar at the three sites. Stable isotope data were then used to re-assign fish species to trophic groups based on the δ^{15}N signatures of fish and their food sources. Herbivorous fish species were clearly distinguished from the other trophic groups by their lower δ^{15}N signatures, consistent with an estimated trophic position of ~2 for all species examined. Scaridae were however characterized by relatively higher δ^{13}C and lower δ^{15}N, which is probably linked with the role of detritus in their diet. The estimated trophic positions of planktivorous fish species were consistent with their gut contents-based classification. Conversely, the isotopic signatures of carnivorous and piscivorous fish species largely overlapped, and their estimated trophic positions were much lower than expected. This suggests that these species feed over a broader range of trophic levels and food sources than implied by the gut contents observations, and indicates that their diet is partly omnivorous. Finally, the relationships between body mass and the isotopic signatures of four fish species were significant for at least one isotopic ratio for each species. Since ontogenetic variations and omnivorous diets are difficult to assess with gut contents data only, stable isotopes revealed essential in estimating the actual trophic status and relationships characterizing the fish species under study.

Key words: Coral reef fish / Gut contents / Stable isotopes / Trophic position / Ontogenetic variability / Pacific Ocean

Résumé – Utilisation des isotopes stables pour l'estimation du régime alimentaire et des relations trophiques des poissons du lagon de Nouvelle-Calédonie (Pacifique Sud-Ouest). Cette étude fournit une analyse du régime alimentaire et des relations trophiques qui caractérisent les poissons du lagon de Nouvelle-Calédonie. Le régime alimentaire de 34 espèces, récoltées dans trois stations contrastées, est décrit par la méthode des contenus stomacaux en utilisant une large base de données locales, associée à une étude bibliographique. Les isotopes stables du carbone et de l'azote sont ensuite mesurés sur les poissons récoltés et sur différentes sources alimentaires potentielles prélevées à chaque station. Malgré des différences spatiales significatives pour la plupart des sources alimentaires et des groupes trophiques de poissons, la structure trophique globale des assemblages se révèle peu variable d'une station à l'autre. Les données isotopiques sont ensuite utilisées pour réassigner les espèces de poissons à différents groupes trophiques, sur la base du rapport entre le δ^{15}N des espèces et de celui de leurs sources alimentaires. Les données isotopiques confirment les résultats des analyses de contenus stomacaux pour les herbivores et les planctivores. Les Scaridae sont cependant caractérisés par des valeurs particulièrement élevées en δ^{13}C et faibles en δ^{15}N, probablement liées à un régime alimentaire en partie détritivore. A l'inverse, pour la plupart des espèces carnivores et piscivores, les données isotopiques mettent en évidence une gamme de sources alimentaires plus diversifiée que celle fournie par les études de contenus stomacaux, et un comportement alimentaire plutôt omnivore. Enfin, la relation entre la masse corporelle et les ratios isotopiques, testée chez quatre espèces, montre des variations ontogéniques significatives pour au moins

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un des isotopes étudiés (carbone ou azote) pour les quatre espèces, mais pas de changement de niveau trophique. Les variations ontogéniques et les comportements alimentaires de type omnivore étant difficiles à évaluer par les seules données de contenus stomacaux, les isotopes stables se révèlent cruciaux pour l'estimation des niveaux trophiques réels des espèces et la représentation des relations trophiques au sein des assemblages.

1 Introduction

The structure and functioning of fish assemblages rely in part on the trophic status and relationships characterizing fish species. The understanding of fish trophic networks has thus become increasingly important for the establishment of ecologically based management programmes (Kulbicki et al. 2005). In ecosystems characterized by a very high species diversity, such as coral reefs, information on the diet of fish species remains incomplete and difficult to assess. Fish diets are often studied using gut contents, which give no information about the origin of the food sources consumed and are representative only of the food ingested by fish at the time of sampling (Pinnegar and Polunin 1999). Conversely, the analysis of the stable isotope signatures of prey and predators provides information about the food-web structure and energy flow over long time periods (Pinnegar and Polunin 2000; Phillips and Gregg 2003). Indeed, the ratio of $^{13}C/^{12}C$, noted $\delta^{13}C$, increases by less than 1.0‰ on average per trophic level (Post 2002), and can thus be used to discriminate between the carbon sources used by consumers (Peterson 1999). The ratio of $^{15}N/^{14}N$, noted $\delta^{15}N$, increases from diet to consumers with a highly variable enrichment level, comprised between 2 and 5‰ (Olive et al. 2003), a mean enrichment of 3.4‰ being generally admitted (Post 2002). Despite its variability, the $\delta^{15}N$ enrichment is consistent throughout successive trophic levels, and can thus provide a measure of trophic position (Post 2002).

In New Caledonia, southwest Pacific, the lagoon extends on an area of 19 000 km^2, thus providing a wide range of environmental conditions, from highly productive coastal ecosystems, influenced by terrigeneous inputs (Tenório et al. 2005) with high chl *a* concentrations (Pinazo et al. 2004) and zooplankton densities (Champalbert 1993), to barrier reef ecosystems influenced by oligotrophic oceanic water flows (Pinazo et al. 2004). This strong environmental variability and the proximity of New Caledonia to the coral reefs biodiversity center located in the China Sea-Philippines-Indonesia region result in highly diverse shorefish assemblages in the lagoon, with a total of 1694 species (Fricke and Kulbicki 2006). However, little is known about the trophic relationships that support this highly diverse shorefish fauna, since the few studies available have only considered specific trophic groups or only used gut contents data (Grimaud and Kulbicki 1998; Bozec et al. 2005; Kulbicki et al. 2005).

The principal aim of the present study was to assess the fish trophic status and relationships in the lagoon of New Caledonia through the use of stable isotope data, while taking into account the high spatial heterogeneity of the lagoon.

This study was therefore conducted in four stages.

- The fish species collected at three sites, chosen for their contrasted environmental conditions, were assigned to trophic groups, relying on previous gut contents data and on a synthesis from the literature.
- The isotopic signatures of those fish and of some of their potential food sources were assessed at each site, and compared between sites, in order to determine whether the trophic functioning of fish assemblages varied spatially.
- The fish species were re-assigned to trophic groups based on stable isotope analyses, in order to check whether any potential food sources had been neglected by previous gut contents analyses.
- The relationships between $\delta^{13}C$ and $\delta^{15}N$ signatures and body mass were tested for four fish species, so as to detect if an ontogenetic variability occurred in their diet.

2 Material and methods

2.1 Sampling sites

Observations from hydrodynamic 3D models developed at the Institute of Research for the Development (IRD) were used in order to select three sampling sites where water column conditions were representative of the contrasts in water column productivity characterizing the lagoon of New Caledonia (see Ouillon et al. 2005; Jouon et al. 2006 for recent applications of the models). The three chosen sites were separated by distances of 11 to 14 km, and included: a fringing reef site (Site 1: 20°10.0'S 166°20.3'E), an intermediate reef site (Site 2: 20°19.2'S 166°23.5'E) and a barrier reef site (Site 3: 22°12.3'S 166°17.7'E), lying approximately 20 km from the coast (Fig. 1).

2.2 Sampling

All samples were collected within a two month period, from July to August 1996, in order to reduce the temporal variations in the isotopic signatures of the organisms (Owens 1987). Except for spanish mackerel *Scomberomorus commerson*, provided by the South Pacific Commission, all the fish samples were collected at the three chosen sites using 7% active substance rotenone. Although it contains carbon, any potential effect of rotenone on the carbon isotope signatures of fish can be considered as negligible. Rotenone residues have indeed been shown to be rapidly cleared from fish plasma, with less than 2% of the dose remaining after 20 min (Gingerich 1986). Moreover, as the same sampling procedure was applied for all fish species and at all sites, the potential resulting error in isotopic signatures was supposed to be standardized across species and sites. Poisoning was performed on 250–300 m^2 areas of coral reef surrounded by a 60 m long, 3 m deep and 10 mm mesh stretch net. The fish were placed on ice immediately after their removal from water.

Three plankton samples, each represented by two replicates, were collected at each site from the upper 5 m layer

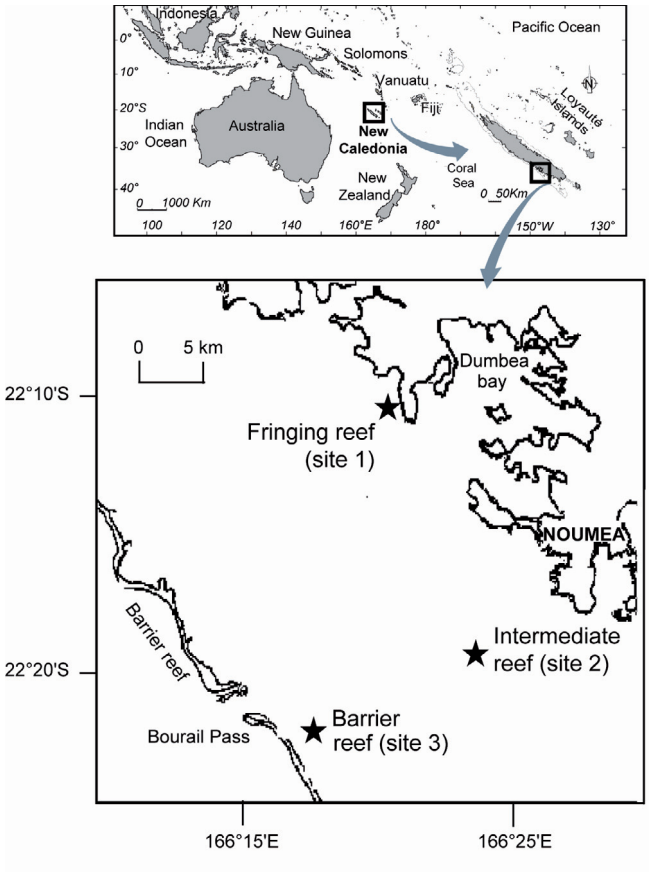

Fig. 1. Position of the study sites (stars) in the southwest lagoon of New Caledonia: Fringing reef (site 1), Intermediate reef (site 2) and Barrier reef (site 3).

of the water column, using five minutes horizontal tows with a 35 μm mesh plankton net. All plankton samples were preserved in formaldehyde. Formaldehyde may alter the isotopic signatures of plankton (Kaehler and Pakhomov 2001), but this alteration has been shown to be low, not exceeding 1.1‰ for ^{13}C and 1.5‰ for ^{15}N, depending on the conservation procedure (Feuchtmayr and Grey 2003). In order to check for any potential effect of formaldehyde on the results of our study, all the ensuing analyses implying calculations based on zooplankton isotopic signatures (i.e., trophic levels calculations) were repeated three times, by using the original δ^{13}C and δ^{15}N zooplankton signatures, and also (δ^{13}C ± 1.1‰) and (δ^{15}N ± 1.5‰). In each case, the three calculations brought to similar interpretations, so we decided to present only the results implying raw signatures of plankton. Furthermore, since a similar procedure was applied for all plankton samples at all sites, the resulting error was expected to be standardized across all samples and sites.

Turf forming microalgae, red calcareous algae and the most common seaweeds encountered were sampled by scuba diving at each site. Each algal type was represented by three samples at each site, each sample being replicated twice. The macrophytes collected were: an unidentified brown macroalga at the fringing reef site, a brown macroalga, *Lobophora* sp. (Phaeophyceae, Dictyotales), at the intermediate reef site, and a calcareous green alga, *Halimeda* sp. (Chlorophyta, Bryopsidales), at the barrier reef site. The algae were placed on ice immediately after their removal from water.

2.3 Fish diets and identification of gut contents-based trophic groups

The feeding habits of the collected fishes were identified by combining several data sets: a large set of unpublished previous data on fish gut contents collected by IRD over long time periods in the same area (Kulbicki et al. 2005; Kulbicki 2006), data from the literature, and the Fishbase website[1] (see Table 1 for the most recent references consulted). The consistency of the diets obtained by this combination of previous data was completed by direct observations of gut contents performed on one to three individuals of each species collected at each site, depending on their respective abundances. Prey items rarely recorded in the literature or rarely observed in combined gut contents data were reported but considered as minor. The fish species were assigned to trophic groups according to the major prey items described in the literature and observed in combined gut contents data. The trophic groups identified were: herbivorous, planktivorous, carnivorous and piscivorous. Although piscivorous fish may be considered as carnivorous, it was decided to distinguish them from the strictly carnivorous ones since they should be on average one trophic level higher (Bozec et al. 2004).

2.4 Sample preparation

Two to six individuals were selected for each fish species from each site. They were weighed (fresh weight, in g) and fork-length measured (FL, in cm). For each individual, two fillets of white muscle tissue taken from the dorsal region were dissected for analysis. Muscle tissue presents the advantage of showing a lower variability in isotopic composition compared to other body parts (Pinnegar and Polunin 1999). Moreover, the use of muscle tissues, whose dependence on oxidative metabolism is limited relative to other body parts (e.g., heart, brain, viscera or the hepatobiliary system), allows to reduce any potential effect of rotenone on fish isotopic signatures (Gingerich 1986). For the smaller fish (<3 g), the whole specimen was used, after removing the head and viscera. Samples were freeze-dried for 24 h.

The plankton samples were filtered on 200 μm and 35 μm mesh filters in order to separate two size ranges of particles: the 35–200 μm size range, constituted by particulate organic matter (POM) consisting of phytoplankton and detritus and representing the base of the trophic food chain, and the >200 μm size range, constituted by zooplankton and representing a primary consumer level. Each filtered sample was washed down with de-ionized water to remove salt, dried at 60 °C during 24 h in an oven and stored with silica gel prior to isotopic analysis (Lajtha and Michener 1994). The turf, red calcareous and macroalgae samples were also freeze-dried for 24 h and stored with silica gel prior to isotopic analysis.

[1] http://www.fishbase.org/

Table 1. Number of individuals, fork length range (cm) and body mass (fresh weight) range (g) for each fish species, with the corresponding collection sites: Fringing reef (site 1), Intermediate reef (site 2) and Barrier reef (site 3), see Fig. 1 for the location of the sampling sites.

Fish family	Fish species	Number of fishes collected	Fork length range (cm)	Body mass (g)	Site
Acanthuridae	*Acanthurus nigrofuscus*	3	8–15	13–81	1
	Ctenochaetus striatus	6	10–17	28–142	1 + 2
	Zebrasoma scopas	2	13–14	48–68	1
Apogonidae	*Cheilidopterus quinquelineatus*	9	4–9	1–10	1 + 2 + 3
	Ostorhinchus doederleini	6	8–9	8–14	1 + 2
Blenniidae	*Cirripectes stigmaticus*	3	6–7	3–5	2
Caesionidae	*Caesio caerulaurea*	6	14–22	54–167	1 + 3
Chaetodontidae	*Chaetodon citrinellus*	2	9–10	13–19	3
	Chaetodon flavirostris	3	5–12	3–7	2
Haemulidae	*Plectorhynchus lineatus*	2	20–31	121–456	2
Holocentridae	*Sargocentron rubrum*	3	15–16	87–94	1
Labridae	*Bodianus perditio*	3	17–27	92–391	3
	Hemigymnus melapterus	3	16–21	83–183	1
Lethrinidae	*Lethrinus atkinsoni*	3	17–19	90–114	1
Mullidae	*Mulloidichthys flavolineatus*	3	15–20	43–94	3
	Parupeneus ciliatus	3	20–22	154–209	2
Nemipteridae	*Scolopsis bilineatus*	5	10–18	18–133	1 + 2
Pomacentridae	*Abudebduf sexfasciatus*	9	7–10	9–25	2 + 3
	Centropyge tibicens	3	8–10	15–36	2
	Chromis viridis	3	4–5	2–3	2
	Chrysiptera notialis	3	5–6	4–5	1
	Dascyllus aruanus	6	4–6	2–7	2 + 3
	Pomacentrus adelus	3	6–7	9–11	1
	Pomacentrus moluccensis	3	7–10	10–20	2
	Stegastes nigricans	9	8–12	12–147	2 + 3
Scaridae	*Chlorurus sordidus*	3	13–19	119–515	3
	Scarus niger	3	15–19	77–147	3
	Scarus schlegeli	3	16–25	69–270	3
Scombridae	*Scomberomorus commerson*	3	73–95	3300–7200	3
Scorpaenidae	*Scorpaenodes guamensis*	3	5–7	3–7	3
Serranidae	*Epinephelus merra*	7	15–23	50–180	1 + 2 + 3
Siganidae	*Siganus doliatus*	3	9–17	79–165	1
Synodontidae	*Saurida gracilis*	3	13–18	18–58	3
	Synodus variegatus	9	9–18	7–58	1 + 2 + 3

All samples (fish, plankton and all algae types) were ground to a homogenized fine powder with a pestle and a mortar. Both the calcareous algae and the plankton samples required an acidification with 1% HCL to remove the inorganic components. Each sample was weight-calibrated in order to permit comparisons with the standard reference material, as determined in trial mass spectrometry runs: 1 mg for fish samples, 5 mg for turf-forming algae, macroalgae and plankton, and 12 mg for red calcareous algae and *Halimeda* sp.

2.5 Stable isotope analyses

Dual analyses of the stable isotope abundances of carbon and nitrogen were conducted at the University of Newcastle for plankton and algae, and at the Scottish Crops Research Institute for fish samples. All the samples of POM and algae (i.e., food sources), zooplankton (i.e., primary consumers) and fish (i.e., secondary consumers) were oxidised, and the N_2 and CO_2 passed through a single inlet dual collector mass spectrometer (Europa Scientific ANCA SL 20-20 system). For calibration of the equipment and compensation for drift with time, the reference standards used were leucine for source materials and cod dorsal muscle tissues for fish samples. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed relative to the internal standards: virtual PeeDee Belemnite (vPDB) for carbon, and atmospheric N_2 for nitrogen. The relative abundances of stable isotopes (‰) were expressed according to the formula:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N,
R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.
Increase or decline in $\delta^{13}C$ or $\delta^{15}N$ indicates enrichment or depletion of the heavy isotope compared to the lighter isotope relative to the internal standard. The difference found in $\delta^{13}C$ and $\delta^{15}N$ data between the two ANCA mass spectrometers when analyzing the same material was <0.2‰.

2.6 Data analysis

A major condition when using stable isotopes in determining food sources is that these food sources have distinct isotopic signatures (Vander Zanden and Rasmussen 2001). Differences in both δ^{13}C and δ^{15}N between food sources were thus tested using one-factor ANOVAs. Differences in δ^{13}C and δ^{15}N signatures between fish trophic groups were similarly tested, with fish individuals as replicates within each trophic group. Since some spatial variability was expected in the isotopic signatures of at least the food sources, one-factor ANOVAs were also used to test for the effect of sites on the δ^{13}C and δ^{15}N signatures of each food source common to the three sites, and on the δ^{13}C and δ^{15}N mean signatures of each fish trophic group, with fish individuals as replicates within each trophic group. As linear analyses are sensitive to departure from normality, the distribution of the δ^{13}C and δ^{15}N signatures were tested for normal distribution using the Kolmogorov-Smirnov test prior to being entered in the various models (Scherrer 1984).

The fish species were re-assigned to trophic groups by calculating trophic positions based on their δ^{15}N mean signatures. The ultimate food sources of fish (i.e., POM and algae) were assigned the basic trophic positions, equal to 1 (Bozec et al. 2004), and the site-specific differences in their δ^{15}N signatures were considered. A fractionation of 3.2‰ per trophic level was used, following the recommendations of Sweetings et al. (2007) for fish muscle tissues. The trophic positions (TP) of each fish species at each site were thus calculated as follows:

$$TP_{fish} = (\Delta\delta^{15}N/3.2) + 1, \text{ with } \Delta\delta^{15}N = \delta^{15}N_{fish} - \delta^{15}N_{source},$$

the source being represented by either POM or different algae types in each case. The expected trophic positions were ~2 for herbivorous fishes, ~2.5 to 3 for planktivorous, ~3 to 3.5 for carnivorous and ~3.5 and more for piscivorous, following Bozec et al. (2004).

Finally, since fish body mass is known to have a significant influence on the δ^{13}C and δ^{15}N fractionation values (Sweeting et al. 2007), the effect of body mass on the isotopic signatures of fish was tested for the species presenting the highest abundances and widest body mass range, using linear regression models. This enabled detection of a potential ontogenetic variability occurring in the diet of these species, a point which has to be taken into account when assigning trophic status to fish species. ANOVAs and regression analyses were performed using Systat v10.2.

3 Results

3.1 Fish sampling

A total of 141 fishes were analyzed: 41 coming from the fringing reef site, 48 from the intermediate reef site and 52 from the barrier reef site. These fishes belonged to 34 species: 14 on the fringing reef site, 16 on the intermediate reef site and 17 on the barrier reef site, and ranged from 4.5 to 95.0 cm FL and from 1.0 g to 7.2 kg in weight (Table 1). Only three species were common to the three sampling sites (*Cheilidopterus quinquelineatus, Epinephelus merra, Synodus variegatus*), all of them being piscivores. Seven were common to at least two sampling sites: two were common to the fringing and the intermediate reefs, three to the intermediate and the barrier reefs and only one to the fringing and the barrier reefs.

3.2 Fish diets and gut contents-based trophic groups (Table 2)

According to the combined gut contents data, among the 34 species of fish collected, 11 were herbivorous (H1 to H11), mainly represented by Acanthuridae, Pomacentridae and Scaridae; seven were planktivorous (Z1 to Z7), including five species of Pomacentridae; nine were carnivorous (C1 to C9), including Mullidae and Labridae; five were piscivorous, with *Scomberomorus commerson* (Pi4) consuming small pelagic fish species, while *Synodus variegatus* (Pi5), *Cheilodipterus quinquelineatus* (Pi1) and *Epinephelus merra* (Pi2) consumed more reef site-attached fish species; two Chaetodontidae were coralivorous, but for statistical analyses they were assimilated to carnivores (C10 and C11, Table 2).

3.3 Trophic structure of fish assemblages (Fig. 2 and Table 3)

The food sources considered were characterized by significant differences in their δ^{13}C and δ^{15}N signatures ("Table 3; ANOVA"[2] – A[1], $p < 0.05$). POM showed a consistently depleted δ^{13}C signature (mean = -20.2 ± 0.4‰) relative to all other food sources (Fig. 2), and significant spatial differences in both δ^{13}C and δ^{15}N (A [3], $p < 0.05$). The green calcareous algae *Halimeda* sp. collected at site 3 also showed a low δ^{13}C signature (mean = 18.5 ± 0.5‰). Conversely, the red calcareous algae showed consistently enriched δ^{13}C signatures (mean = –3.9 ± 0.3‰), and neither did their δ^{13}C or δ^{15}N signatures vary spatially (A [3], $p > 0.05$). The brown unidentified macroalgae and *Lobophora* sp. collected at sites 1 and 2 presented intermediate values of δ^{13}C, with means of –10.5 ± 0.2‰ and –10.9 ± 0.5‰ respectively. The turf microalgae presented variable δ^{13}C at the three sites (A [3], $p < 0.05$), with a particularly enriched signature at site 3 (Fig. 2), but their δ^{15}N signatures were similar at the three sites (A [3], $p > 0.05$). Among the food sources collected at the three sites, turf microalgae presented the most depleted mean δ^{15}N signature (mean = 3.1 ± 0.2‰), followed by POM (mean = 4.0 ± 0.5‰) and red calcareous algae (mean = 4.5 ± 0.3‰). The zooplanktonic primary consumers showed a mean δ^{13}C signature varying from –18.5‰ at site 2 to –20.1‰ at site 1, with weak but significant spatial differences (A [3], $p < 0.05$). The δ^{15}N mean signature of zooplankton was enriched by ~3‰ relative to POM, with a mean of 6.4‰ and no differences between sites (A [3], $p > 0.05$). Finally, as indicated by their position along the δ^{13}C axis, red calcareous algae were probably not a major source of food for any of the fish species examined at any site. A similar observation can be made for

[2] "Table 3; ANOVA": A.

Table 2. Trophic groups of the 34 fish species assigned from combined gut contents data, including direct observations from the present study; previous unpublished data from the same area and published data from the literature. Food items between brackets indicate prey rarely observed in gut contents or rarely reported in the literature.

Trophic group	Fish species	Prey items	Code	References
Herbivorous				
	Acanthurus nigrofuscus	Microalgae	H1	Polunin et al. 1995
	Centropyge tibiscens	Microalgae (corals and tunicates)	H2	Shirai 1986
	Cirripectes stigmaticus	Microalgae	H3	Sano et al. 1984
	Ctenochaetus striatus	Microalgae (detrital material)	H4	Choat et al. 2004
	Pomacentrus adelus	Filamentous algae (green algae)	H5	Allen 1991
	Scarus niger	Microalgae (detrital material)	H6	Ochavillo et al. 1992
	Scarus schlegeli	Microalgae (detrital material)	H7	Choat et al. 2004
	Chlorurus sordidus	Microalgae (detrital material)	H8	Choat et al. 2002
	Siganus doliatus	Microalgae	H9	Woodland 1997
	Stegastes nigricans	Microalgae (microinvertebrates)	H10	Hata and Kato 2004
	Zebrasoma scopas	Microalgae (macroalgae)	H11	Choat et al. 2004
Planktivorous				
	Abudebduf sexfasciatus	Zooplankton (microalgae)	Z1	Myers 1991
	Ostorhinchus doederleini	Zooplankton (nekton, zoobenthos)	Z2	Myers 1991
	Caesio caerulaurea	Zooplankton	Z3	Ter Kuile 1989
	Chromis viridis	Zooplankton (microalgae)	Z4	Allen 1991
	Chrysiptera notialis	Zooplankton	Z5	Allen 1991
	Dascyllus aruanus	Zooplankton (microalgae)	Z6	Booth 2004
	Pomacentrus moluccensis	Zooplankton (microalgae)	Z7	Pratchett et al. 2001
Carnivorous				
	Bodianus perditio	Macroinvertebrates	C1	Kulbicki et al. 2005
	Hemigymnus melapterus	Macroinvertebrates (zooplankton)	C2	Westneat 2001
	Lethrinus atkinsoni	Macroinvertebrates (nekton)	C3	Kulbicki et al. 2005
	Mulloidichthys flavolineatus	Macroinvertebrates (nekton)	C4	Kulbicki et al. 2005
	Parupeneus ciliatus	Macroinvertebrates (zooplankton)	C5	Kulbicki et al. 2005
	Plectorhynchus lineatus	Macroinvertebrates (nekton)	C6	Myers 1991
	Sargocentron rubrum	Macroinvertebrates (nekton)	C7	Kulbicki et al. 2005
	Scolopsis bilineatus	Macroinvertebrates (nekton)	C8	Russell 1990
	Scorpaenodes guamensis	Macroinvertebrates	C9	Myers 1991
	Chaetodon citrinellus	Corals (microalgae)	C10	Allen et al. 1998
	Chaetodon flavirostris	Corals (microalgae)	C11	Coleman et al. 1981
Piscivorous				
	Cheilidopterus quinquelineatus	Reef nekton	P1	Nakamura et al. 2003
	Epinephelus merra	Reef nekton	P2	Kulbicki et al. 2005
	Saurida gracilis	Nekton	P3	Kulbicki et al. 2005
	Scomberomorus commerson	Pelagic nekton	P4	Blaber et al. 1990
	Synodus variegatus	Reef nekton	P5	Shibuno et al. 1996

the green calcareous alga *Halimeda* sp. collected at site 3. The δ^{13}C signatures presented by brown macroalgae and turf microalgae were more consistent with those of most fishes. The links between the δ^{15}N signatures of food sources and fish will be examined in more detail below.

Each trophic group of fish was characterized by a specific δ^{13}C and δ^{15}N range of values (A [2], $p < 0.05$). At the three sites, the herbivorous fish species were clearly separated from the other trophic groups by their low δ^{15}N signatures (Fig. 2), except for *Stegastes nigricans* (H10) at sites 2 and 3, and *Centropyge tibiscens* (H2) at site 2, which presented higher δ^{15}N signatures (Figs. 2b and 2c). The Scaridae species (H6, H7 and H8) collected at site 3 showed particularly low δ^{15}N and high δ^{13}C signatures (Fig. 2c). Consequently, the mean δ^{15}N and δ^{13}C values of herbivores displayed significant spatial variations (A [4], $p < 0.05$). Contrary to the herbivorous species, the planktivorous, carnivorous and piscivorous species were poorly discriminated by their isotopic signatures (Fig. 2), especially at site 2 where their values largely overlapped (Fig. 2b). Spatial variations in δ^{13}C signatures were only found for carnivores and for piscivores when the pelagic species *Scomberomorus commerson* was excluded (A [4], $p < 0.05$). Conversely, only the δ^{15}N signatures of piscivores did not vary spatially (A[4], $p > 0.05$) and *Synodus variegatus* (P5) showed the

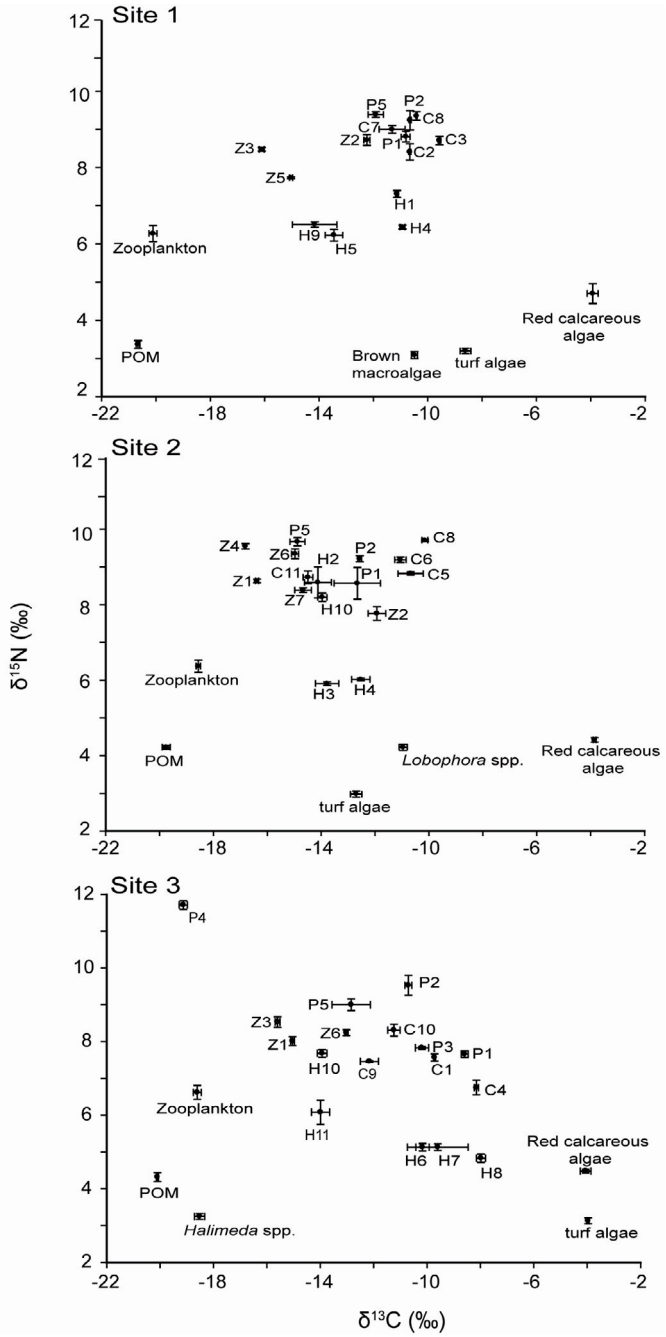

Fig. 2. Plots of δ^{15}N against δ^{13}C signatures of food sources, zooplankton and fish species at the fringing (site 1), intermediate (site 2) and barrier reef (site 3) sites. The points represent the mean values and the bars the standard deviations. See Table 2 for species codes and Fig. 1 for the position of the sampling sites.

highest δ^{15}N values at all sites (Fig. 2). Site 3 was also characterized by a wide dispersion of δ^{13}C and δ^{15}N values among carnivorous and piscivorous species, whereas these species were plotted more narrowly at site 1 (Figs. 2a and 2c).

3.4 Re-assessment of fish trophic groups based on isotopic data (Table 4)

Generally, the estimated trophic positions based on either POM or algae as the first trophic level were close (Table 4). For seven out of the 11 herbivorous-classified species, the $\Delta\delta^{15}$N estimated trophic positions were consistent with gut contents data, with mean positions ranging from 1.8 to 2.5 (i.e. ~2; Table 4). However, the three Scaridae species (*Scarus niger*, *S. schlegeli* and *Chlorurus sordidus*, H6 to H8) and *Cirripectes stigmaticus* (H3) were characterized by lower trophic positions, with means ranging from 1.4 to 1.6 (i.e. <2; Table 4). The estimated trophic positions of the seven planktivorous-classified species ranged from 2.4 to 2.8 (Table 4), logically indicating one higher trophic level relative to herbivores and confirming the gut contents-based classification. For carnivorous and piscivorous species however, the estimated trophic positions were generally lower than expected. The mean estimated trophic positions of the eleven carnivorous-classified species ranged from 2.0 to 2.9, which suggest that these species feed over a broader range of food items than indicated by gut contents data alone. The values for *Mulloidichthys flavolineatus* (C4), *Bodianus perditio* (C1) and *Scolopsis bilineatus* (C9) were particularly low, always < to 2.4. Among the five piscivorous-classified species, only did *Scomberomorus commerson* (P4) show a high estimated trophic position > 3.5, consistent with its gut contents-based classification, whereas the mean values for *Saurida gracilis* (P3) and *Cheilidopterus quinquelineatus* (P1) were as low as 2.3 to 2.5 respectively (Table 4).

3.5 Ontogenetic variability in fish feeding behaviour (Fig. 3)

The four species selected for the study of the relationship between body mass and isotopic variations were: *Synodus variegatus* (P5), *Stegastes nigricans* (H10), *Abudebduf sexfasciatus* (Z1) and *Cheilidopterus quinquelineatus* (P1). These species were indeed the only ones to provide at least seven individuals with a body mass difference of at least 8.5 g between the smallest and the biggest fish. The δ^{13}C signature of muscle tissue increased with body mass for *Abudebduf sexfasciatus* and *Cheilidopterus quinquelineatus* (Figs. 3c and 3d; $r^2 = 0.83$, $p < 10^{-6}$ and $r^2 = 0.31$, $p = 0.016$ respectively), whereas it decreased with body mass for *Stegastes nigricans* (Fig. 3b; $r^2 = 0.79$, $p < 10^{-6}$). The relationship was not significant for *Synodus variegatus* (Fig. 3a; $p > 0.05$). Conversely, the δ^{15}N signature of muscle tissue decreased with body mass for *Synodus variegatus* and *Abudebduf sexfasciatus* (Figs. 3a and 3b, $r^2 = 0.38$, $p = 0.006$ and $r^2 = 0.61$, $p < 10^{-6}$ respectively) and increased with body mass for *Stegastes nigricans* (Fig. 3b; $r^2 = 0.22$, $p < 10^{-6}$). The relationship was not significant for *Cheilidopterus quinquelineatus* (Fig. 3d). In no case did the variation in δ^{15}N with body mass exceed 2.4‰, which suggests that no changes in trophic position occurred for any species within the range of body mass values available in the present study.

Table 3. F ratio and probability levels associated with one way ANOVAs testing for differences in δ^{13}C and δ^{15}N between food sources [1], between fish trophic groups [2], and between sites for each food source [3] and each fish trophic group [4]. NS: non significant, POM: Particulate Organic Matter, Turf: turf-forming microalgae, Piscivorous(*) once *Scomberomorus commerson* excluded.

Test type	Degree of freedom	δ^{13}C		δ^{15}N	
		F-ratio	$p-$value	F-ratio	p-value
[1] Differences between food sources	6	72.661	$<10^{-6}$	155.414	$<10^{-6}$
[2] Differences between fish trophic groups	3	44.949	$<10^{-6}$	102.053	$<10^{-6}$
[3] Differences between sites for:					
POM		22.288	$<10^{-6}$	28.060	$<10^{-6}$
Red calcareous algae	2	0.395	0.690 NS	0.864	0.468 NS
Turf		7.467	6×10^{-3}	2.337	0.131 NS
Zooplankton		26.046	$<10^{-6}$	0.922	0.419 NS
[4] Differences between sites for:					
Herbivorous		7.324	1×10^{-3}	6.581	2×10^{-3}
Planktivorous	2	1.614	0.206 NS	5.780	5×10^{-3}
Carnivorous		7.177	1×10^{-3}	68.172	$<10^{-6}$
Piscivorous		2.703	0.076 NS	0.613	0.545 NS
Piscivorous(*)		13.764	$<10^{-6}$	1.729	0.189 NS

4 Discussion

Significant spatial variations were observed in the present study for most of the food sources and fish trophic groups examined. These spatial variations can be accounted for by the strong heterogeneity of water column productivity characterizing the lagoon of New Caledonia (Pinazo et al. 2004), and confirm that contrasts in water column conditions can affect the stable isotope signatures of both sources and consumers. Once these variations were considered, the general trophic structures of fish assemblages appeared globally similar at the three sites. Stable isotope data were also generally useful in determining the major trophic pathways sustaining these structures, although with a variable efficiency depending on the trophic group examined.

Stable carbon and nitrogen isotopic ratios were very efficient in separating herbivorous fish species from the other groups. The trophic position of these species, calculated according to the δ^{15}N fractionation between algal sources and fish, confirmed the herbivory of most of the species revealed by gut contents analysis. However, it seems that some of the potential algal sources collected in this study only contribute poorly to the diet of the herbivorous fish sampled. Being largely ^{13}C enriched relative to all herbivores, red calcareous algae, for example, do not appear to constitute a significant food source in any herbivore diet. Carbonate is a common constituent of herbivorous fish stomach contents as these fish graze the algal film on rocks and corals (Bruggemann et al. 1994) and also feed on the epiphytic algae growing on carbonate substrata (Van Rooij et al. 1995). Therefore, it seems that calcareous-algal carbon is negligibly used by the grazers sampled in the present study. Similarly, the calcareous green alga *Halimeda* sp. sampled on the barrier reef tends to be rejected by rabbitfish in favour of more nutritional algal species like *Enteromorpha* (Montgomery and Gerking 1980). Consequently, *Halimeda* is unlikely to have been a substantial food source for the grazers examined in this study. Former stomach contents analyses have indicated that, despite a relatively high energy, protein and carbohydrate content (Montgomery and Gerking 1980), macroalgae in general are unlikely to constitute the major component of herbivore diets on coral reefs (Russ and St John 1988). The low δ^{15}N values found for the parrotfishes *Scarus schlegeli*, *S .niger* and *Chlorurus sordidus* at the barrier reef suggest that their main food source is more likely to have been turf algae, characterized by the lowest δ^{15}N values among primary producers. However, the substantial ^{13}C-enrichment of these algae relative to all three scarids could indicate that detrital material represents a more important part of scarids' diet than previously thought (Chen 2002; Choat et al. 2002, 2004), and might explain the low ^{15}N and high ^{13}C values characterizing these species. A similar diet-mixing hypothesis might be postulated for most of the herbivorous fish sampled in this study. Some surgeonfish like *Acanthurus nigrofuscus* (H1), *Ctenochaetus striatus* (H4) or *Zebrasoma scopas* (H11) indeed exhibit a somewhat detritivorous feeding habit related to dentition and feeding behaviour (Purcell and Bellwood 1993). The substantial enrichment of nitrogen relative to reef sediments in the stomach contents of *Ctenochaetus striatus* indicates that such feeding is nutritionally advantageous (Nelson and Wilkins 1988). Such detritus may derive from sources other than the algae sampled in this study, and these may include the faecal detritus of other fishes which are widely used as a food source in the reef community (Rothans and Miller 1991). Furthermore, this faecal material has been shown to contain significant levels of phosphorus, copper, iron, manganese and zinc (Geesey et al. 1984). *Zebrasoma scopas* is known to consume benthic algae on reefs, but also to consume large quantities of faecal material originating from zooplanktivorous *Chromis atripectoralis* (Bailey and Robertson 1982). Cophrophagy could thus account for the δ^{13}C and δ^{15}N data of the herbivores that were sampled in the present study.

Table 4. Trophic positions of fish species based on the difference between their δ^{15}N signatures and those of their ultimate food sources (both POM and algae) at each site, with POM: Particulate Organic Matter; TmA: turf-forming microalgae; BMA: brown unidentified macroalga, *Lob*.: brown macroalga *Lobophora* sp., *Hal*: green macroalga *Halimeda* sp. A mean enrichment of 3.2‰ for ^{15}N per trophic level has been used, following Sweetings et al. (2007)'s recommendations for fish muscle tissues. A trophic position of 1 is assumed for the food sources. Fish species are ranked in alphabetical order, as in Table 1.

Fish species	Site 1			Site 2			Site 3		
	1^{rst} trophic level								
	POM	TmA	BMA	POM	TmA	*Lob*.	POM	TmA	*Hal*.
Abudebduf sexfasciatus (Z1)				2.4	2.8	2.4	2.2	2.5	2.5
Acanthurus nigrofuscus (H1)	2.2	2.3	2.3	-	-	-	-	-	-
Bodianus perditio (C1)	-	-	-	-	-	-	2.0	2.4	2.3
Caesio caerulaurea (Z3)	2.6	2.6	2.7	-	-	-	2.3	2.7	2.6
Centropyge tibiscens (H2)	-	-	-	2.4	2.8	2.3	-	-	-
Chaetodon citrinellus (C10)	-	-	-	-	-	-	2.2	2.6	2.6
Chaetodon flavirostris (C11)	-	-	-	2.4	2.8	2.4	-	-	-
Cheilidopterus quinquelineatus (P1)	2.7	2.8	2.8	2.4	2.7	2.3	2.0	2.4	2.4
Chlorurus sordidus (H8)	-	-	-	-	-	-	1.2	1.5	1.5
Chromis viridis (Z4)	-	-	-	2.7	3.1	2.6	-	-	-
Chrysiptera notialis (Z5)	2.4	2.4	2.5	-	-	-	-	-	-
Cirripectes stigmaticus (H3)	-	-	-	1.5	1.9	1.5	-	-	-
Ctenochaetus striatus (H4)	2.0	2.0	2.0	1.6	2.0	1.5	-	-	-
Dascyllus aruanus (Z6)	-	-	-	2.6	3.0	2.6	2.2	2.6	2.6
Epinephelus merra (P2)	2.8	2.9	2.9	2.6	3.0	2.5	2.6	3.0	3.0
Hemigymnus melapterus (C2)	2.6	2.6	2.7	-	-	-	-	-	-
Lethrinus atkinsoni (C3)	2.7	2.7	2.8	-	-	-	-	-	-
Mulloidichthys flavolineatus (C4)	-	-	-	-	-	-	1.8	2.1	2.1
Parupeneus ciliatus (C5)	-	-	-	2.4	2.8	2.4	-	-	-
Plectorhynchus lineatus (C6)	-	-	-	2.6	2.9	2.5	-	-	-
Pomacentrus adelus (H5)	1.9	1.9	2.0	-	-	-	-	-	-
Pomacentrus moluccensis (Z7)	-	-	-	2.3	2.7	2.3	-	-	-
Ostorhinchus doederleini (Z2)	2.7	2.7	2.8	2.1	2.5	2.1	-	-	-
Sargocentron rubrum (C7)	2.8	2.8	2.8	-	-	-	-	-	-
Saurida gracilis (P3)	-	-	-	-	-	-	2.1	2.5	2.4
Scarus niger (H6)	-	-	-	-	-	-	1.3	1.6	2.0
Scarus schlegeli (H7)	-	-	-	-	-	-	1.3	1.6	1.6
Scolopsis bilineatus (C8)	2.9	2.9	3.0	2.7	3.1	2.7	-	-	-
Scomberomorus commerson (P4)	-	-	-	-	-	-	3.3	3.7	3.7
Scorpaenodes guamenis (C9)	-	-	-	-	-	-	2.0	2.4	2.3
Siganus doliatus (H9)	2.0	2.0	2.1	-	-	-	-	-	-
Stegastes nigricans (H10)	-	-	-	2.2	2.6	2.2	2.1	2.4	2.4
Synodus variegatus (P5)	2.9	2.9	3.0	2.7	3.1	2.7	2.5	2.8	2.8
Zebrasoma scopas (H11)	-	-	-	-	-	-	1.5	1.9	1.9

The fish species usually classified as carnivorous and piscivorous sampled in this study actually appear to feed over a broader range of trophic levels and food sources than expected from the gut contents observations. Their isotopic ranges of values indeed largely overlapped at the three sites, and their estimated trophic positions revealed to be lower than expected. This result might be explained by the underestimation of the importance of mixed omnivorous diets by gut contents analysis. Omnivorous feeding behaviours have indeed been shown to be widespread among many temperate reef fishes (La Mesa et al. 2007) and coral reef fishes (Kavanagh and Olney 2006; Silvano and Guth 2006). Ontogenetic variations, which occurred in the present study for the four fish species examined, could also play a role. Ontogenetic variations in feeding behaviours have indeed been reported for many demersal reef fish species (Kawakami and Tachihara 2005; Tibbetts and Carseldine 2005) and pelagic tropical species (Graham et al. 2007). Both processes might also be associated to explain the wide range of isotopic values and trophic positions observed for the carnivorous fish species in the present study. Kulbicki et al. (2005) indeed demonstrated that the number of prey types consumed by over 100 carnivorous coral-reef fish species from the lagoon of New Caledonia increased with fish size, and thus that omnivorous behaviours may become increasingly important as fish grow. Since such omnivorous diets are difficult to determine by using gut content data alone, stable isotopes were

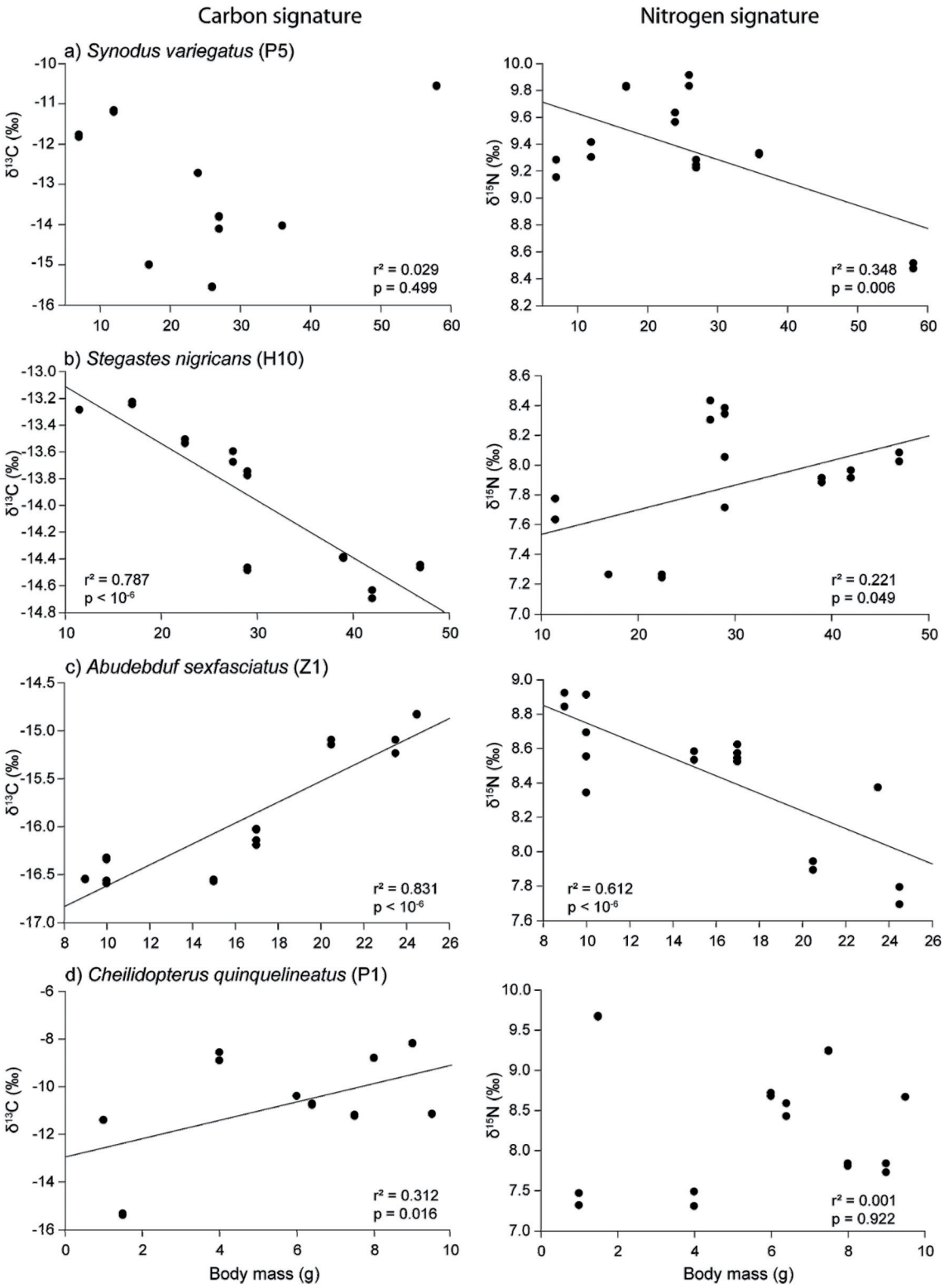

Fig. 3. Relationship between δ^{13}C and body mass (left column) and between δ^{15}N and body mass (right column) in the four species for which at least seven individuals were collected, with a body mass difference of at least 8.5 g between the smallest and the biggest fish. *Synodus variegatus*, piscivorous (a), *Stegastes nigricans,* herbivorous (b), *Abudebduf sexfasciatus*, planktivorous (c) and *Cheilidopterus quinquelineatus*, piscivorous (d). The lines correspond to the linear regression models.

essential in estimating the trophic status and feeding relationships of the fish species under study.

5 Conclusion

In the present study, stable isotope data facilitated the assessment of the major trophic relationships structuring fish assemblages in the lagoon of New Caledonia. Stable isotopes of carbon and nitrogen were very efficient for discriminating herbivorous fish species and for identifying their major food sources. Conversely, carnivorous and piscivorous fish trophic groups were poorly discriminated from one another, and their estimated trophic positions were lower than expected when considering gut contents data alone. This was probably due to a partly omnivorous diet, or to an ontogenetic variation in the food sources consumed by some species. This study thus emphasizes the importance of mixed dietary, including coprophagy and omnivorous diet, in the feeding habits of many coral reef fish species usually classified as carnivorous by gut contents studies. This type of feeding behaviour should thus be paid greater attention when assigning fish species to trophic groups and when attempting to model the trophic structure of fish assemblages in such diversified ecosystems.

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