



Complex food webs in highly diversified coral reefs: Insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes



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ABSTRACT

We studied the trophic network architecture of the coral reef ecosystem of the New Caledonian lagoon. To encompass the main trophic levels, we assayed carbon and nitrogen stable isotopes in various organic matter sources, intermediate consumers (invertebrates and fish), and 19 species of predatory fish (total of 1229 samples). At each level, wide range of variations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ suggested multiple sources for the OM, and complex trophic relationships among the different organisms. Despite this complexity, four trophic structures were identified. 1) The predominant reef benthic food web (R-BFW) based on the OM produced by algal turf supplies most of intermediate consumers and all anguilliform fish studied. 2) The sedimentary benthic food web (S-BFW), and 3) the lagoon pelagic food web (L-PFW), respectively based on sedimentary OM (SOM) and particulate OM (POM) involve a wide range of organisms and represent complementary food webs for most anguilliform fish. 4) Finally, the detrital benthic food web (D-BFB) where the OM issued from seagrass is indirectly utilised by reef consumers plays a secondary role. Anguilliform fish are widespread sedentary predators that live in various habitats; the species sampled were respectively associated with the three main trophic structures identified, depending on their diet and habitat. This study reveals several major structures that are inter-connected to form an overall complex trophic network in the coral reefs.

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1. Introduction

In highly diversified environments, intersecting food chains can form complex networks that influence the functioning and the resilience of the ecosystems (Folke et al., 2004). Describing the food web architecture and gathering accurate information on the trophic relationships across species is a critical prerequisite to assess the persistence of ecosystems threatened by global changes (Wilson et al., 2010). In most tropical ecosystems, food webs involve very large numbers of species from which available trophic information (e.g. diet) is generally limited; their trophic architecture remains poorly understood (Link, 2002). Although essential, filling up this lack of knowledge poses considerable difficulties. Indeed, studying the foraging ecology of numerous species spread over a wide range of taxa, that displaying contrasted ecology, physiology, and body sizes, is demanding in terms of logistics, funding, and expertise.

Carbon and nitrogen stable isotope analyses offer useful tools to assess the trophic position of organisms and provide valuable information about their spatial distribution (Layman et al., 2012). Because they offer

complementary information to stomach content analyses, they have been widely employed to study the trophic structure of ecosystems (e.g. Peterson and Fry, 1987; Davenport and Bax, 2002; Koenigs et al., 2015). Notably to study major marine ecosystems like *Posidonia* seagrass beds (Lepoint et al., 2000), rocky reefs (Cresson et al., 2014), estuaries (Lee, 2000) or continental shelves (Darnaude et al., 2004). However, most marine studies focused on specific segments of the trophic web and did not consider the whole trophic structures. For instance, the origin of the particulate organic matter (Buscail et al., 1995), macrophytes (Cooper and McRoy, 1988), pelagic and benthic invertebrates (Bouillon et al., 2000), or fish (Greenwood et al., 2010) have been often studied separately. This segmentation precludes a global assessment of the trophic web, especially in complex ecosystems.

Coral reefs are characterized by a very rich biodiversity and a great variability of their trophic parameters across space and time (Harmelin-Vivien, 2002; Wyatt et al., 2012). Despite significant advances based on stable isotope analyses (e.g. Wyatt et al., 2010; Dromard et al., 2013; McMahon et al., 2015) no global assessment of their trophic structure is available (Wilson et al., 2010). Several major sources for the primary production of OM have been described recently (De Goeij et al., 2013; Wyatt et al., 2013; Briand et al., 2015), and different studies focused on reef fish (Carassou et al., 2008; Wyatt et al., 2012;

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Letourneur et al., 2013, Dromard et al., 2015). But very few data are available about reef invertebrates that occupy key (often intermediate) positions in the food webs (Mallela and Harrod, 2008; Davis et al., 2015). Overall, information of the trophic relationships across the whole range of producers, consumers and predators is fragmentary. Investigations that include a wide spectrum of organisms from each trophic level are timely in order to encompass the whole trophic architecture of coral reefs.

Sampling all organisms living in diverse and complex coral reefs is unfeasible, notably for fish. Therefore, selecting pertinent organisms is necessary. The isotopic values of the targeted species should be relevant of the sampled habitats; sedentary species should be thus preferred over vagrant ones. Similarly, abundant and largely distributed species should be preferred over rare ones to better identify major food chains. These precautions are notably important for predatory fish that are situated at the apex of the food chains. In this study, we mainly focused on anguilliform fish species (moray eels, congers, and snake-eels). These predators can be very abundant in coral reefs (Ineich et al., 2007), are widely distributed across habitats (Brischoux et al., 2009a), and usually occupy a high trophic level in food webs (Brischoux et al., 2011). Their diet has been partly elucidated and each species feeds preferentially on several major types of organisms: crustaceans, fish, annelids, cephalopods or snails (Harmelin-Vivien, 1979; Gilbert et al., 2005; Vaslet et al., 2011). They are sedentary, characterized by high site fidelity after maturity, and exhibit long-life expectancy (Böhlke et al., 1989). Those traits are useful to integrate trophic information into a precise spatial and temporal context. Anguilliform fish represent an abundant and diverse group that plays key roles both as predators and prey (Ineich et al., 2007). However, anguilliform fish received limited attention and few studies have assessed their trophic position (Marguillier et al., 1997; Vaslet et al., 2011, Brischoux et al., 2011), likely because their cryptic lifestyle complicated observation. Yet, in many reef ecosystems of the West Pacific Ocean, sea snake sampling offers a cost/efficient method to rapidly collect large numbers of anguilliform fish belonging to various taxa (Reed et al., 2002; Ineich et al., 2007; Bonnet, 2012).

Using C and N stable isotope analyses, the main goal of this study was to describe the whole trophic structure(s) of a complex coral reef ecosystem. Consequently, our sample included a wide range of organisms, encompassing major trophic levels from the main putative sources of organic matter (OM) to various intermediate consumers and ultimately including a wide range of predatory anguilliform fish. We sampled different habitats during two seasons to 1) reconstruct food webs' architecture, from OM sources up to the anguilliform fish, to 2) identify the main trophic pathways through which OM flows up to the higher levels, and to 3) determine the trophic status of the anguilliform fish that represent typical insufficiently studied major predators of many coral reefs.

2. Material and methods

2.1. Study sites and sampling

New Caledonia located in the SW Pacific (21°30'S, 165°30'E) contains the second largest continuous reef ecosystem in the world (~1600 km of barrier reef, enclosing ~24,000 km²). The study was carried out in two areas of the southwest lagoon of New Caledonia, Grand Nouméa (GN) and Grand Sud (GS) (Fig. 1). Three stations located on a coast-barrier reef gradient were sampled in each area (total six stations). Sampling was performed seasonally, during summer (January to March) and winter (June to September) 2011.

We attempted to sample the main compartments potentially representative of the whole food webs: various OM sources, a large amount of intermediate consumers (invertebrates and fish), and various top predators (i.e. different species of anguilliform fish). More precisely, we sampled twenty different macrophytes (algal turf, macroalgae and seagrass, $N = 183$), the particulate organic matter (POM) of the marine surface

layer (top 1 m, $N = 32$) and the sedimentary organic matter (SOM) of the bottom substrate (top 3 cm, $N = 34$), plus about 60 species of micro- and macro-invertebrates (small and large crustaceans, gastropods, echinoderms and annelids, $N = 331$) (Tables 1 and 2). Fish from 61 species presenting various characteristics (i.e. demersal, benthic and/or cryptic lifestyle, small to medium average size) were selected as potential preys of anguilliform fish ($N = 247$, Table 2). Anguilliform fish were obtained from the stomach content of their main predators, the amphibious sea kraits (*Laticauda laticaudata* and *L. saintgironsi*), via gentle forced regurgitation (Brischoux et al., 2007; Briand et al., 2014). Sea kraits are phylopatric predators that exhibit typical central place foraging strategies; they rapidly return to their home islet to digest their prey (Shetty and Shine, 2002, Brischoux et al., 2009b). Recently ingested prey (i.e. poorly digested regurgitated items) are captured nearby (<5 km away) the home islet of the sea kraits, and thus they provide a high spatial resolution (Brischoux et al., 2007). In this study, we used only poorly digested prey to ensure that the isotopic values of the anguilliform fish were representative of each station. Nineteen anguilliform species were studied, including fifteen Muraenidae species, two Ophichthidae species and two groups of Congridae ($N = 402$, Table 3). Isotopic differences have been found between conger eels consumed by *L. laticaudata* and *L. saintgironsi* that use distinct habitats (Brischoux et al., 2011). Accordingly, conger eels were separated in two different groups, *Conger* "LI" and *Conger* "Ls" (meaning congers caught by *Laticaudata laticaudata* and *L. saintgironsi*, respectively).

All samples were identified at the lowest possible taxonomic level. Thalli of macrophytes were cleared of their epiphytes and each fish was measured to the nearest mm (total length, TL). A total of 1229 individuals were sampled and analysed to determine their C and N isotopic ratios.

2.2. Stable isotope analyses

Tissues that provide the most reliable isotopic values were taken and immediately frozen at $-30\text{ }^{\circ}\text{C}$ for subsequent analyses: a piece of thallus for macrophytes, soft muscle for all macro-invertebrates and dorsal white muscle for all fish (Pinnegar and Polunin, 1999). For small invertebrates (crustaceans and polychaetes), whole individuals were used to obtain sufficient amount of material (e.g. 5 mg) for analysis.

Carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analysed for all samples. Sediment was dried and reduced to a fine powder. POM in seawater was collected on GF/F filters (porosity $0.7\text{ }\mu\text{m}$) and dried. Tissue samples of plants (macrophytes) and animals (macro-invertebrates and fish) were freeze-dried and grounded to fine powder with a porcelain mortar and pestle. Approximately 1 mg of powder was weighed and encapsulated for vegetal/animal samples, 15–20 mg for SOM and 15–30 mg for POM (matter extracted by scrubbing the filter). Samples were first analysed without prior treatment. For calcareous algae and crustaceans (e.g. *Halimeda* spp., shrimps and crabs), as well as for POM and SOM, two subsamples were analysed. One was treated for $\delta^{13}\text{C}$ analysis, after acidification (details in Letourneur et al., 2013), as carbonates present higher $\delta^{13}\text{C}$ than organic carbon (DeNiro and Epstein, 1978). The second subsample, tested for $\delta^{15}\text{N}$, was not acidified to limit alteration of nitrogen isotopes (Pinnegar and Polunin, 1999).

The $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ ratios were measured by continuous-flow isotope-ratio mass spectrometry. Measurement precision estimated using standards included in the analyses was of 0.1‰ for $\delta^{13}\text{C}$ and 0.15‰ for $\delta^{15}\text{N}$. Isotope ratios were expressed as parts per 1000 (‰) differences from a standard reference material:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N , R is the corresponding ratio ($^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$) and δ is the proportion of heavy to light isotope in the sample. The

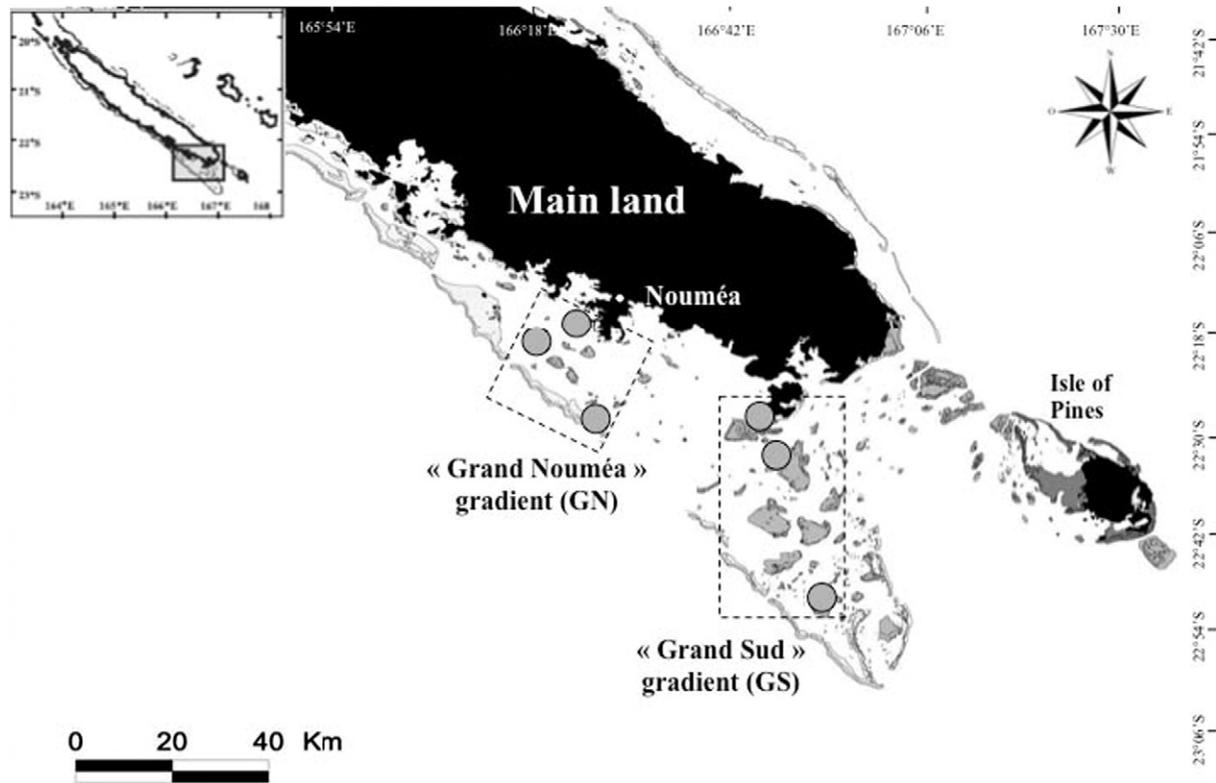


Fig. 1. Location of study sites in the southwest lagoon of New Caledonia, SW Pacific Ocean. Sites were distributed over two coast-barrier reef gradients, “Grand Nouméa” (GN) and “Grand Sud” (GS). Land is black; grey areas represent coral reefs.

international standard references are Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen.

2.3. Statistical analyses

Prior to analyses, data distributions were examined for normality (Shapiro-Wilk test) and homogeneity of variances (Levene test). Spatial and seasonal patterns in the $\delta^{13}C$ and $\delta^{15}N$ isotopic values of OM sources and invertebrates were analysed either using three-way ANOVAs (area x site x season) or non-parametric Kruskal-Wallis tests. For anguilliform

fish, a possible size effect was taken into account using ANCOVAs with total length (TL) as a covariate. Other fish that were not sampled in all stations and only in summer were not included in the analyses.

Hierarchical Ascendant Classification method (HAC) was run to obtain a cluster of species according to their $\delta^{13}C$ and $\delta^{15}N$ values. Euclidian distances were used to calculate dissimilarities between species. Clusters were performed using the Ward method that target to minimize inertia within a group and maximize variation between groups. Isotopic clustering was carried out in two steps. First, some close species belonging to a given taxon were pooled (e.g. seagrass, sea stars, blennies, etc.). Second, the closest previous groups belonging to a given ecological group were pooled (e.g. macrophytes, invertebrates, fish, etc.). No substantial difference emerged comparing the results from each steps. For conciseness, only the results from the second step analyses are presented. The statistics were performed using R (R project, version 2.13.2). The level of significance for statistical analyses was set at $\alpha = 0.05$.

Table 1

Mean $\delta^{13}C$ and $\delta^{15}N$ isotopic ratio (\pm sd) of organic matter sources (pools and macrophytes) sampled in the SW lagoon of New Caledonia. Within each subgroup (obtained after the first HAC), organisms were presented by increasing $\delta^{13}C$ values. For each subgroup are also indicated: the number of individuals sampled (N), the identification code (IC) and the Hierarchical Ascendant Classification number (HAC – for example 1.2 means group 1, sub-group 2; see Fig. 2).

Organic matter sources (S)		N	IC	HAC	$\delta^{13}C$	$\delta^{15}N$
Pools	POM	32	POM	3.2	-19.38 \pm 1.68	4.50 \pm 0.84
	SOM	34	SOM	2.2	-14.04 \pm 1.68	2.81 \pm 0.75
Macrophytes	<i>Halimeda</i> spp1	27	H1	3.1	-18.68 \pm 0.94	1.78 \pm 0.57
	Algal turf	24	AT	3.1	-18.53 \pm 1.97	2.02 \pm 0.56
	<i>Sargassum</i> sp2	11	Sa2	2.2	-14.41 \pm 1.77	3.77 \pm 0.70
	<i>Halimeda</i> spp2	10	H2	2.2	-13.95 \pm 3.68	2.33 \pm 1.29
	<i>Sargassum</i> sp1	3	Sa1	2.2	-13.93 \pm 0.92	2.36 \pm 0.24
	<i>Halimeda</i> spp3	29	H3	2.1	-13.63 \pm 1.84	0.42 \pm 1.34
	<i>Acanthophora</i> sp.	3	A	2.1	-11.71 \pm 0.62	2.09 \pm 0.22
	<i>Cystoseira</i> sp.	3	C	2.1	-11.56 \pm 0.88	1.86 \pm 0.10
	<i>Cymodocea</i> sp2	6	S2	1.3	-8.92 \pm 0.69	2.84 \pm 0.69
	<i>Turbinaria</i> spp.	32	T	1.3	-8.72 \pm 1.58	2.60 \pm 0.73
	<i>Halodule</i> sp	12	S3	1.2	-8.40 \pm 0.89	1.82 \pm 1.06
	<i>Padina</i> sp.	11	P	1.2	-7.52 \pm 0.78	2.10 \pm 0.46
	<i>Cymodocea</i> sp1	6	S1	1.2	-7.24 \pm 0.64	0.64 \pm 1.54
<i>Liagora</i> spp.	6	L	1.1	-4.72 \pm 1.93	2.72 \pm 0.25	

3. Results

3.1. Isotopic values of food web compartments

Hierarchical clustering analyses (HAC) enabled us to identify several important groups in each major ecological compartment, mainly on the basis of the carbon value of the sampled organisms (Fig. 2).

3.1.1. Organic matter sources

Three groups of sources were differentiated (Table 1 and Fig. 2a): group S1, characterized by high $\delta^{13}C$ values (-4.72 to -8.92‰) is composed of three species of seagrass (*Cymodocea* sp1, sp2 and *Halodule* sp.), plus different algae belonging to *Liagora*, *Padina* and *Turbinaria* genus; group S2, characterized by intermediate $\delta^{13}C$ values (-11.60 to -14.40‰) is characterised of SOM and includes several *Halimeda*, *Acanthophora*, *Cystoseira* and *Sargassum* species; and group S3,

Table 2

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratio (\pm sd) of intermediate consumers (invertebrates and potential prey fish) sampled in the SW lagoon of New Caledonia. Within each subgroup (obtained after the first HAC), organisms were presented by increasing $\delta^{13}\text{C}$ values. For each subgroup are also indicated: the number of individuals sampled (N), the identification code (IC) and the Hierarchical Ascendant Classification number (HAC – for example 1.2 means group 1, sub-group 2; see Fig. 2).

		N	IC	HAC	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		
<i>INVERTEBRATES (I)</i>									
Crustaceans	Mysidacea	5	I27	4.2	−17.81	± 2.08	4.24	± 1.20	
	Euphausiacea	1	I28	4.2	−16.29		4.85		
	Other - large shrimps	4	I29	4.2	−15.96	± 2.36	5.68	± 1.14	
	Amphipoda	12	I26	4.2	−15.56	± 1.48	2.97	± 0.97	
	Dardanus spp2	4	I19	3.3	−12.54	± 0.47	5.88	± 0.8	
	Isopoda	8	I17	3.3	−12.20	± 2.31	5.55	± 1.56	
	Anomura - small 2	18	I12	3.2	−12.52	± 1.10	4.77	± 0.88	
	Brachyura - small 2	9	I13	3.2	−12.50	± 0.83	5.13	± 1.10	
	Brachyura - small 1	7	I25	2.2	−10.75	± 1.03	8.15	± 0.38	
	Dardanus spp1	5	I5	1.3	−9.29	± 1.47	5.39	± 1.51	
	Anomura - small 1	5	I2	1.2	−9.00	± 2.04	3.32	± 0.46	
	Brachyura - large	36	I6	1.1	−8.55	± 0.96	5.91	± 1.38	
	Gastropods	Turbinidae	11	I11	3.2	−12.28	± 2.4	4.64	± 0.94
		Trochidae	21	I8	3.1	−11.89	± 1.82	3.64	± 0.54
		Planaxidae	18	I9	3.1	−11.19	± 1.08	4.17	± 1.18
		Neritidae 2	14	I10	3.1	−11.18	± 1.4	4.56	± 2.22
		Strombidae	4	I7	3.1	−11.11	± 0.21	3.04	± 0.81
		Muricidae	22	I22	2.1	−10.07	± 1.38	7.08	± 1.14
Conidae		10	I21	2.1	−9.65	± 1.56	6.92	± 1.25	
Nassariidae		5	I15	1.3	−9.93	± 0.73	5.45	± 0.9	
Neritidae 1		19	I14	1.3	−9.89	± 1.3	5.21	± 1.1	
Cerithidae 1		3	I3	1.3	−9.42	± 0.24	3.31	± 0.07	
Cerithidae 2		15	I16	1.2	−9.97	± 1.11	5.62	± 1.01	
Neritidae 3		7	I1	1.2	−8.47	± 1.71	3.10	± 0.94	
Echinoderms		Asteroidea 1	6	I31	4.1	−14.72	± 0.78	7.07	± 0.29
		Echinoidea 1	4	I30	4.1	−14.08	± 0.88	7.02	± 0.87
	Echinoidea 2	12	I23	2.2	−10.93	± 0.65	6.89	± 1.34	
	Asteroidea 2	20	I24	2.2	−10.83	± 2.58	7.15	± 0.66	
	Ophiuroidea	15	I20	2.1	−9.96	± 1.59	6.42	± 0.49	
	Asteroidea 3	2	I4	1.1	−6.89	± 0.51	5.18	± 0.88	
Others	Polychaeta	9	I18	3.3	−12.91	± 1.37	5.76	± 1.87	
<i>FISH – POTENTIAL PREYS (F)</i>									
	Pomacentridae 4	16	F34	3.2	−18.08	± 0.18	8.37	± 0.33	
	Pomacanthidae 2	1	F36	3.2	−17.60		9.00		
	Pomacentridae 7	4	F28	3.2	−17.56	± 0.29	7.76	± 0.19	
	Pomacentridae 3	8	F35	3.2	−17.29	± 0.13	8.93	± 0.38	
	Apogonidae 2	5	F38	3.2	−16.77	± 0.17	9.49	± 0.24	
	Cirrhitidae	1	F37	3.2	−16.22		9.10		
	Apogonidae 3	14	F39	3.2	−15.89	± 1.30	9.91	± 0.45	
	Apogonidae 7	3	F33	3.1	−16.60	± 0.23	8.60	± 0.05	
	Pomacentridae 6	2	F32	3.1	−16.37	± 0.10	8.49	± 0.37	
	Pomacentridae 1	10	F29	3.1	−16.23	± 0.93	7.94	± 0.74	
	Pomacanthidae 1	21	F27	3.1	−15.92	± 1.05	7.83	± 0.38	
	Pomacentridae 9	4	F31	3.1	−15.88	± 0.25	8.51	± 0.13	
	Pomacentridae 8	11	F24	3.1	−15.55	± 0.55	7.58	± 0.23	
	Pseudochromidae	3	F30	3.1	−15.48	± 0.08	8.44	± 0.29	
	Pomacentridae 5	23	F25	3.1	−15.37	± 0.35	7.69	± 0.56	
	Tetraodontidae	5	F26	3.1	−15.37	± 0.08	7.86	± 0.46	
	Acanthuridae 2	8	F12	2.3	−15.58	± 0.87	5.58	± 0.30	
	Labridae 1	9	F16	2.2	−14.60	± 0.58	8.00	± 0.51	
	Pinguipedidae 1	2	F15	2.2	−14.44	± 0.03	7.51	± 0.32	
	Scorpaenidae	2	F14	2.2	−14.28	± 0.34	7.49	± 0.04	
	Opistognathidae	2	F13	2.2	−14.16	± 0.12	7.21	± 0.50	
	Chaetodontidae 3	2	F17	2.2	−14.05	± 0.14	8.09	± 0.35	
	Chaetodontidae 1	3	F23	2.1	−14.36	± 0.56	9.34	± 0.06	
	Apogonidae 9	8	F20	2.1	−14.32	± 0.62	8.86	± 0.37	
	Apogonidae 1	16	F18	2.1	−14.23	± 0.77	8.51	± 0.62	
	Apogonidae 4	3	F19	2.1	−14.15	± 0.97	8.57	± 0.25	
	Pomacentridae 2	1	F21	2.1	−13.81		8.84		
	Labridae 2	1	F22	2.1	−13.37		9.48		
	Blenniidae	12	F2	1.2	−13.42	± 0.98	6.39	± 0.44	
	Monacanthidae	2	F3	1.2	−12.52	± 0.10	6.91	± 0.47	
	Acanthuridae 1	4	F4	1.2	−12.09	± 0.86	6.80	± 0.35	
	Scaridae	4	F1	1.2	−11.89	± 1.05	5.15	± 0.63	
	Platycephalidae	2	F5	1.2	−11.87	± 0.38	6.91	± 0.05	
	Apogonidae 8	17	F8	1.1	−13.16	± 1.07	8.02	± 0.66	
	Apogonidae 6	4	F7	1.1	−12.72	± 0.31	7.73	± 0.31	
	Chaetodontidae 2	4	F10	1.1	−12.44	± 0.62	8.44	± 0.34	
	Apogonidae 5	3	F11	1.1	−11.61	± 0.91	8.42	± 0.34	
	Apogonidae 10	6	F6	1.1	−11.17	± 1.07	7.45	± 0.34	
	Pinguipedidae 2	1	F9	1.1	−10.88		7.96		

Table 3
Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratio (\pm sd) of anguilliform fish in the SW lagoon of New Caledonia. Within each taxa, organisms were presented by increasing $\delta^{13}\text{C}$ values. For each taxa are also indicated: the number of individuals sampled (N), the identification code (IC) and the Hierarchical Ascendant Classification number (HAC – for example 1.2 means group 1, sub-group 2; see Fig. 2).

Anguilliform fish (A)		N	IC	HAC	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$		
Congridae	<i>Conger</i> Ll	52	C14	3.2	−16.26	± 1.69	8.75	± 0.99
	<i>Conger</i> Ls	21	C10	2.2	−13.37	± 2.24	8.39	± 0.74
Muraenidae	<i>Cirrimaxilla formosa</i>	4	M18	3.3	−16.83	± 0.70	9.76	± 0.70
	<i>Gymnothorax moluccensis</i>	16	M19	3.3	−16.52	± 1.19	10.01	± 0.72
	<i>Gymnothorax margaritophorus</i>	10	M13	3.2	−15.34	± 1.21	8.67	± 0.98
	<i>Gymnothorax eurostus</i>	33	M15	3.2	−14.94	± 1.26	9.25	± 0.92
	<i>Gymnothorax pindae</i>	14	M16	3.1	−14.37	± 1.67	9.46	± 0.89
	<i>Scuticaria tigrina</i>	11	M17	3.1	−14.31	± 1.28	9.69	± 0.33
	<i>Gymnothorax reticularis</i>	4	M6	2.3	−14.48	± 0.84	7.55	± 0.58
	<i>Gymnothorax albimarginatus</i>	13	M11	2.2	−14.21	± 2.05	8.52	± 1.10
	<i>Uropterygius</i> sp1	1	M9	2.2	−14.04		8.11	
	<i>Uropterygius supraforatus</i>	1	M12	2.2	−13.45		8.63	
	<i>Uropterygius</i> sp2	1	M7	2.1	−13.17		7.73	
	<i>Gymnothorax chilospilus</i>	133	M8	2.1	−12.83	± 1.12	7.86	± 0.65
	<i>Gymnothorax undulatus</i>	35	M1	1.1	−11.65	± 0.81	7.89	± 0.55
	<i>Gymnothorax fimbriatus</i>	39	M3	1.1	−11.61	± 0.96	8.43	± 0.87
	<i>Uropterygius macrocephalus</i>	1	M2	1.1	−10.98		8.27	
Ophichthidae	Ophichthidae sp1	5	O5	2.3	−14.16	± 1.01	7.49	± 0.48
	<i>Muraenichthys</i> sp.	8	O4	2.3	−13.41	± 0.76	6.23	± 0.95

characterized by low $\delta^{13}\text{C}$ values (−18.50 to −19.40‰) comprises algal turf and two species of *Halimeda*. The POM was classified by HAC in this last group as well, but nonetheless was discriminated in a different sub-group owing to a peculiar $\delta^{15}\text{N}$ value (4.50‰). Consequently, the POM was distinguished as a group S4.

3.1.2. Intermediate consumers

Four groups of invertebrates were identified (Table 2 and Fig. 2b): group I1, characterized by high $\delta^{13}\text{C}$ values (−6.89 to −9.42‰) and low to intermediate $\delta^{15}\text{N}$ values (3.10 to 5.91‰) contained several crustaceans (large Brachyura, small Anomura1 and Dardanus spp1) and gastropods (Cerithidae, Nassariidae and Neritidae1), plus Asteroidea3; group I2, characterized by high $\delta^{13}\text{C}$ (−9.65 to −10.93‰) and $\delta^{15}\text{N}$ (6.42 to 8.15‰) values contained few crustaceans (small Brachyura1), some gastropods (Conidae and Muricidae) and most echinoderms (Asteroidea2, Echinoidea2 and Ophiuroidea); group I3, characterized by intermediate $\delta^{13}\text{C}$ values (−11.11 to −12.91‰) and low to intermediate $\delta^{15}\text{N}$ values (3.04 to 5.88‰) contained several benthic crustaceans (isopoda, small Brachyura2, small Anomura2 and Dardanus spp2) and gastropods (Trochidae, Strombidae, Planaxidae, Turbinidae and Neritidae2), plus polychaeta; and group I4, characterized by low $\delta^{13}\text{C}$ values (−14.08 to −17.81‰) contained small planktonic crustaceans (amphipoda, Euphausiacea, Mysidacea, large shrimps) and of other echinoderms (Asteroidea1 and Echinoidea1).

Three groups of demersal fish were identified (Table 2 and Fig. 2c): group F1, characterized by high $\delta^{13}\text{C}$ values (−10.88 to −13.42‰) contained Blenniidae, Monacanthidae, Platycephalidae, Scaridae, several Apogonidae, plus Acanthuridae1, Chaetodontidae2 and Pinguipedidae2 species; group F2, characterized by intermediate $\delta^{13}\text{C}$ values (−13.37 to −15.58‰) contained Opistognathidae, Scorpaenidae, Labridae, several Apogonidae, Chaetodontidae, plus Acanthuridae2, Pomacentridae2 and Pinguipedidae1 species; group F3, characterized by low $\delta^{13}\text{C}$ values (−15.37 to −18.08‰) and high $\delta^{15}\text{N}$ values (7.58 to 9.91‰) contained Cirrhitidae, Pomacentridae, Pseudochromidae, Tetraodontidae, several of Apogonidae and most Pomacentridae.

3.1.3. Predatory anguilliform fish

Three groups of anguilliform fish were distinguished (Table 3 and Fig. 2d): group A1, characterized by high $\delta^{13}\text{C}$ values (−10.98 to −11.65‰), contained three Muraenidae species (*Gymnothorax fimbriatus*, *G. undulatus* and *Uropterygius macrocephalus*); group A2, characterized by intermediate $\delta^{13}\text{C}$ values (−12.83 to −14.48‰)

contained several Muraenidae species (*G. albimarginatus*, *G. chilospilus*, *G. reticularis*, *Uropterygius* sp1, sp2 and *U. supraforatus*), *Conger* Ls and all Ophichthidae species; and group A3, characterized by low $\delta^{13}\text{C}$ values (−14.31 to −16.83‰) contained the other Muraenidae species (*Cirrimaxilla formosa*, *G. eurostus*, *G. margaritophorus*, *G. moluccensis*, *G. pindae* and *Scuticaria tigrina*), plus *Conger* Ll. Anguilliform fish were also separated by their nitrogen values, according to whether their $\delta^{15}\text{N}$ values were low (*G. reticularis*, *Muraenichthys* sp. and Ophichthidae sp1) or high (*C. formosa*, *G. moluccensis*, *G. pindae* and *S. tigrina*).

3.2. Reconstruction of food webs from OM sources to anguilliform fish

Although we observed spatio-temporal variations for some OM sources and for intermediate consumers (see 3.3 Spatial and temporal variations paragraph below), the global structure of coral reef food webs was conserved between seasons at each site and in both areas. Therefore, we pooled the data from the different sites to obtain a global picture of coral reef food webs in the lagoon of New Caledonia. Four main food webs were identified (Fig. 3).

3.2.1. D-BFW

The detrital benthic food web is based on OM issued from seagrass (*Cymodocea* spp. and *Halodule* sp.) and some few palatable macroalgae (*Liagora* spp., *Padina australis* and *Turbinaria* spp.). Only some benthic herbivorous and omnivorous-detritivorous invertebrates possibly depend on these sources of OM; large Anomura (*Dardanus scutellatus*), Cerithidae (*Clypeomorus batillariaoformis*), Neritidae, large Brachyura (*Grapsus albolineatus*, *G. tenuicrustatus*, *Eriphia sebana*) and Asteroidea (*Fromia milleporella*). No demersal fish or Anguilliform fish were involved in this trophic pathway.

3.2.2. S-BFW

The sedimentary benthic food web where OM originates from SOM and from several macroalgae (*Sargassum* spp., *Acanthopora* spp., *Cystoseira* spp. and *Halimeda* spp.). Many reef organisms are involved in this food web. Among them, most of the sampled invertebrates, notably supposedly herbivorous species (Strombidae, Trochidae, Planaxidae, Turbinidae and some Neritidae), detritivores-omnivores (most Anomura, some small Brachyura, some Neritidae and Cerithidae, Nassariidae, isopoda, polychaeta and Ophiuroidea) and carnivores (Conidae, Muricidae, Asteroidea and some small Brachyura), as well as Echinoidea with high $\delta^{15}\text{N}$ values. This web also includes half of

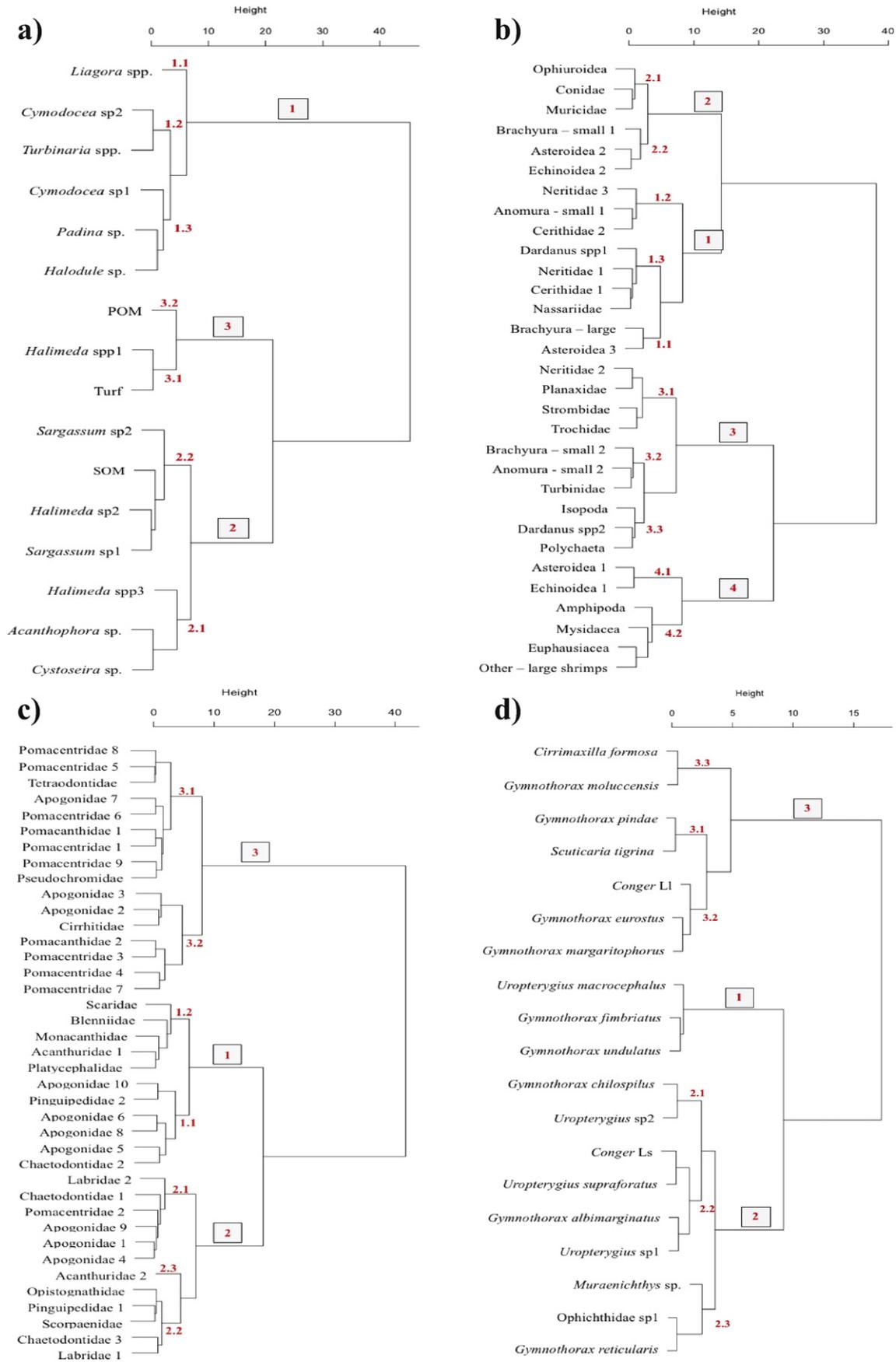


Fig. 2. Dendrograms of a) organic matter sources, b) invertebrates, c) potential prey fish and d) anguilliform fish, obtained from isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) with the Hierarchical Ascendant Classification method (HAC). The “height”-axis is a measure of closeness of either individual data points or clusters, or in other word distance between groups.

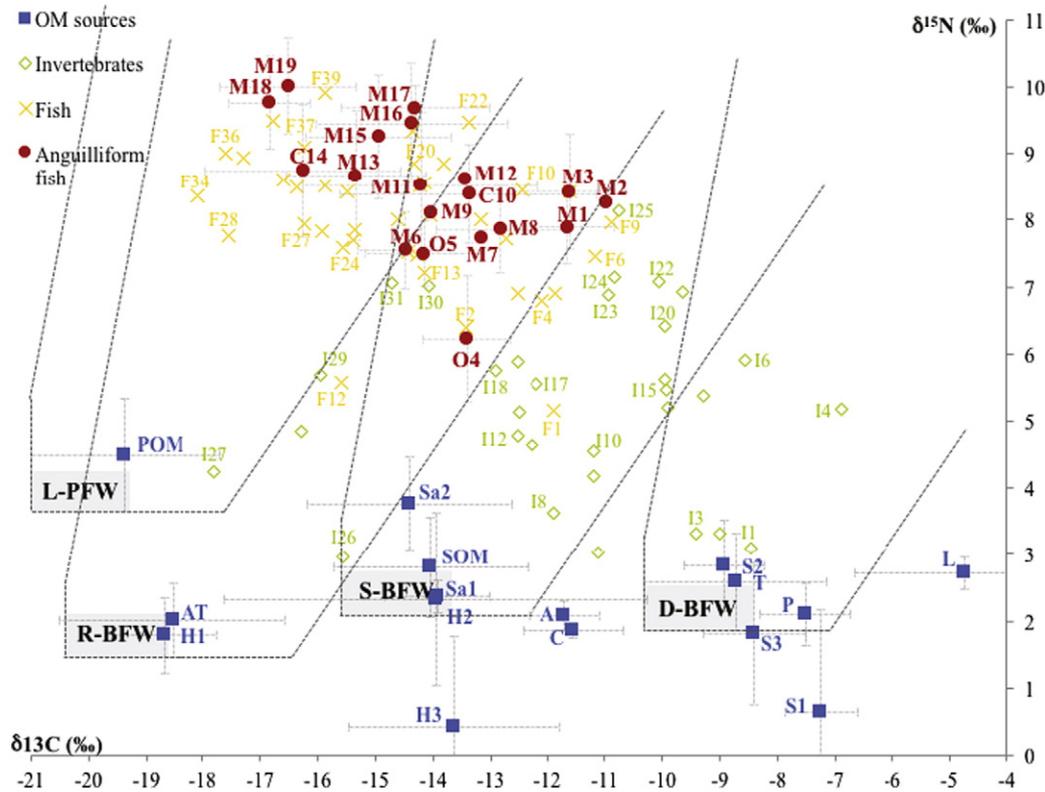


Fig. 3. Plot of $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ (mean \pm SD) for the various compartments and taxa from coral reefs of the SW New Caledonian lagoon. Dotted lines show the limits of the isotopic value ranges expected for trophic transfer of the four major OM sources; we chose the min-max trophic enrichment factors of +1‰ in $\delta^{13}\text{C}$ and +4.5‰ in $\delta^{15}\text{N}$ (left line) and of +2‰ in $\delta^{13}\text{C}$ and +2.5‰ in $\delta^{15}\text{N}$ (right line), in order to get a global view of the OM transfer (Letourneur et al., 2013, codes and taxa as in Tables 1, 2 and 3).

the potential prey fish, with some herbivores-detritivores (Scaridae, Blenniidae, *Ctenochaetus striatus*), some strict and facultative corallivores (*Oxymonacanthus longirostris* and Chaetodontidae) and some micro- and macrocarnivores (Labridae, Platycephalidae, Scorpaenidae, Pinguipedidae, Opistognathidae, *Plectroglyphidodon dickii* and most of Apogonidae). Many anguilliform fish depend on this food web; mainly those with high $\delta^{13}\text{C}$ values (*Gymnothorax fimbriatus*, *G. undulatus* and *Uropterygius macrocephalus*), substantially for anguilliforms with intermediate $\delta^{13}\text{C}$ values (*G. albimarginatus*, *G. chilospilus*, *G. reticularis*, *Uropterygius supraforatus*, sp1 and sp2, *Conger* Ls, *Muraenichthys* sp. and Ophichthidae sp1) and to a lesser extent for others with low $\delta^{13}\text{C}$ values (*G. pindae* and *Scuticaria tigrina*).

3.2.3. R-BFW

The reef benthic food web is based on algal turf and some calcareous macroalgae (*Halimeda opuntia* and *H. heteromorpha*). It involves only few studied invertebrates, that display varied diets (herbivorous, planktonophagous and carnivorous) and lifestyles (benthic vs. planktonic); amphipoda, large shrimps, Mysidacea, Euphausiacea, the Echinoidea *Parasalenia gratiosa*, plus the Asteroidea *Fromia* cf. *monilis* and *Gomphia egyptica*. On the other hand, this trophic pathway included most of the potential prey fish and lead to all anguilliform species examined in this study.

3.2.4. L-PFW

The lagoon pelagic food web where POM used by the phytoplankton is then consumed by many planktonophagous organisms with C-depleted values, such as micro-crustaceans (large shrimps and Mysidacea), Apogonidae (*Archamia fucata*, *Cheilodipterus artus* and *Ostorhinchus angustatus*) and most of non-herbivores Pomacentridae (*Chromis*, *Amphiprion*, etc.). Other fish depend on this OM source, like some micro-, macro-carnivores and piscivores (Cirrihitidae, Labridae, Pseudochromidae, Tetraodontidae and some Apogonidae). POM

appears also to be an important OM source for several anguilliform fish having the lowest $\delta^{13}\text{C}$ values (*Cirrimaxilla formosa*, *Gymnothorax eurostus*, *G. margaritophorus*, *G. moluccensis*, *G. pindae*, *Scuticaria tigrina* and *Conger* L1) and an occasional source for other species (*G. albimarginatus*, *G. reticularis*, *Uropterygius supraforatus* and sp1).

3.3. Spatial and temporal variations

Organic matter sources showed significant spatial variations (see Tables 3 and 4 in Briand et al., 2015); notably in OM pools (POM and SOM) compared to most primary producers (*Halimeda* spp., *Sargassum* sp., *Turbinaria* spp., *Cymodocea* spp., *Halodule* sp.). Isotopic values of OM pools were relatively stable over seasons. Primary producers displayed limited seasonal variation (see Table 4 in Briand et al., 2015). On average, isotopic values of intermediate reef consumers were moderately variable across space (invertebrates and potential prey fish) or time (invertebrates only, Table 4), although marked fluctuations were observed in several organisms (e.g. *Nardoa novaecaledonia*). Overall, no clear general pattern was revealed for intermediate reef consumers. Significant variations across space and time were observed for three anguilliform species; *Conger* Ls, *Gymnothorax fimbriatus* and *G. undulatus* showed slight fluctuations (Table 4).

4. Discussion

Isotopic analyses performed on a wide range of species belonging to various taxa enabled us to assign individuals to major trophic levels from producers to top predators. Our results confirm that highly diverse ecosystems like coral reefs involve complex interconnected trophic structures. Importantly, these structures are variable across space and time. Despite this complexity and variability, four major partly overlapping trophic pathways were identified. We also showed that different anguilliform fish occupy a high trophic level in these four trophic

Table 4

Summary of the statistical significance of spatio-temporal variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures of invertebrates, fish (potential preys) and anguilliform fish in the SW lagoon of New Caledonia (only most abundant species in each category are given and information for OM sources are given in Briand et al., 2015). Analysis were done with three-way ANOVAs or ANCOVAs, or non parametric Kruskal-Wallis test: area (Grand Nouméa versus Grand Sud) x site (coastal versus intermediate versus barrier reef) x season (summer versus winter). ns = $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; (–) = untested.

		Area	Site	Season	Area x site	Site x season	Area x site x season
<u>Invertebrates</u>							
<u>Crustaceans</u>							
Amphipoda	$\delta^{13}\text{C}$	–	ns	ns	ns	–	–
	$\delta^{15}\text{N}$	–	***	***	ns	–	–
Eriphia sebana	$\delta^{13}\text{C}$	***	ns	ns	***	–	–
	$\delta^{15}\text{N}$	**	ns	ns	*	–	–
Grapsus albolineatus	$\delta^{13}\text{C}$	ns	*	*	ns	ns	ns
	$\delta^{15}\text{N}$	**	*	**	*	ns	ns
<u>Gastropods</u>							
Clypeomorus brevis	$\delta^{13}\text{C}$	ns	ns	**	ns	ns	ns
	$\delta^{15}\text{N}$	ns	ns	**	ns	ns	ns
Nerita plicata	$\delta^{13}\text{C}$	***	***	ns	***	**	**
	$\delta^{15}\text{N}$	***	ns	ns	***	ns	ns
Planaxis sulcatus	$\delta^{13}\text{C}$	ns	ns	ns	ns	ns	ns
	$\delta^{15}\text{N}$	ns	***	*	**	ns	ns
Tectus niloticus	$\delta^{13}\text{C}$	***	***	***	ns	***	***
	$\delta^{15}\text{N}$	*	**	ns	ns	ns	ns
<u>Echinoderms</u>							
Echinometra mathaei	$\delta^{13}\text{C}$	**	ns	ns	ns	–	–
	$\delta^{15}\text{N}$	***	***	ns	***	–	–
Nardoa novaecaledonia	$\delta^{13}\text{C}$	–	***	*	***	–	–
	$\delta^{15}\text{N}$	–	***	***	***	–	–
<u>Fish (potential preys)</u>							
Apogon sp.	$\delta^{13}\text{C}$	–	ns	–	–	–	–
	$\delta^{15}\text{N}$	–	ns	–	–	–	–
Cheilodipterus artus	$\delta^{13}\text{C}$	–	***	–	–	–	–
	$\delta^{15}\text{N}$	–	ns	–	–	–	–
Ostorhinchus doederleini	$\delta^{13}\text{C}$	–	***	–	–	–	–
	$\delta^{15}\text{N}$	–	***	–	–	–	–
Pomacentrus moluccensis	$\delta^{13}\text{C}$	–	*	–	–	–	–
	$\delta^{15}\text{N}$	–	***	–	–	–	–
<u>Anguilliform fish</u>							
<u>Congridae</u>							
Conger Ll	$\delta^{13}\text{C}$	ns	ns	ns	ns	ns	ns
	$\delta^{15}\text{N}$	ns	ns	ns	ns	ns	ns
Conger Ls	$\delta^{13}\text{C}$	ns	*	**	ns	ns	ns
	$\delta^{15}\text{N}$	ns	ns	*	ns	ns	ns
<u>Muraenidae</u>							
Gymnothorax chilospilus	$\delta^{13}\text{C}$	*	ns	ns	ns	ns	ns
	$\delta^{15}\text{N}$	*	ns	ns	ns	ns	ns
Gymnothorax eurostus	$\delta^{13}\text{C}$	ns	ns	ns	ns	ns	–
	$\delta^{15}\text{N}$	ns	ns	ns	ns	ns	–
Gymnothorax fimbriatus	$\delta^{13}\text{C}$	***	ns	ns	ns	–	–
	$\delta^{15}\text{N}$	ns	***	ns	ns	–	–
Gymnothorax moluccensis	$\delta^{13}\text{C}$	–	ns	ns	–	ns	–
	$\delta^{15}\text{N}$	–	ns	ns	–	ns	–
Gymnothorax undulatus	$\delta^{13}\text{C}$	**	*	ns	ns	–	–
	$\delta^{15}\text{N}$	ns	ns	ns	ns	–	–

pathways; thereby confirming their position as important predators in coral reefs. Therefore, although stable isotopes should be used with caution (e.g. due to fractionation factors, baseline variations, Cabana & Rasmussen 1996, Post 2002, Boecklen et al. 2011, Woodcock et al. 2012) they provided the first global assessment of OM flows across the whole trophic structure of a complex coral reef ecosystem. Below we review our results regarding the main trophic levels and then discuss their interactions.

4.1. Organic matter sources

A great diversity of isotopic values characterized the potential OM sources sampled. However, four main groups were distinguished,

mostly based on $\delta^{13}\text{C}$ variations, and were associated with different habitats (Fig. 4). First, macrophytes characterized by high $\delta^{13}\text{C}$ values are typical from sandy plains and/or detrital substrate (seagrass species, *Padina australis*, *Turbinaria* spp. and *Liagora* spp.). Second, different macrophytes (*Acanthophora spicifera*, *Cystoseira* sp., *Sargassum* spp., *Halimeda* spp.) and the SOM characterized by lower $\delta^{13}\text{C}$ values are mostly found on sedimentary bottoms near coral colonies. Third, algal turf, *Halimeda opuntia* and *H. heteromorpha*, were strongly ^{13}C -depleted sources generally found on hard coral substrates. Lastly, POM from the water column exhibited ^{15}N -enriched value (4.50‰) that strongly contrasts with the other OM sources ($\delta^{15}\text{N}$ from 0.42 to 3.77‰). Our values are close to those measured in other coral reefs of the same very broad oceanic region (e.g. POM $\delta^{15}\text{N}$ of 4.15‰ in Wallis Island, Central-West Pacific, Letourneur Y., unpublished data).

Other potential OM sources include symbiotic dinoflagellates in Scleractinian corals, encrusting calcified coralline algae, microphytobenthos and bacterial biofilm (Fig. 4). Additionally, the number of macrophyte species sampled in this study, although comprising dominant species, was relatively modest in relation to their high diversity in New Caledonia. Consequently, the four structures identified might not fully represent the actual complexity of the studied ecosystem.

4.2. Intermediate consumers

Invertebrates and demersal fish exhibited a wide range of carbon and nitrogen values, mirroring the great diet diversity of the organisms sampled (Cresson et al., 2014, Dromard et al., 2015). Importantly, the isotopic values of consumers mainly reflected their feeding habits rather than their phylogeny. The $\delta^{15}\text{N}$ values revealed several trophic levels (Fig. 4) that match well with the functional groups issued from gut content analyses (Guille et al., 1986; Kulbicki, 1991; Green and Bellwood, 2009). But some species were not well classified (e.g. urchins with ~7‰ $\delta^{15}\text{N}$), suggesting a more opportunistic diet (Wangensteen et al., 2011, Rodríguez-Barreras et al., 2015) than previously described (e.g. herbivorous diet, Khamala, 1971). Likewise, several discrepancies about the published trophic position of several fish were observed (e.g. *Centropyge flavissimus*, *Ctenochaetus striatus* and *Paraperis hexophthalma*). Our isotopic analyses suggest that these presumably consumers exploit a higher range of nutritive resources than previously suspected.

Although a great diversity of consumers was sampled, many other potential consumers were not, and this may explain several gaps in the food webs proposed. Among invertebrates, several potential prey of the anguilliforms (e.g. cephalopods, stomatopods, prawns) or important groups like bivalves were not sampled. The taxonomic and functional diversity of the fish sampled was not comprehensive. However, our sample comprises many small and cryptic fish generally overlooked by visual census techniques (blennies and gobies) and thus provides novel insights.

4.3. Predatory fish

The isotopic ratios of anguilliform fish also encompassed a wide range of values, likely in relation with the respective diverse foraging habits and contrasted habitats of the various species sampled ($\delta^{13}\text{C}$ from –16.83 to –10.98‰). Our results also suggest that anguilliform fish occupy three different elevated trophic levels ($\delta^{15}\text{N}$ ranging from 6.23 to 10.01‰; Fig. 4): micro-carnivorous (*Gymnothorax chilospilus*, *G. reticularis*, *Muraenichthys* sp., *Ophichthidae* sp1, and *Uropterygius* sp2), macro-carnivorous (*Conger* Ls and *Conger* Ll, *G. albimarginatus*, *G. eurostus*, *G. fimbriatus*, *G. margaritophorus*, *G. undulatus*, *U. macrocephalus*, *U. supraforatus*) and piscivorous (*Cirrimaxilla Formosa*, *G. moluccensis*, *G. pindae*, and *Scuticaria tigrina*). This categorisation fits well with the limited studies available (e.g. *G. eurostus*, *G. moluccensis* and *G. reticularis*, Harmelin-Vivien, 1979; Thollot, 1996) and provides new information for many other species.

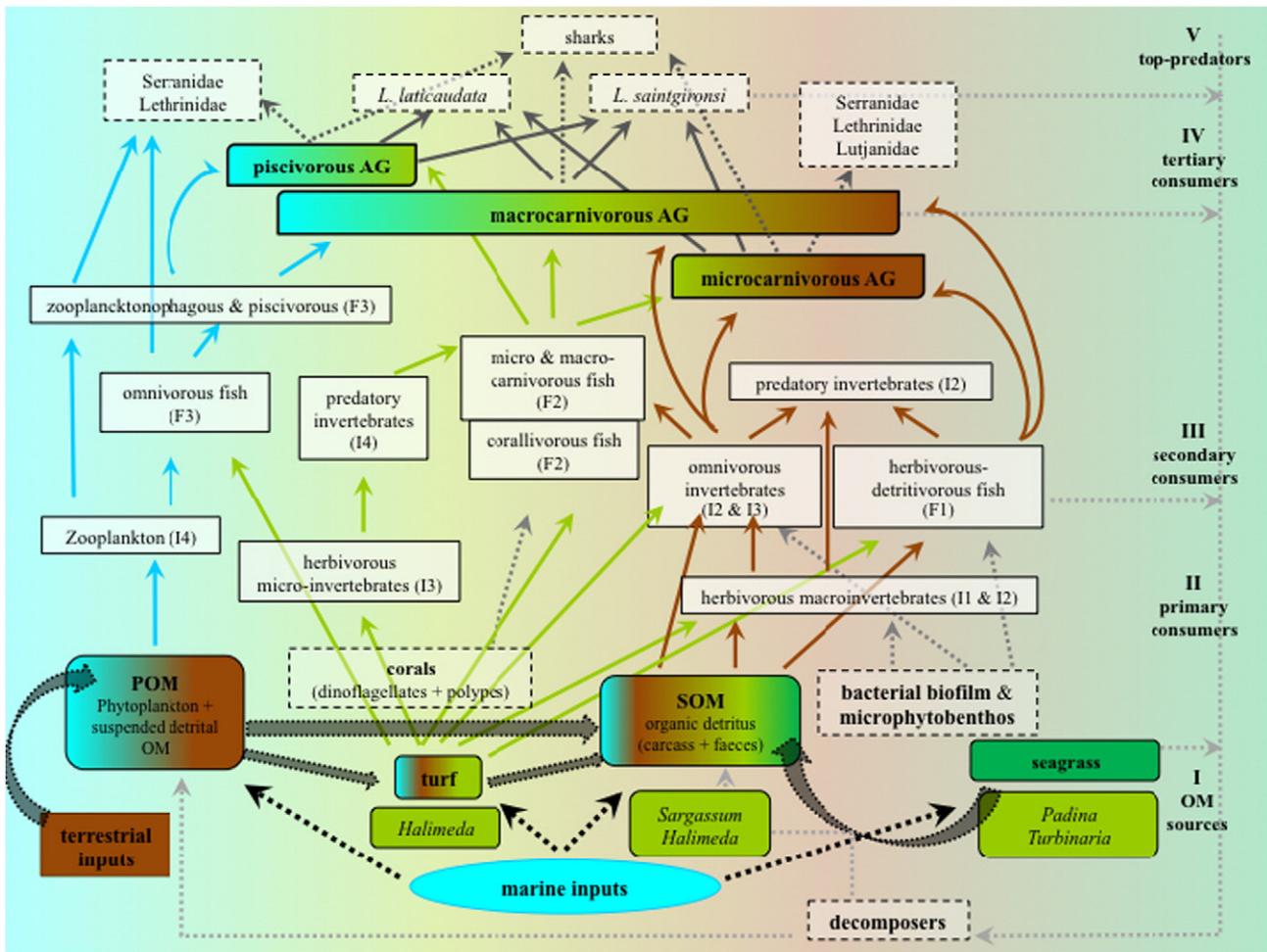


Fig. 4. Simplified functional schema of New Caledonian coral reefs' trophic networks involving predatory anguilliform fish. Major OM fluxes are qualitatively symbolized by arrows, for which the size is not equivalent to their intensity. Hypothetical fluxes, not estimated in this study, are also represented (dotted lines). The main trophic pathways as well as the influence of their major OM sources on other food webs are identified by different colours; the «lagoon pelagic» food web (L-PFW, blue), the «reef» benthic food web (R-BFW, light green), the «sedimentary» benthic food web (S-BFW, maroon) and the «detrital» benthic food web (D-BFW, dark green). Codes I1 to I4 and F1 to F3, see corresponding species in results 3.1 Isotopic values of food web compartments.

Different anguilliform fish mainly feed on fish and macro-crustaceans (brachyurans and shrimps), but supplement their diet with smaller invertebrates (isopods, amphipods, polychaetes, Fig. 4), and thus should be considered as 'feeding opportunists'. They play an important role as of high level-predators (Fig. 4), but they also represent the main (almost exclusive) prey of two very abundant sea snakes (Fig. S1, Ineich et al., 2007; Bonnet, 2012).

Isotopic values of several other fish confirm their potential place in the predator list (Fig. S1). Further, our results suggest that Serranidae (*Cephalopholis sonnerati*, *Plectropomus leopardus*, *P. maculatus*) and large Lethrinidae (*Lethrinus lentjan* and *L. miniatus*) consume prey from high trophic levels, thus possibly including anguilliforms such as *G. eurostus*, *G. moluccensis* or *Conger* L1. Large *Epinephelus howlandi* and *E. merra*, *Lethrinus atkinsoni* may occasionally feed on *G. chilospilus*, *G. reticularis* or Ophichthidae (Fig. S1). Finally, sharks might be situated at the apex of the food webs as suggested by isotopic data collected in Australia (Speed et al., 2012, Fig. S1). However anguilliform fish are rarely observed in stomach content of sharks and of other fish; (Olin et al., 2013).

4.4. Food web architecture

Our results based on the measurements of the isotopic values of many organisms are in accordance with a crude model of the trophic structure proposed in a smaller coral reef lagoon of New Caledonia

situated 200 km northeast of our sampling area (Bozec et al., 2004). More important, our analyses suggest that four main OM trophic pathways co-exist (Fig. 4).

The reef benthic food web (R-BFW, Fig. 3) based on algal turf represents the major trophic web for many reef consumers and for all anguilliform fish. The high nutritive quality of algal turf compared to less digestible benthic macroalgae and its abundance in shallow waters of reef habitats may explain the importance of this trophic web (Cribb, 1973). Accordingly, algal turf is the main food resource of many herbivorous fish in various coral reefs (Choat et al., 2002). However, algal turf lacks important nutritive elements (Dromard et al., 2013). Consumers must complement their diet with additional items; for instance, microphytobenthos, small invertebrates, coral or detritus (e.g. fish faeces and small seaweed fragments, Choat et al., 2002; Dromard et al., 2013).

Two other pathways are essential for many organisms and utilised as complementary food sources (Fig. 4). The sedimentary benthic food web (S-BFW, Fig. 3), mainly based on SOM, is utilised by benthic organisms (mostly invertebrates) with ^{13}C -enriched isotopic values, whereas the lagoon pelagic food web (L-PFW, Fig. 3) based on POM mainly involves plankton-feeders consumers with ^{13}C -depleted values. Because few consumers depending directly on POM were sampled, this information remains incomplete. Nevertheless, we suggest that numerous filter feeders and deposit feeders (sponges, ascidians, bivalves, bryozoans, polychaetes) use this pathway (Glynn, 2004; Cresson et al.,

2014). Unpublished isotopic results of bivalves respectively studied in the lagoon of New Caledonia (*Anadara antiquata*: $-17.3 \pm 0.6\%$ $\delta^{13}\text{C}$ and $4.7 \pm 0.4\%$ $\delta^{15}\text{N}$, Lorrain A. personal communication, 2015) and Wallis Island, Central Pacific (clams: -15.80 ± 0.71 $\delta^{13}\text{C}$ and $5.11 \pm 0.42\%$ $\delta^{15}\text{N}$, Letourneur Y., unpublished data) support this view. In addition, the trophic position of omnivorous fish in the L-PFW (*Centropyge bispinosus*, *C. flavissimus*, *C. tibicens*, *Chrysiptera rex*, *Stegastes* spp.) known to consume at least occasionally filter-feeding invertebrates (Parrish, 1989; Dromard et al., 2013) is in agreement with the proposed structure.

Finally, the detrital benthic food web (D-BFW, Fig. 3) that transfers OM issued from seagrass and some poorly nutritive macroalgae appears secondary (Danovaro et al., 2001, Fig. 4). However, this OM is probably indirectly integrated under a detrital form in other food webs, as suggested in other marine environments (Cebrián et al., 1997; Cresson et al., 2014), or is used by few specialized albeit important organisms such as dugongs or sea turtles.

Our study emphasizes the importance of algal turf and macroalgae compared to vascular plants as major OM sources in coral reef ecosystem of New Caledonia (Lepoint et al., 2000) along with the essential place of pools (i.e. POM and SOM) in OM flows (Dromard et al., 2013; Letourneur et al., 2013; McMahon et al., 2015). The critical role of the sedimentary reservoir in potential OM exchanges was revealed by a partial overlapping of the major food webs. For instance, the sedimentary food web played a key role in the circulation of OM issued from seagrass detritus and POM deposited particles.

Overlapping across pathways might reflect the fact that organisms upgrade the nutritive quality of the food associated to their main trophic-pathway (e.g. R-BFW) by incorporating items from other pathways and possibly from other habitats. Automatically, this crossing process increases the complexity of higher trophic levels that depend on varying contributions from multiples food sources. Anguilliform fish exhibited precisely such an expected trophic complexity.

4.5. Influences of sites and seasons

Marked fluctuations in isotopic ratios were found among sites whereas time variations were less important (we note however that only two seasons were available for analyses). Such variations were buffered along food webs, from producers up to anguilliform fish and were more visible considering the lower trophic levels.

An important proportion of terrestrial and marine inputs were integrated into OM pools (POM and SOM). POM is a transitory reservoir regularly renewed and mixed by currents. Its isotopic composition is influenced by terrestrial inputs near shores and by open ocean waters near the barrier reef, and thus reflects changing seawater characteristics of the SW lagoon of New Caledonia (Briand et al., 2015). The SOM, associated to primary producers and some reef consumers, integrated local features. Coastal sites were more or less equally influenced by terrestrial inputs; season effects were notably visible in coastal sites, likely because terrestrial inputs carried by rivers and seasonal rainfalls are more pronounced near river mouths (Le Borgne et al., 2010). However, despite these spatial and seasonal fluctuations, the global structure of the food web remained relatively stable.

5. Conclusion

This study assessed an important part of the trophic relationships existing in complex coral reefs, and therefore improved our understanding of the functional of these ecosystems. This study also markedly improved current knowledge of the ecology of major cryptic predators. Anguilliform fish are diverse, abundant and involved into various high trophic levels. Consequently, they play important roles in the functioning of coral reefs, and most likely not only in New Caledonia. Further studies are needed to support our findings, notably through the inclusion of other organisms that were not sampled, and also to examine

more accurately spatial and temporal fluctuations. In this endeavour, our study provides a useful baseline covering the main trophic levels.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.fooweb.2016.07.002>.

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