Isotopic discrimination in helminths infecting coral reef fishes depends on parasite group, habitat within host, and host stable isotope value

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Stable isotopes of carbon and nitrogen characterize trophic relationships in predator–prey relationships, with clear differences between consumer and diet (discrimination factor Δ13C and Δ15N). However, parasite–host isotopic relationships remain unclear, with Δ13C and Δ15N remaining incompletely characterized, especially for helminths. In this study, we used stable isotopes to determine discrimination factors for 13 parasite–host pairings of helminths in coral reef fish. Differences in Δ15N values grouped according to parasite groups and habitat within the host with positive Δ15N values observed for trematodes and nematodes from the digestive tract and variable Δ15N values observed for cestodes and nematodes from the general cavity. Furthermore, Δ13C values showed more complex patterns with no effect of parasite group or habitat within host. A negative relationship was observed between Δ15N and host δ15N values among different host-parasite pairings as well as within 7 out of the 13 pairings, indicating that host metabolic processing affects host-parasite discrimination values. In contrast, no relationships were observed for Δ13C values. Our results indicate that parasite group, habitat within host, and host stable isotope value drive Δ15N of helminths in coral reef fish while their effect on Δ13C is more idiosyncratic. These results call for use of taxon- or species-specific and scaled framework for bulk stable isotopes in the trophic ecology of parasites.

Parasitism is a common life strategy for consumers and is ubiquitous amongst food webs1. The role of parasites in aquatic food chains has been shown to be fundamental2,3 and the inclusion of parasitic relationships within food webs dramatically increases the number of trophic links within ecosystems4. Despite this, host-parasite relationships remain a neglected component during the evaluation of biodiversity5, especially for systems with high biodiversity such as coral reefs6. Trophic relationships for parasites7 remain poorly characterized within food webs as small size, multidisciplinary requirements for identification, and cryptic lifestyles (e.g. multiple hosts associated to multiple larval stages) make identification and characterization of these relationships difficult.

Stable isotope techniques are routinely utilized to study trophic relationships within food webs5,8 by using trophic discrimination factors for carbon and nitrogen (Δ13C and Δ15N) to account for the stepwise increase in δ13C and δ15N (%) that occurs between diet and consumer during metabolism9–12. However, parasites do not generally follow this relationship with parasite–host discrimination factors (Δ13C or Δ15N) observed ranging from considerably higher than typical trophic discrimination between predator and prey to negative values for Δ13C or Δ15N across a variety of taxa1,3,13–15.
Amongst helminths in fish hosts, cestodes and nematodes are usually depleted in δ\(^{15}\)N values versus their hosts\(^{13,15-17}\) and vary in Δ\(^{13}\)C, while trematodes have been found to vary in both Δ\(^{13}\)C and Δ\(^{15}\)N\(^{18,19}\). However, there can also be considerable variation within these helminth groups\(^{14,20}\) and within other coral reef parasites such as copepods, cymothoids, gnathiids, isopods, and monogeneans\(^{2,21-23}\). Distinct differences for trophic discrimination in parasitic relationships are potentially caused by the combined effects of unique feeding ecologies, often reduced metabolic capabilities of the parasitic taxa being investigated\(^{14,26}\), and host metabolic effects due to parasitism\(^{26}\). Feeding ecology varies depending on whether the parasite feeds upon host tissue exclusively (on host or within; tissue type dependent\(^{18}\)), is able to supplement with material from within the dietary tract (on host or within; tissue type dependent18), is able to supplement with material from within the dietary tract or from the environment (e.g. prey items, detritus, mucus, or blood\(^{27}\)), or can directly uptake nutrients from host tissues\(^{26}\). In addition, it has been suggested that trophic discrimination factors of parasites may not be fixed but scale with the isotopic signature of their hosts, both within\(^{18}\) and among parasite species\(^{14}\).

Despite multiple investigations, clear stable isotope discrimination patterns between major parasite groups have not emerged, making simple incorporation of parasites into food web studies using a single universal trophic discrimination factor impossible. This knowledge gap warrants further investigation into the drivers of discrimination factors in helminths. In this study, we examined both δ\(^{13}\)C and δ\(^{15}\)N values from whole tissue of 136 helminth parasite–host pairings from coral reef fish to determine the isotopic relationship between taxonomically distinct groups of helminth parasites and to investigate the effect of the habitat within the host and host isotopic value on helminth isotopic discrimination. We expected that parasite isotopic enrichments and variability versus their host will be larger in parasites located in the dietary tract as their diet may not only include host material while parasites in the body cavity that solely utilize host tissues will have less variability in their isotopic discrimination. In addition, we expect a negative scaling of parasite discrimination factors with the δ\(^{13}\)C and δ\(^{15}\)N values of their hosts.

### Results

We examined the isotopic discrimination of 136 helminth parasite–host pairings including trematodes (n = 27), cestodes (n = 19), and nematodes (n = 90) from 4 host reef lagoon-associated fish species (from the families Lethrinidae, Nemipteridae, Siganidae and Synodontidae; Table 1, Fig. 1). One trematode species and five of the nematode species were sampled from the dietary tracts (DT) of host species while the remaining one cestode and 4 nematode species were samples from the general cavity (GC). Six out of the 13 Δ\(^{13}\)C values for parasite–host pairs were negative (Supplementary Table 1), with positive relationships (1.05 to 1.58‰) predominately occurring in dietary tract associated parasites (Fig. 1). In 9 out of 13 cases, δ\(^{15}\)N values were significantly different between parasite–host pairs within the same host, either positive or negative, except for carbon in A. novacaledonica (0.47‰, L. genivittatus versus -1.10‰) (Supplemental Table 1, Fig. 2). For Δ\(^{15}\)N values, we found significant differences between trematodes, cestodes and the two habitats (DT & GC) of nematodes within hosts (One-way ANOVA: F\(_{3,15}=26.9\) p < 0.001; Fig. 3). Host δ\(^{15}\)N was examined versus Δ\(^{15}\)N and we found that a linear regression for all of the predatory host pairings (e.g. with the herbivore host pairing white nematode—Siganus lineatus removed) had a negative slope of −1.2 (R\(^2 = 0.071\); Fig. 4) with negative slopes observed within individual pairings that were different than 0 for 7 of the parasite–host pairings at α = 0.05 (Fig. 4; Supplementary Table 2).

Δ\(^{13}\)C values of the pairings were generally negative with lower δ\(^{13}\)C in the parasite than those of the host fish, except for Philometra sp./Saurida undosquamis (Δ\(^{13}\)C = 0.06 to 1.19‰), white nematode/S. lineatus (Δ\(^{13}\)C = 0.38 to 3.81‰) and A. novacaledonica / L. genivittatus (Δ\(^{13}\)C 0.47 to 0.98‰, Figs. 2 and 3). The first two of these relationships occur for parasites in the digestive tract and the last one in the general cavity of the host.

### Table 1.

| Fish host (size range, cm; trophic level; family; feeding style) | Parasite | Attachment site on host (DT/GC) | N |
|---------------------------------------------------------------|---------|---------------------------------|---|
| Lethrinus genivittatus (11.0–21.5; 2.9; Lethrinidae; invertivore) | A. novacaledonica (Trematode) | DT | 16 |
| | Pseudophyllidae (Cestode) | GC | 8 |
| | Callamanus sp. (Nematode) | DT | 9 |
| | Unidentified white nematode | GC | 8 |
| Nemipterus furcosus (12.1–25.0; 3; Nemipteridae; invertivore) | A. novacaledonica (Trematode) | DT | 16 |
| | Pseudophyllidae (Cestode) | GC | 11 |
| | Callamanus sp. (Nematode) | DT | 11 |
| | Rhaphidascaris sp. (Nematode) | DT | 7 |
| | Unidentified white/cream nematode | GC | 10 |
| | Unidentified nematode (cyst form) | GC | 13 |
| | Unidentified white nematode | DT | 7 |
| Siganus lineatus (17.8–25.6; 2.5; Siganidae; herbivore) | Philometra sp. (Nematode) | GC | 18 |
| Saurida undosquamis (28.1–38.0; 2.8; Synodontidae; piscivore) | Unidentified white nematode | DT | 7 |
Among the 13 parasite–host pairings tested, significant differences between host and parasite δ13C were observed for 10 cases with a Δ13C range from −0.73 to −1.97‰. There was no clear Δ13C distinction observed between parasites found in the digestive tract versus those found in the general cavity. For Δ13C values, we found no significant differences between trematodes, cestodes and the two habitats (DT and GC) of nematodes within hosts (One-way ANOVA: F3, 132:1.4 p = 0.2; Fig. 3). Host δ13C was examined versus Δ13C and found that a linear regression for all of the pairings combined minus the herbivore pairing had a negative slope of −0.56 (R2 = 0.196, p < 0.001; Fig. 4), but that linear regressions for individual pairings indicated no significant difference from 0 for those relationships (Supplementary Table 2).

Mean δ13C and δ15N values for the host species L. genivittus were −14.04 ± 0.51‰ and 8.97 ± 0.52‰ (mean ± SD; Δ13C then Δ15N throughout), N. furcosus were −14.16 ± 0.49‰ and 9.31 ± 0.50‰, S. undosquamis were −16.25 ± 0.49‰ and 8.07 ± 1.09‰, and S. lineatus were −15.75 ± 0.40‰ and 8.97 ± 0.59‰, respectively (Fig. 1; Supplementary Table 1), with significant differences observed between species for both δ13C and δ15N values (One-way ANOVA: δ13C, F3, 177:52.6, p < 0.001; δ15N, F3, 177:22.8, p < 0.001). Body size did not influence δ13C and δ15N values for S. undosquamis and S. lineatus for the size range and number of individuals considered here (Pearson correlation, p > 0.05 in all cases). By contrast, fish size significantly influenced δ15N values for L. genivittus and N. furcosus (p < 0.001 for both species; Fig. 5) but not for δ13C values (p > 0.05). Calculated trophic levels (Table 1) were similar for the whole populations of fish sampled in this study for L. genivittus and S. undosquamis (2.9 and 2.8, respectively), S. lineatus having the lowest, and N. furcosus having the highest trophic levels (2.5 and 3.0, respectively; One-way ANOVA: F3, 137:42.7, p < 0.001). Trophic levels were also higher for larger fish for both L. genivittus (2.6 and 2.9 for 11–15 cm and 18–21.5 cm individuals, respectively; One-way ANOVA: F1, 39:35.9, p < 0.001) and N. furcosus (2.8 and 3.0 for 12.1–15 cm and 20–25.3 cm individuals, respectively; One-way ANOVA: F1, 61:27.6, p < 0.001).

Discussion

Δ15N varied inconsistently between and within taxa, with the most consistent result being elevated Δ15N (>0‰) for dietary tract associated nematodes, likely associated with feeding on host dietary items in addition to tissue. Δ13C was consistently negative between parasite taxa and likely indicates increased reliance on fatty acids from the host to support tissue growth in reef fish-associated helminths. The varied relationships amongst and between taxa provide further evidence that parasite–host pairings are distinctly different than typical trophic relationships and warrant further investigation to adequately characterize parasite contributions to food webs.

Figure 1. Mean δ15N and δ13C composition (± SD) for parasite and reef fish host pairings. Parasites and hosts are displayed with open and filled symbols, respectively. Dietary tract (DT) and general cavity (GC) refer to the parasite habitat within fish hosts.
Δ15N differences for parasite–host pairings. Δ15N values showed no difference or were positive for the dietary tract associated trematode and nematodes (Allardia, Callamanus, Rhaphidascaris, and unidentified white) while the cestodes had negative values for both pairings examined. Δ15N values for the general cavity-associated nematodes varied, with a strong positive value for the gonad-associated Philometra sp.–S. undosquamis pairing, no difference observed for unidentified white nematode—N. furcosus pairing, and strong negative relationships for both the nematode cyst-type—N. furcosus and the unidentified white nematode—L. genivittatus pairings (Fig. 2).

Figure 2. Δ15N and Δ13C values (‰) for parasite–host couplings examined in this study. Asterisks indicate significant differences between host and parasite at α = 0.05. Dietary tract (DT) and general cavity (GC) refer to the parasite habitat within fish hosts. For the boxplots, squares indicate mean, lines indicate median, boxes indicate upper and lower quartiles, and whiskers indicate 1.5 quartile ranges. Black diamonds are outliers.
utilization of host-metabolized compounds from tissue or the taxa-dependent ability for nematodes to biosynthesize amino acids from nitrogenous compounds.

**Δ¹³C differences for parasite–host pairings.** Δ¹³C values were predominately neutral or negative for ten of the parasite–host pairings examined, with positive Δ¹³C only observed for the A. novacaledonica—L. genivittatus, white nematode—S. lineatus, and Philometra sp.—S. undosquamis pairings. No change or depletion in δ¹³C does not agree with the expected 0.5–1‰ increase that is usually expected for trophic interactions, but likely reflects reliance on lipids and fatty acids directly derived from the host or host diet to support helminth tissue growth. Platyhelminthes and some nematodes have been found to be incapable of de novo fatty acid synthesis and to have to rely on fatty acids derived from the host due to incomplete metabolic pathways for lipid biosynthesis. Direct uptake of fatty acids and other lipids from the host would be expected to coincide with a

**Figure 3.** Δ¹⁵N and Δ¹³C values (‰) for trematodes and cestodes, and nematodes separated by parasite habitat within host. Letters indicate significant differences (post hoc Tukey’s test, α = 0.05). Dietary tract (DT) and general cavity (GC) refer to the parasite habitat within fish hosts. For the boxplots, black dots indicate mean, lines indicate median, boxes indicate upper and lower quartiles, and whiskers indicate 1.5 quartile ranges. Black diamonds are outliers.
minimum carbon fractionation as no further metabolic processing is required, thereby maintaining the relatively low δ¹³C values associated with lipids as they are incorporated into the parasite. The relatively uniform neutral or negative relationships for Δ¹³C values across the pairings located from both the dietary tract and the general cavity indicate that lipid carbon is likely utilized to support tissue growth beyond species closely associated with fatty tissues (e.g. blood and liver)¹³,¹⁴. This relationship should be examined further with methods that incorporate metabolic pathway techniques for target species beyond model organisms targeted for pathogenicity²⁴,²⁵. Pairings that have elevated Δ¹³C values likely reflect decreased utilization of host lipids and increased reliance on either host sugars or proteins processed through more complete metabolic pathways within the helminths to provide tissue carbon or potentially different δ¹³C compositions from different host tissues¹⁸.

Figure 4. Host δ¹⁵N values versus Δ¹⁵N values classified for each individual parasite–host pairing. Labeling follows the pairing order 1–13 from Fig. 2 with X indicating trematodes, + indicating cestodes, squares indicating dietary tract nematodes and triangles indicating general cavity nematodes. Regression lines indicate the significant relationships for the combined pairings from the three predatory (invertivore or piscivore) fish in the dataset (i.e. excluding samples from the herbivore host S. lineatus (open squares, 9)) for nitrogen (slope = – 1.2, R² = 0.071, p < 0.001) and carbon (slope = – 0.56, R² = 0.196, p = 0.17).
Comparing host isotopic values and $\Delta^{13}C$ and $\Delta^{15}N$ of parasite–host pairings. $\delta^{15}N$ values for both fish host species *L. genivittatus* and *N. furcosus* increased with body size leading to higher trophic levels in larger fish, a pattern commonly observed for coral reef-associated invertivore/carnivore fish, while there was no corresponding increase or shift in $\delta^{13}C$ throughout ontogeny. No change in $\delta^{13}C$ indicates that both smaller and larger individuals are relying on similar sources of underlying carbon production, and that the larger individuals are feeding on larger prey with an elevated trophic level, i.e. elevated $\delta^{15}N$ values.

Additionally, a negative linear relationship was observed for both $\Delta^{13}C$ and $\Delta^{15}N$ values versus $\delta^{13}C$ and $\delta^{15}N$ values for predatory fish hosts were observed with significant negative slopes for nitrogen in 7 of the 13 parasite–host pairs (Fig. 4; Supplementary Table 2), while no significant within-pairings relationships were found for carbon (Supplementary Table 2). A negative linear relationship for trophic discrimination factors with increased host carbon and nitrogen values has previously been observed for parasite–host, predator–prey and herbivore–plant relationships and may be associated with dietary quality. In this study, there appeared to be an increased spread in the fractionation ($\Delta^{15}N$ values) observed within the herbivore *S. lineatus*, with the lowest $\delta^{15}N$ values occurring with the highest $\Delta^{15}N$ values and a distinct grouping of individuals with lower $\Delta^{15}N$ values corresponding with the highest $\delta^{15}N$ values (Fig. 4). This wide range of values may represent the relative richness in diet, with strictly herbivorous individuals causing a shift in their parasites towards exclusive utilization of host tissues, while individuals that supplement with animal protein (more omnivorous) provide additional material within their diet for their parasites to supplement from. Increased protein quality in a predator’s diet results in a smaller % difference between the diet and consumer, i.e. a smaller trophic fractionation. This relationship coincides with the trend of decreased $\Delta^{15}N$ values being observed for increased trophic level.
predation within predators in this study (Fig. 4). In herbivores, larger trophic discrimination factors for nitrogen are often observed37, and supplementation with protein (omnivory) would be expected to generate a negative offset in \( \Delta^{15}N \) if the parasites are supplementing from dietary protein in addition to host tissues.

**Conclusion**

In conclusion, we found that positive discrimination for nitrogen occurred more often in dietary tract associated helminths, while neutral or negative discrimination occurred for helminths from within the general cavity. Increased discrimination in the dietary tract is likely due to a combination of the increased need for metabolism of food taken from the host’s diet and the host tissue in comparison to the helminths in the general cavity that appear to make use of direct uptake pathways for host nitrogen compounds with minimal metabolic reworking. No differences were observed between the two parasite habitats for discrimination of carbon. This study characterized discrimination factors for carbon and nitrogen within helminths living in coral reef fish and highlights the uncertainties that remain in adequately describing parasitic relationships within food webs. These uncertainties call for the development of a taxon- or species-specific and scaled framework for using bulk stable isotope analysis to study the trophic ecology of parasites. In addition, further work using metabolomics and compound specific stable isotope techniques is warranted to better characterize the underlying metabolic differences that are driving the differences observed for trophic discrimination factors between parasite and hosts.

**Methods**

**Sample areas and studied species.** Individual fish from the three species *Lethrinus genivittatus* (Cuvier & Valenciennes, 1830), *Nemipterus furcosus* (Cuvier & Valenciennes, 1830), and *Saurida undosquamis* (Richardson, 1848) were caught using hand lines in the lagoon off the city of Nouméa (22°18′S and 166°25′E) in New Caledonia, southwestern Pacific Ocean at approximately 10–12 m depth, in August 2011, 2013, and 2014. Three years of data from catches were pooled as a preliminary two-way ANOVA (year × size) and revealed that year was not a significant factor (p > 0.05). *L. genivittatus* mostly feeds on crabs and worms, *N. furcosus* mostly feeds on crabs and shrimp and *S. undosquamis* is predominantly piscivorous46. The species *Siganus linearis* (Cuvier & Valenciennes, 1835) was caught in coastal mangroves in the southeast coast at Yâte (22°16′S and 167°01′15E) using gillnets in June–August 2014. This species is usually considered an herbivore39, but has been observed to feed predominantly on algae and to supplement with minor consumption of invertebrates in Yâte40. Parasites were present in all fish that were examined and appear to be ubiquitous within the species examined in this study.

All individuals caught were immediately placed in ice until further processing in the laboratory. Each fish was measured to the nearest 0.1 cm (total length) and a small piece of dorsal muscle of each fish was sampled and immediately frozen at −20 °C for further stable isotope analyses. To extract the parasites, the general cavity was first examined to collect parasites embedded in or attached to fish tissues outside of the digestive tract. In a second step, the method presented in Justine et al.41 was applied to flush and extract living parasites from within the digestive tract using a 9% saline solution that was then briefly brought to near boiling to fix the parasites prior to transfer to 95% ethanol. All helminth parasites (i.e. nematodes, cestodes and trematodes) having a sufficient biomass were collected and immediately frozen. A total of 54 *L. genivittatus* were caught with 36 exploitable parasite-fish pairings, 99 *N. furcosus* with 75 exploitable parasite-fish pairings, and respectively 7 *S. undosquamis* and 18 *S. linearis* were exploitable as parasite-fish pairings (Table 1). All animal experimentation met the ABS/ASAB guidelines for ethical treatment of animals and sampling protocols were approved by the internal ethics committee for the Université de la Nouvelle-Calédonie.

**Stable isotope preparation and analyses.** Carbon and nitrogen stable isotope ratios (\( \delta^{13}C \) and \( \delta^{15}N \)) were determined for dorsal muscle tissue of all fishes collected. Fish muscle tissue is routinely utilized for stable isotope analyses. To extract the parasites, the general cavity was first examined to collect parasites embedded in or attached to fish tissues. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. Carbon and nitrogen stable isotope ratios (\( \delta^{13}C \) and \( \delta^{15}N \)) were determined for dorsal muscle tissue of all fishes collected. Fish muscle tissue is routinely utilized for stable isotope analyses. To extract the parasites, the general cavity was first examined to collect parasites embedded in or attached to fish tissues. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment. This same procedure was used for parasites and ground into a fine powder using a mortar and pestle. One milligram of powdered material was loaded into tin capsules and analyzed for each sample without prior treatment.

\[
\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^{3}, \quad \text{where} \ X = ^{13}C \ or \ ^{15}N
\]  \hspace{1cm} (1)

where \( R \) is the corresponding ratio \( ^{13}C/^{12}C \) or \( ^{15}N/^{14}N \) for both sample and reference standard and \( \delta X \) is the measured isotopic value in per mil (‰) relative to the international standard references are Vienna Pee Dee Belemnite (vPDB) for carbon and atmospheric \( N_2 \) for nitrogen.

Parasite–host discrimination factors were calculated using:

\[
\Delta^{13}C \ or \ \Delta^{15}N = \delta X_{\text{parasite}} - \delta X_{\text{host tissue}}
\]  \hspace{1cm} (2)

where \( \delta X \) represents the isotopic value of carbon or nitrogen for each parasite–host tissue pairing examined.

**Data analysis.** The significance of differences in \( \delta^{13}C \) and \( \delta^{15}N \) between a fish and its parasite was tested with the Wilcoxon signed rank test when homogeneity of variances was not verified or paired samples t-tests.
when homogeneity of variances was verified, dependant on fish species. The relationships between fish size and isotopic values ($\delta^{15}$N or $\delta^{13}$C) were investigated with Pearson correlation coefficients. One-way analysis of variance (ANOVA) was used to determine significant differences between host and parasite $\delta^{15}$N and $\delta^{13}$N values and to explore the relationship between host size and trophic level. The relationship between host $\delta^{15}$N and $\delta^{13}$N values and $\Delta^{13}$C and $\Delta^{15}$N values were determined through linear regression followed with subsequent application of an F test of the modelled slope against a slope of 0. This was done among and within the host-parasite pairings. For the analysis among pairings we excluded samples from the herbivorous fish host S. lineatus (18 samples) due to their very different isotope values to avoid skewing the relationship due to explained outliers.

The trophic level (TL) of fish individuals was calculated following the formula of\(^7\):

$$\text{TL} = \lambda + \left( \frac{\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{source}}}{\Delta^{15}\text{N}} \right)$$  

(3)

where $\lambda$ is the trophic level of the source of organic matter, i.e. 1.; $\delta^{15}\text{N}_{\text{fish}}$ is the isotopic value of nitrogen for the considered fish, $\delta^{15}\text{N}_{\text{source}}$ is the isotopic value of the source of organic matter at the base of the food web, i.e. 3.59 for sedimentary organic matter\(^33\) that concerns L. genivittatus, N. furcosus, and S. undosaquarium, all caught of sandy unvegetated bottom; and 2.12 for the most eaten algae by Siganus lineatus and $\Delta^{13}$N that is the trophic enrichment factor (TEF) between a food item and its consumer. Here, we adopted a value of 3.9‰ for S. lineatus\(^40,43\) reflecting usually higher TEF for herbivores compared to the conventional 3.4‰ value\(^27\). For the three other species, we adopted a TEF of 3.0‰ because TEF are usually lower than the conventional value for carnivores\(^37,44\).

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Competing interests
The authors declare no competing interests.

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