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The same but different: stable isotopes reveal two distinguishable, yet similar, neighbouring food chains in a coral reef

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Stable isotope compositions were studied in particulate organic matter (POM), zooplankton and different trophic groups of teleosts to compare food chains based on plankton at two sites (lagoon and outer slope) in a New Caledonian coral reef. For each trophic compartment, \( ^{13}C \) values were always lower in the outer slope than in the lagoon. This result may be explained by potential differences in POM composition between the two environments, suggesting that the two food chains are based on different primary sources of carbon. In contrast, \( ^{15}N \) values did not vary between the lagoon and the outer slope, indicating that these two food chains presented similar length and trophic levels, despite being distinguishable.

Keywords: barrier reef, particulate organic matter, zooplankton, reef teleosts, stable isotopes, Pacific Ocean

INTRODUCTION

Food webs encompass various food chains which structure marine communities. Variations in the relative importance of one component of a food chain (from nutrients to predators) may change abundances of the different species that are part of the food web (Friedlander & DeMartini, 2002; Smith et al., 2010). Coral reefs are a habitat for numerous species and provide various ecological goods and services (Moberg & Folk, 1999). Consequently, knowing the food web functioning of these habitats is critical for their management.

Coral reefs were formerly considered as food webs isolated in an oceanic desert. The surrounding ocean, however, is also an important food source for coral reefs, as oceanic zooplankton may be imported into the reef by waves and tidal currents, and then consumed by planktivorous teleosts (Hammer et al., 1988, 2007). While benthic sources represent an important carbon source to reef teleosts (Carassou et al., 2008; Wyatt et al., 2012; Briand et al., 2016), numerous species rely principally or exclusively on planktonic sources for food (Hobson, 1974; Frédéric et al., 2009) and even non-planktivorous species may rely on oceanic productivity (Wyatt et al., 2012). Barrier reefs act as border zones between oceanic and lagoon areas, leading to differences in habitat conditions (Delesalle & Sournia, 1992; Leichter et al., 2013) and community composition (Carleton & Doherty, 1998; Lecchi et al., 2003; Leichter et al., 2013). Marked differences between food webs could thus be expected (Wyatt et al., 2012; Briand et al., 2015), as an indicator of water retention (Leichter et al., 2013) and of separation between neighbouring outer slope and lagoon communities.

Stable isotope analyses are commonly being used in food web studies. They offer a basis for studying food web components as stable isotope composition can be measured in most organisms, including photosynthetic ones, as well as in organic particles (e.g. Davenport & Bax, 2002; Carassou et al., 2008). Carbon isotopic composition \( (^{13}C) \) is generally used to determine the baseline sources of carbon in food webs (Michener & Kaufman, 2007; Briand et al., 2015) because of the differences in stable isotope composition generally observed between the different types of primary producers (phytoplankton, phytoendophytes) or organic matter and the low enrichment in \( ^{13}C \) (0.5 – 1‰) in organisms relative to their diet (DeNiro & Epstein, 1978; Michener & Kaufman, 2007). Nitrogen isotopic composition \( (^{15}N) \) is used to estimate the trophic level of consumers, as organisms are generally enriched in \( ^{15}N \) (**3.4‰ on average**) relative to their diet (DeNiro & Epstein, 1981; Schoeninger & DeNiro, 1984; Michener & Kaufman, 2007) although important variations of the trophic enrichment from prey to predators occur (Wyatt et al., 2010). Furthermore, spatial and temporal variations of \( ^{13}C \) and \( ^{15}N \) in the baseline sources of food webs and organisms (e.g. Harmelin-Vivien et al., 2008; Veit-Köhler et al., 2013) may help to identify feeding areas (Hobson, 1999).

In this study, the planktonic food chain of the southwestern New Caledonian coral reef environment was
investigated by analysing C and N stable isotope ratios in particulate organic matter, two size classes of zooplankton and four trophic groups of teleosts. The chosen study area was the Ouano lagoon. Most studies on reef food webs of New Caledonia using stable isotopes were conducted in the Nouméa lagoon (e.g. Carassou et al., 2008; Briand et al., 2016) but the Ouano lagoon has not been studied, to our knowledge. Furthermore, analysis of the isotopic signatures of different size classes of plankton has not been done before on New Caledonian coral reefs. The aims of this study were (1) to identify the pathways of organic matter from sources to demersal zooplanktivorous teleosts through stable isotope analysis, (2) to compare the architecture of the two identified food chains between lagoon and outer slope assemblages.

MATERIALS AND METHODS

Study area
The Ouano lagoon (south-west of New Caledonia, Pacific Ocean; Figure 1) is delimited by a large barrier reef and comprises several islets and intermediate reefs within the lagoon, i.e. coral reefs located in the middle of the lagoon between the coastline and the barrier reef. It is connected to the external ocean by the St-Vincent pass (southern passage) and the îles pass (northern passage). It has a mean depth of 10 m. Previous studies have shown that water circulation in the Ouano lagoon is driven by both tide and waves (Chevalier et al., 2012, 2015): inward and outward flows of water through the passes occur during the flood and the ebb respectively. Oceanic water may also enter into the lagoon by going over the barrier reef during high wave events. The path of the lagoon water can be determined by the method of water origin (de Brye et al., 2013), with the numerical hydrodynamic model developed and validated in Chevalier et al. (2015). This method highlights that water near the barrier reef inside the lagoon is predominantly coming from the outer slope (Figure 1).

Sampling
Sampling was performed within the lagoon at ~2–3 m depth and on the outer slope at ~10–15 m depth from 2–9 October 2013. Particulate organic matter (POM) was considered as the baseline of the studied food chain as it included phytoplankton and other edible particles such as mucus, faeces and phytobenthos debris (Wyatt et al., 2013). POM was obtained by sampling and filtering seawater on pre-combusted (500°C, 2 h) GF/F filters (N ¼ 25). These filters were dried (60°C, 48 h) prior to subsequent analysis. Zooplankton was sampled at ~330 m on the outer slope and ~4 m in the lagoon and was sampled horizontally to obtain more biomass, by using an 80 mm mesh-sized WP2 net (N ¼ 3). Zooplankton samples were separated into two size classes (80 – 200 and ≥200 mm) using sieves and then freeze-dried. Teleosts were opportunistically collected using 7% rotenone or by spearfishing inside the lagoon and on the outer slope (Figure 1) and then were frozen. In the laboratory, species were identified and classified in trophic groups according to the origin of their food given in the literature (Supplementary Table S1 in the supplemental material section): diurnal planktivorous teleosts feeding on pelagic plankton; nocturnal planktivorous teleosts feeding at night; non-planktivorous teleosts feeding on benthic prey (phytobenthos, sessile and/or mobile invertebrates) and teleosts with a mixed diet feeding on both pelagic and benthic food (e.g. consumption of both phytobenthos and planktonic crustaceans). Total length (TL) was measured. Digestive tracts of teleosts were removed and preserved in 95% ethanol. Anterior dorsal muscles of teleosts were sampled and freeze-dried for subsequent stable isotope analyses.

Stable isotope analysis
Zooplankton and teleost samples were ground into a fine powder. Carbonates present in POM and zooplankton (i.e. crustacean carapaces, mollusc shells) are more enriched in 13C than other tissues (DeNiro & Epstein, 1978). Consequently, analyses were carried out separately for measurements of d13C and d15N values. For d13C measurements,

Fig. 1. Sampling area (light grey: reefs) of particulate organic matter (POM) and zooplankton and sampling stations of teleosts inside the Ouano lagoon (black square) and on the outer slope (white square). Colours represent the percentage of water coming from the outer slope in the Ouano lagoon with a wave height of 0.3 m, i.e. the mean wave height during the sampling campaign.
one half of POM samples and one half of each zooplankton sample received 1% HCl treatment before being rinsed and dried to remove carbonates (Kennedy et al., 2005; Jaschinski et al., 2008; Kolasinski et al., 2008). For δ15N measurements, the rest of the raw samples was washed without acidification as acidification may affect nitrogen isotopic composition (Bunn et al., 1995; Kennedy et al., 2005; Kolasinski et al., 2008). Six replicates were analysed per station for POM and per zooplankton sample (three for d13C, three for d15N). For teleosts, a maximum of nine individuals (three individuals selected in three size classes) per species available were selected for stable isotopes analysis. Lipid removal or correction for δ13C values was not necessary as levels of lipids in teleosts were low (C/N < 3.5) (Post et al., 2007; Skinner et al., 2016).

Powdered samples were precisely weighed (~0.4 mg for non-acidified zooplankton and teleosts; 1 mg for non-acidified POM and 2 mg for acidified POM and zooplankton; precision of 0.01 mg) in 5 × 8 tin cups (6 cups per station for POM and per zooplankton sample), and analysed with an elemental analyser (Flash EA 1112, Thermo Scientific, Milan, Italy) coupled to a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Bremen, Germany). Analyses were conducted at the LIENSs stable isotope facility at the University of La Rochelle, France. d13C and δ15N are expressed in δ notation in ‰ as deviations from standards (Vienna Pee Dee Belemnite for d13C and N2 for d15N) according to the formula: dXsample/2000 = 1000, where X is 13C or 15N. Rsample is the isotopic ratio of the sample and Rstandard is the isotopic ratio of the standard. Calibration was done using reference materials (USGS-24, IAEA-CH6, -600 for carbon; IAEA-N2, -NO-3, -600 for nitrogen). Analytical precision was ± 0.15‰ based on the analyses of acetanilide (Thermo Scientific) used as laboratory internal standard.

Stomach content analysis

Stomach contents of teleosts from the outer slope were analysed and the food items were identified to the lowest feasible taxonomic level. A technical failure prevented the analysis of the stomach contents of teleosts sampled inside the lagoon. Dry weight (DW) of ingested organisms was measured or estimated from data or mathematical formulas available in the literature (e.g. Uye, 1982; Chisholm & Roff, 1990; Salapoomin, 1995). Consequently, for some prey, total length and cephalosome length were measured to estimate DW. Food composition was expressed by frequency of occurrence (%O; percentage of non-empty stomachs containing a given prey item), numerical percentage (%N; mean percentage per stomach of the number of a given prey item as a proportion of the total number of all prey in each stomach), weight percentage (%W; mean percentage per stomach of the weight of a given prey item as a proportion of the total weight of all prey in each stomach). The index of relative importance (IRI; Pinkas et al., 1971) for each prey item was then calculated according to the formula: IRI ¼ %O × (%N + %W), and then transformed into percentage by dividing it by the sum of IRI for all prey items (%IRI; Cortés, 1997).

Data analysis

Data analyses were performed with the R statistical software (version 2.15.0; R core team, 2013). Isotopic compositions were analysed separately on POM, zooplankton and teleosts. Differences in d13C and d15N values in POM inside the lagoon and on the outer slope were compared with Student’s t-tests as data were normally distributed. After checking normality of residuals (Shapiro test) and homoscedasticity (Levene test), type III ANOVA were performed to compare d13C and d15N values among the fixed factors sampling zones (lagoon and outer slope) and size classes of zooplankton (80–200 and ≥200 mm). Both factors were orthogonal with each other.

For teleosts, after checking normality of residuals (Shapiro test) and homoscedasticity (Levene test), type III ANCOVA were performed to compare d13C and d15N values among the fixed factors trophic groups (diurnal planktivorous; nocturnal planktivorous; non-planktivorous and mixed diet) and sampling zones (lagoon and outer slope), with total body length as a co-variable to account for any size effect. Both factors were however not orthogonal with each other. Consequently, post hoc Games – Howell tests were performed if trophic groups had a significant effect on isotopic ratios. Hierarchical clustering (Euclidean distance, Ward method) was also performed to compare isotopic ratios among species. Trophic levels of the different trophic groups of teleosts were calculated using the formula proposed by Post (2002):

\[ TL = \frac{1}{2} \sqrt{2 + (d^{15}N_{\text{trophic group}} - d^{15}N_{\text{zoozooplankton}}) / 2.4} \]

\[ d^{15}N_{\text{trophic group}} \]

is the mean d15N value of the trophic group considered in the lagoon or on the outer slope. \[ d^{15}N_{\text{zoozooplankton}} \]

is the mean d15N value in the zooplankton larger than 200 mm sampled in the lagoon or on the outer slope. d15N value in the zooplankton larger than 200 mm was chosen as stomach contents showed that teleosts fed mainly on prey larger than 200 mm (mean ± SD 140 ± 10 163 ± 7 mm).

RESULTS

POM had a lower d13C on the outer slope (mean ± SD 225 ± 0.4%) than inside the lagoon (221.0 ± 1.5%) (t ¼ 22.814, P ¼ 0.020) but d15N values did not significantly differ between the two zones (t ¼ 22.0639, P ¼ 0.534) (Figure 2, Table 1).

In zooplankton, d13C values were not influenced by size class but were significantly lower on the outer slope (220.4 ± 0.3%) than inside the lagoon (219.0 ± 0.0%) (Figure 2, Tables 1 and 2(a)). For d15N values, there was a significant interaction between size class and zone, with higher values for small zooplankton inside the lagoon and for large zooplankton on the outer slope (Figure 2, Tables 1 and 2(b)).

ANOVA results (Table 3(a)) showed that the interaction between sampling zone and trophic group influenced d13C values. This just significant interaction showed that the effect of the lagoon was slightly more important in some teleost trophic groups, but, as for POM and zooplankton, teleosts of all groups sampled on the outer slope had lower d13C values (217.9 ± 1.2%) than those sampled in the lagoon (214.8 ± 2.4%). The trophic group also influenced d13C but Figure 2 shows that trophic groups have rather similar values on the outer slope and more different ones inside the lagoon, in accordance with the interaction between the trophic groups and the sampling zone. Length had no effect on d13C.

ANOVA results (Table 3(b)) showed that d15N values were not influenced by the interaction between sampling zone and trophic group. There were also no significant differences in mean d15N values between teleosts sampled inside the
lagoon (8.3 ± 0.6‰) and those sampled on the outer slope (8.5 ± 0.5‰). The trophic group influenced d13C values with diurnal planktivorous being the most 13N-enriched teleosts among all trophic groups (4.374 ≤ t ≤ 5.552; p = 0.01) while the d15N values of nocturnal planktivorous teleosts, non-planktivorous teleosts and teleosts with a mixed diet are not significantly different (0.737 ≤ t ≤ 51.842; p = 0.05).

Length had a nearly significant effect on d15N because of increasing values of d15N with length in nocturnal planktivorous teleosts sampled inside the lagoon and non-planktivorous teleosts.

The cluster analysis on isotopic values (Figure 3) indicated that trophic group and zone of sampling influenced isotopic values in teleosts, as highlighted by the ANCOVA results. Three clusters appeared. The first one contained essentially non-planktivorous teleosts, including all those sampled inside the lagoon, but also contained a sub-cluster of nocturnal species. The second cluster contained only nocturnal species with a high d15C. The last cluster contained nearly all diurnal planktivorous species and is divided into two sub-clusters, one containing almost exclusively diurnal planktivorous teleosts sampled on the outer slope.

Diurnal planktivorous teleosts had the highest trophic level (3.29 in the lagoon and 3.24 on the outer slope), followed by the nocturnal planktivorous (3.15 in the lagoon and 3.24 on the outer slope), the non-planktivorous (2.97 in the lagoon and 3.06 on the outer slope) and the teleosts with a mixed diet (3.03 in the lagoon and 2.97 on the outer slope).

Stomach contents of teleosts sampled on the outer slope are summarized in Supplementary Table S2. Diurnal planktivorous teleosts fed on gastropod larvae (%IRI ¼ 32.50), phyto-benthos (%IRI ¼ 23.07) and various copepod species (%IRI ¼ 20.67). The importance of phyto-benthos for this group is explained by the consumption of this food by Genicanthus watanabei (%IRI ¼ 84.55), which constitutes a quarter of stomach contents of analysed planktivorous teleosts on the outer slope, while consumption of phyto-benthos was negligible in the other planktivorous species (%IRI < 5).

Non-planktivorous teleosts fed on phyto-benthos (%IRI ¼ 45.41), polyps (%IRI ¼ 19.24), benthic gastropods (%IRI ¼ 13.79) and eggs (%IRI ¼ 10.03). The number of analysed individuals, however, was rather low (Supplementary Table S2).

Nocturnal planktivorous teleosts and teleosts with a mixed diet were both represented by a single species (Ostiorhinchus angustatus and Pomacentrus brachialis respectively) and few individuals (N ¼ 1 and N ¼ 2, respectively). Their diet was composed of five amphipods (%IRI ¼ 83.19) and one small shrimp (%IRI ¼ 16.81) for Ostiorhinchus angustatus and of copepods (mainly the genus Oncaea and Claudio/ Paracalanus, %IRI ¼ 50.68), gastropod larvae (%IRI ¼ 18.14) and Rhabdonema diatoms (%IRI ¼ 18.06) for Pomacentrus brachialis.

**DISCUSSION**

**Differences and similarities between two neighbouring food chains**

Stable isotope analysis revealed that both food chains sampled in the Ouano lagoon and on the outer slope are distinguishable despite being close to each other (less than 10 km) and despite an important part of the water in the lagoon coming from the outer slope. For each trophic compartment (i.e. POM, zooplankton size classes and different teleost trophic groups), d13C values were significantly higher in the lagoon than on the outer slope despite both areas being close (less than 10 km) while d15N was not influenced by the sampling zone.

Differences in d13C values between the lagoon and the outer slope may be explained by two hypotheses regarding POM composition. Firstly, d13C values may be linked to potential differences in primary producer compositions between these two zones, namely by differences within pico-cyanobacteria assemblages that are important components in the oligotrophic ocean. In the Noumâa lagoon (400 km south-east of Ouano lagoon), Prochlorococcus was shown to be dominant in oceanic waters, while Prochlorococcus and Synechococcus co-occur in the lagoon (Jacquet et al., 2006). Differences in d13C values linked to potential co-existence of Prochlorococcus and Synechococcus in the Ouano lagoon seem to indicate that water exchanges between lagoon and ocean do not lead to the homogenization of the community structure of phytoplankton at a large spatial scale because of quick renewal of water inside the Ouano lagoon and grazing of imported picophytoplankton by coral reef community (Houbreïque et al., 2006; Cuet et al., 2011). Therefore, few picophytoplankton cells may be imported from the bordering ocean inside the lagoon by water passing over the reef. Further studies on phytoplankton communities of the Ouano lagoon may confirm this hypothesis.

Secondly, different contributions of materials (mucus, faces, zooplankton, marine photosynthetic organism debris, barrier reef erosion debris) to POM among sites may explain the differences in d13C values between the lagoon and the outer slope (Wyatt et al., 2013; Briand et al., 2015). Wyatt et al. (2013) observed that allochthonous...
phytoplankton mainly contributed to POM near the reef crest at Ningaloo Reef (**40 – 75%), while inside the lagoon autochthonous releases, i.e. detritus, mainly contributed to POM despite phytoplankton contribution remaining important (**20 – 25%). Detritus may include, for example, sedimentary matter resuspended by cross-reef flows (Chevalier et al., 2015), phytobenthos debris and coral mucus (Wyatt et al., 2013), and are known to be more enriched in 13C than phytoplankton (Wyatt et al., 2013; Briand et al., 2015).

Similar results were found at Ningaloo Reef, Western Australia, where 13C values of POM were lower on the outer slope than in the lagoon while no spatial variations of 15N occurred (Wyatt et al., 2013). In contrast, the inverse phenomenon was observed in two neighbouring bays of Moorea Island (French Polynesia), with 13C values of POM decreasing from the entrance of the bays to the coastal areas (Letourneur et al., 2013). This difference may be explained by the lack of river inputs in the Ouano lagoon and the Ningaloo Reef (Wyatt et al., 2012, 2013) while the two bays of Moorea island are subjected to river inputs reducing 13C of POM (Letourneur et al., 2013).

Spatial variations of stable isotope values in zooplankton followed the same trend as in POM. Higher or similar densities of zooplankton were observed in lagoons of New Caledonia than on outer slopes, with highest densities observed in coastal areas (Champalbert, 1993). Planktivorous teleosts, however, are known to form a ‘wall of mouths’ over reef flats that reduce the density and

<table>
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<th></th>
<th>Lagoon</th>
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<th>Outer slope</th>
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<td>d15N</td>
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<td>2.4 + 0.7</td>
<td>6</td>
<td>NA</td>
<td>222.5 + 0.4</td>
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<td>217.8 + 0.1</td>
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<td>6</td>
<td>NA</td>
<td>219.6 + 0.5</td>
<td>3.9 + 0.2</td>
</tr>
<tr>
<td>Zooplankton &gt; 200 mm</td>
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<td>8.6 + 0.3</td>
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<td>8.2</td>
<td>3.18</td>
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<td>–</td>
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<td>9.2</td>
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<td>7.9 + 0.3</td>
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<td>Pomacentrus moluccensis</td>
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The trophic ecology of zooplankton in the Outer Reef may differ significantly from that in the inner lagoon. Consequently, zooplankton in the Outer Reef may be predominantly herbivorous, as evidenced by stable isotope ratios between zooplankton in the lagoon and from the outer slope. Zooplankton in the lagoon may also be more variable in isotope ratios between different communities. Differences in stable isotope ratios between zooplankton from the inner lagoon and the outer slope may also be explained by changes in trophic ecology. Detritus in the POM of the lagoon can be used as food by organisms, including zooplankton (Gottfried & Roman, 1983; Crossman et al., 2001; Dromard et al., 2013). For example, Roman et al. (1990) showed that consumption of phytoplankton by reef zooplankton does not satisfy their dietary nutritional requirements, leading reef zooplankton to consume edible detritus such as mucus (Gottfried & Roman, 1983). As a result, zooplankton in the lagoon and on the outer slope may exploit different food sources, and thus different isotope values are observed in both communities.

**Trophic ecology of teleosts**

The differences in δ13C values between lagoon and outer slope in teleosts were noticeable and consistent with the spatial variations observed in POM and zooplankton, indicating that δ13C values of teleosts are partially due to δ13C values of POM and zooplankton in their respective sampling area. Similar results were obtained at Ningaloo Reef (Wyatt et al., 2012), with increasing δ13C values in teleosts from the outer slope to the lagoon. In contrast, in Moorea Island, δ13C values of the teleost Stegastes nigricans decreased from the entrances of the bays to the coastal areas (Letourneur et al., 2013). This trend, however, follows the decreasing trend of δ13C values in POM across the bays. These results suggest that the teleosts mostly rely on local food resources, and that migrations between lagoon and ocean are at best scarce. This hypothesis is consistent with their sedentary and even territorial behavior, and the limited home range of most coral reef teleosts (Sale, 1978; Ceccarelli, 2007; Nash et al., 2015). As a result, higher contribution of reef-derived materials to the diet of teleosts, and thus higher δ13C values, are expected in the lagoon in the different trophic groups. This phenomenon was observed for the planktivorous teleost Amblyglyphidodon indicus in the Red Sea. On oceanic reefs (steep-walled pinnacles rising from deep water), analysis of stable isotope ratios in this planktivorous species revealed that it exploits a food chain with planktivorous basal sources. On shelf reefs (situated on the continental shelf, in water between 25 and 60 m depth), although it still relied mainly on plankton-based food chains, this teleost appeared to also exploit a food chain based on phytoplankton (McMahon et al., 2016). As in other trophic compartments, δ15N values of teleosts did not differ between lagoon and outer slope and computed trophic levels appear to be similar. This result is consistent with the lack of spatial variations of δ15N values in POM and zooplankton but differs from the results at Ningaloo Reef where δ15N values of teleosts differ.

**Table 2.** Influence of size class (smaller or larger than 200 mm) and zone of sampling (interior, outer slope) on (a) δ13C and (b) δ15N values of zooplankton.

<table>
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<th>F</th>
<th>P</th>
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<tr>
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<td>0.07</td>
<td></td>
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</tr>
<tr>
<td>(b)</td>
<td></td>
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<td>Size class</td>
<td>1</td>
<td>0.16</td>
<td>0.970</td>
<td>0.341</td>
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<td>Zone</td>
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<tr>
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<td>1.14</td>
<td>7.133</td>
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</tr>
<tr>
<td>Residuals</td>
<td>14</td>
<td>0.15</td>
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</table>

Bold results are significant.

**Table 3.** Influence of trophic group (diurnal planktivorous, nocturnal planktivorous, non-planktivorous and mixed diet) and zone of sampling (interior, outer slope) on (a) δ13C and (b) δ15N values of teleosts.

<table>
<thead>
<tr>
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<th>MS</th>
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<tbody>
<tr>
<td>(a)</td>
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<td>0.001</td>
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<td>4.66</td>
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<tr>
<td>Residuals</td>
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<td>11.10</td>
<td></td>
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<tr>
<td>(b)</td>
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<td>1.17</td>
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</table>

Bold results are significant.
declined across the reef despite the lack of spatial variation of d^{15}N in POM (Wyatt et al., 2012, 2013). By using Bayesian mixing models with zooplankton, phyto-benthos and coral mucus as prey, Wyatt et al. (2012) conclude that the contribution of zooplankton to the diet of teleosts decreased across the reef because of the rarity of oceanic zooplankton in the lagoon. Consequently, spatial variations of d^{15}N at least in the diurnal planktivorous teleosts would have been expected if the zooplankton contribution to their diet had declined from the ocean to the lagoon. Nevertheless, because densities of zooplankton are higher or similar in lagoons than in ocean in south-western New Caledonia (Champalbert, 1993) this zooplankton appears to be reef-produced, enough zooplankton may be available for planktivorous teleosts inside the lagoon. As a result, the absence of difference in d^{15}N values between teleosts of the lagoon and of the outer slope may reflect the absence of difference in d^{15}N values between zooplankton of the lagoon and of the outer slope.

d^{13}C and d^{15}N values differed significantly among trophic groups of teleosts. These differences, however, are the result of one trophic group having higher stable isotope values than the other ones (nocturnal planktivorous teleosts for d^{13}C and diurnal planktivorous teleosts for d^{15}N). The unusually high d^{13}C values of nocturnal planktivorous teleosts sampled inside the Ouano lagoon may be explained by the diets of several species. Indeed, Aponog anoxostigma, Cheilodipterus quinquelineatus and Ostorhinbus cyanosoma feed primarily on benthic prey, including small teleosts (Barnett et al., 2006), that are generally enriched in d^{13}C compared with POM (Briand et al., 2015). Furthermore, the nocturnal emergence of zooplankton (Roman et al., 1990) may also change d^{13}C values of zooplankton (Pitt et al., 2008), as the emerging organisms may rely on d^{13}C-enriched sedimentary organic matter (Briand et al., 2015) rather than on POM during daylight. Thus, the nocturnal emergence of zooplankton may influence d^{13}C values of their predators and upper trophic levels. In the lagoon, three species of sampled nocturnal planktivorous teleosts had isotopic compositions similar to those of non-planktivorous teleosts. Isotopic analyses on diurnal and nocturnal samples of zooplankton and POM should be carried out to confirm the existence of two different trophic pathways between day and night.

Stomach contents of the teleosts sampled on the outer slope indicated that several trophic groups may feed on similar prey. For example, Genicanthus watanabei feeds mainly on phyto-benthos like non-planktivorous teleosts. Such a phenomenon, already observed for the Genicanthus genus (Randall, 1975; Howe, 1993), may indicate that the trophic groups may have greater trophic plasticity or a less specific diet than indicated by stable isotopes. Further studies on the food web of the Ouano lagoon should also be done on stomach contents of teleosts sampled inside the lagoon in order to confirm the results presented here.

Nevertheless, previous studies showed that open ocean particles may still be a source of carbon for lagoon food webs and that water passing over the barrier reef may resuspend benthic particles inside the lagoon. These two combined phenomena may lead to the differentiation of composition and thus d^{13}C values of POM between the lagoon and the outer slope. Consistent differences in d^{13}C values between the lagoon and the outer slope in each trophic compartment indicate reliance on POM by the two food chains. Furthermore, while the planktonic food chain on the outer slope of the Ouano lagoon probably relies more on oceanic sources, the planktonic food chain in the lagoon may rely on both oceanic (imported particles) and benthic (mucus aggregates and resuspended particles) sources because of tidal and wave induced external inputs and autochthonous releases.

Consequently, benthic-pelagic coupling may occur in the Ouano Lagoon. The lack of spatial differences in d^{15}N values of POM, zooplankton and teleosts, however, indicates a similar chain length in the lagoon and in the outer slope. Consequently, although distinguishable, the two food chains are similar.

The oceanic water typically passes over the barrier reefs in many lagoons. Consequently, this result is very likely to be generalizable on the general ecology of the trophic networks of many lagoons which are well separated from surrounding oceanic waters by a well delineated barrier reef.

SUPPLEMENTARY MATERIAL
The supplementary material for this article can be found at https://doi.org/10.1017/S0025315417001370

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REFERENCES


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email: baptiste.lebourg@doct.ulg.ac.be
**Supplementary material:** The same but different: stable isotopes reveal two distinguishable, yet similar, neighbouring food chains in a coral reef

Baptiste Le Bourg, Yves Letourneur, Daniela Banaru, Jean Blanchot, Cristèle Chevalier, Gérard Mou-Tham, Benoit Lebreton, Marc Pagano

**Table S1.** Trophic groups of the 32 teleost species sampled in the Ouano lagoon and determined from the literature

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- **Note:** The values for %D, %N, %W, and %H represent the percentage of each organism in the diet. The values for %D, %N, %W, and %H for the non-planktivorous diet are taken from a different source.
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References


Hobson E.S. (1991) Trophic relationships of fishes specialized to feed on zooplankters above coral


