Pathways of organic matter in an estuarine mangrove trophic network assessed by carbon and nitrogen stable isotopes

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*Carbon and nitrogen stable isotopes were used to describe an estuarine mangrove food web in New Caledonia, SW Pacific. Isotopic values were measured for all components of the ecosystem, from various organic matter (OM) sources to predators. Primary producers showed δ¹³C values from −32.29‰ (*Bruguiera gymnorhiza*) to −24.67‰ (mouth particulate organic matter), whereas δ¹⁵N values ranged from 1.48‰ (*Avicennia marina*) to 10.17‰ (*Eichomia crassipes*). Two potential organic matter sources, i.e. the mangrove species and* E. crassipes*, appeared not to be directly used by consumers although were indirectly entering the food web through particulate and sedimentary organic matter pools (POM and SOM). Overall, invertebrates showed C-depleted and N-depleted values compared with fish, highlighting their lower trophic level. The highest trophic levels in this estuarine mangrove were represented by carangids (δ¹⁵N of 11.24‰ for* Caranx *sp. and 10.81‰ for* Carangoides fulvoguttatus*) and gerrids (δ¹⁵N of 10.42‰ for* Gerres filamentosus*). Two main pathways of organic matter were identified from sources of OM to end-members, i.e. from estuarine POM and SOM toward gerrids and from marine POM towards carangids. The food chain comprised three or four trophic levels, depending on the pathway of organic matter. The position of some consumer species within the reconstructed food web might imply that an important source of organic matter was probably missing, i.e. microphytobenthos. Despite an obvious connection, the role of river inputs as potential drivers of mangrove food web dynamics appeared important only during the wet season.*

Keywords: food webs, organic matter sources, consumers, Bayesian mixing model, New Caledonia

INTRODUCTION

Mangrove forests constitute a critical ecosystem for several countries and islands in the intertropical and sub-tropical zones, where they extend over large areas (Hogarth, 1999). Although dominated by a relatively low number of tree species, mangrove forests are usually highly productive systems (Alongi, 1998; Rozas & Minello, 2006) that support great biodiversity (Nagelkerken & van der Velde, 2004; Sepúlveda-Lozada *et al.*, 2015) and high biomass (Dixon *et al.*, 1994; Leopold *et al.*, 2015). They play a key role in stabilizing sediments of marine and/or terrestrial origin, which provide effective protection of coastlines against hydrodynamic disturbances (Alongi, 1998). Mangrove areas also provide good protection against predators for many marine species due to the structural complexity of the root entanglement. These habitats are often considered as nursery grounds offering safety and high food availability, particularly for fish (Cocheret de la Morinière *et al.*, 2003; Mumby *et al.*, 2004; Lugendo *et al.*, 2007; Vaslet *et al.*, 2012, 2015; Sepúlveda-Lozada *et al.*, 2015; Serafy *et al.*, 2015).

Located at the interface between terrestrial and marine ecosystems, mangroves play an important role in the export of nutrients and dissolved/particulate matter originating from coastal watersheds (Marchand *et al.*, 2006; Nagelkerken *et al.*, 2008; Molnar *et al.*, 2013; Briand *et al.*, 2015). This export concept can be applied to some fish species as well; juveniles use mangroves, whereas with increasing size and age, subadults and adults move towards seagrass beds and adjacent coral reefs (Nagelkerken *et al.*, 2000; Cocheret de la Morinière *et al.*, 2003; Mumby *et al.*, 2004; Huxham *et al.*, 2007; Honda *et al.*, 2013; Vaslet *et al.*, 2015).

In various parts of the world many mangroves are threatened by natural and anthropogenic disturbances such as hurricanes (Imbert *et al.*, 1998), tsunamis (Alongi, 2008), sewage pollution (Howarth & Farber, 2002; Molnar *et al.*, 2013), human coastal pressure (Serafy *et al.*, 2015) and deforestation for the fast growing shrimp aquaculture industry (Duke *et al.*, 2007). It thus becomes increasingly crucial to better understand mangrove ecosystem functioning, and one way to achieve this goal is to study food webs with a stable isotope approach (carbon and nitrogen). Indeed, the δ¹³C ratio is mainly used to determine the origin of the organic matter (OM) sources, while the δ¹⁵N ratio is used as a proxy to estimate the trophic level of an organism within a food chain. Both combined allow the tracking of OM pathway(s) from potential sources (i.e. primary producers and pools of OM,

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see below) to various consumers belonging to different trophic levels.

Apart from some pioneering studies in the 1980s (Hackney & Haines, 1980; Rodelli *et al.*, 1984), the relatively recent utilization of stable isotopes (C and N) in mangrove ecology has already provided very useful information. For instance, several studies have unambiguously highlighted the importance of suspended OM, phytoplankton and/or primary producers in sustaining consumer communities in various mangrove forests (Bouillon *et al.*, 2000, 2002; Thimdee *et al.*, 2004; Kon *et al.*, 2007; Abrantes & Sheaves, 2008, 2009; Faye *et al.*, 2011; Abrantes *et al.*, 2014, 2015; Sepúlveda-Lozada *et al.*, 2015).

The objective of this study is to improve the knowledge of mangrove ecosystem functioning, by comparing the food web structure in two contrasted sites and during two seasons of an estuarine mangrove in a Pacific island. This sampling design is based on the expectation that riverine sources would be more influential on the estuarine location and marine sources more influential on the mouth location, and these contributions would change seasonally with wet/dry seasons. To test this hypothesis, we aim (1) to determine the isotopic values of various OM sources and of several consumers having different feeding strategies and belonging to different trophic levels, (2) to characterize and quantify the mix of several sources in the two OM pools identified (i.e. particulate and sediment OM; see below), and (3) to reconstruct food web structures in this estuarine mangrove.

MATERIALS AND METHODS

Study sites and sampling

The estuarine mangrove studied is located in La Foa, in the western part of the New Caledonian lagoon (SW Pacific Ocean) (Figure 1). This area is relatively dry, although strong rainy episodes may occur during the hot and wet season, and its watershed includes agricultural activities requiring an important irrigation system that takes water from the river. Two sites were sampled, i.e. the middle and mouth of the estuary, in April (hot and wet season) and August (cool and dry season) 2011. The two sites were chosen to capture the relative influence of marine *vs* river inputs on the estuarine functioning, and the two seasons were chosen to capture the differences in river flow according to wet *vs* dry periods.

At each site and each month three mangrove species were collected, i.e. *Avicennia marina*, *Bruguiera gymnorhiza* and *Rhizophora stylosa*. Two main heterogeneous pools of OM, composed of allochthonous and autochthonous materials, were also collected. The first one is sedimentary organic matter (SOM) (subsurface layer of sediment <3 cm depth, excluding macro-detritus). The SOM is a complex mixture of phytoplankton, bacteria, dead cells and faecal pellets, and detrital particles plus microphytobenthos and meiofauna to a lesser extent. The second one is particulate organic matter (POM) (the subsurface water, approximate depths <10 cm) of the river fresh water, estuarine water (mid-estuary and mouth) and marine water from the coral reef lagoon (~9 km south-east from the river mouth). The particulate organic matter in water is a mixture of phytoplankton, bacteria, dead cells and faecal pellets, and detrital particles (Tesi
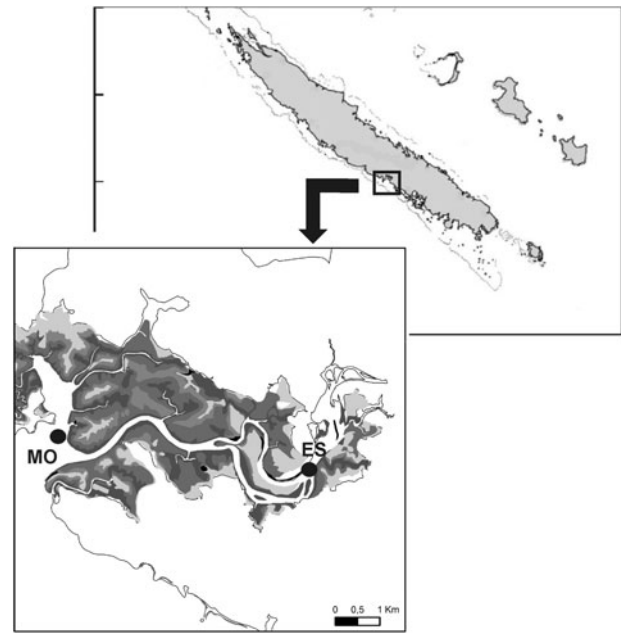

Fig. 1. Location of sampled sites (black dots) in the mouth (MO) and estuary (ES) in the mangrove forest of La Foa, New Caledonia. From the dark to light grey, coloured areas represent dense *Rhizophora* spp., mix between *Rhizophora* and other species, *Avicennia* spp. and sandflats.

et al., 2007; Harmelin-Vivien *et al.*, 2008; Frangoulis *et al.*, 2011).

At each season and only at the estuary site (due to absence in the mouth site) additional potential sources of OM were sampled, i.e. benthic macro-detritus and the invasive water hyacinth *Eichornia crassipes* because of its abundance in upstream parts of the river and thus transport to the estuary by river flow.

Gill-nets were used to catch fish and some large invertebrates such as the mud crab *Scylla serrata*. Other invertebrates were carefully caught by hand when possible (oysters, hermit crabs, gastropods) or with a small trap. Biodiversity in New Caledonian mangroves is high (for instance, ~250 fish species were listed by Thollot (1992) in a neighbouring mangrove) and it is thus obviously impossible to sample all invertebrate or fish species. Although opportunistic, our sampling aims at catching species with various feeding strategies and that are representative of different trophic levels. Our study does not provide a complete view of the existing food webs in the sampled area, but rather adopts a general approach in order to reveal pathways for OM flows.

Stable isotope preparation and analyses

Organic matter was obtained by filtration of waters on pre-weighed Whatman GF/F filters (porosity 0.7 μm), then pre-combustion at 450°C for 4 h. The 63–200 μm-sized fraction was considered to be the best proxy for analysing the main phytoplankton components of the community (Rau *et al.*, 1990; Rolff & Elmgren, 2000). In this study, we focused on obtaining broad isotopic values of freshwater, estuarine and marine POM, rather than analysing the various fractions of phytoplankton (e.g. pico- and nanoplankton). The largest particles and detritus were, however, removed to avoid bias in isotopic values. Marine, estuarine and freshwater

POM samples were oven-dried at 60°C for 24 h and scraped to collect the dried organic material. Vegetal, animal and sediment samples were freeze-dried and ground into a fine powder (<6 μm) using a mortar and pestle. Mangrove samples (leaves), animal muscles (fish, large crustaceans and large bivalves) and freshwater POM samples were analysed without any prior treatment. For marine and estuarine POM, SOM and small crustaceans, two sub-samples were analysed: one for carbon isotope analysis, after acidification by 1% HCl solution to remove carbonates, rinsed with distilled water and oven-dried at 60°C for 24 h, as carbonates present higher $\delta^{13}C$ than organic carbon (De Niro & Epstein, 1978); and the other for nitrogen isotope analysis, requiring no prior acidification as the process results in an enrichment in $\delta^{15}N$ (Pinnegar & Polunin, 1999).

The $^{13}C{:}^{12}C$ and $^{15}N{:}^{14}N$ ratios were analysed by continuous-flow isotope-ratio mass spectrometry. The spectrometer (Delta V Plus stable-isotope analyser coupled with a Flash EA 2000 analyser; Thermo Scientific, Bremen, Germany) was operated in dual isotope mode. The analytical precision was 0.2‰ for both N and C, estimated from standards analysed along with the samples. Internal standards were 1 mg leucine calibrated against 'Europa flour' and IAEA standards N1 and N2. Isotope ratios were expressed as parts per 1000 (‰) differences from a standard reference material:

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

where X is ^{13}C or ^{15}N, R is the corresponding ratio ($^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$) and δ is the measure of heavy to light isotope in the sample. The international standard references are Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen.

Assessments of the contributions of potential OM sources to the estuarine POM and SOM pools

Different models can be used to evaluate the contribution of various OM sources to a pool (Phillips & Gregg, 2003; Parnell et al., 2010). The starting point is to consider that a pool's isotopic signature is the mean of the values of the various constitutive or incorporated sources (Phillips, 2001). For a pool constituted by three potential sources, each of them characterized by its own $\delta^{13}C$ and $\delta^{15}N$ values, the percentage of each source contributing to the pool is described by the following equations (Fry, 2008):

$$\delta^{13}C_{pool} = f_1\delta^{13}C_1 + f_2\delta^{13}C_2 + f_3\delta^{13}C_3$$
$$\delta^{15}N_{pool} = f_1\delta^{15}N_1 + f_2\delta^{15}N_2 + f_3\delta^{15}N_3$$
$$f_1 + f_2 + f_3 = 1$$

where $\delta^{13}C$ and $\delta^{15}N$ are the isotopic values for sources 1 to 3 and f is the relative proportion of the contribution of a source to the pool.

Thus the relative contributions of various OM sources to POM and SOM pools from the estuarine mangrove were assessed with Bayesian mixing-models (SIAR package in R, Parnell et al., 2010). These models calculate the most feasible solutions that could explain isotopic ratios measured for POM or SOM and allow the integration of all uncertainties linked to sources of OM. A major concern is the choice of trophic

enrichment factors (TEFs), as the model outputs can be strongly influenced by the use of incorrect TEFs (Bond & Diamond, 2011). However, as our cases studied concerned only the mix of several potential OM sources and no consumption process, the TEF was considered to be null in the model.

For the estuarine POM, the $\delta^{13}C$ and $\delta^{15}N$ values of the river and marine POM were computed to assess their different influences. For the estuarine SOM, the same OM sources were considered plus those of mangroves (three species), benthic detritus and water hyacinth.

Data analyses

After verification of data normality with the Kolmogorov–Smirnov test, the variance homogeneity of OM sources (i.e. POM, SOM, detritus and mangrove leaves), invertebrates and fish was tested using the Levene test. Then two-way analyses of variance (site × month) plus post-hoc comparisons of means using t-tests were performed. If variances were not homogeneous, data were analysed with Kruskal–Wallis tests, a non-parametric equivalent of ANOVA. Sources, vegetal or animal taxa sampled during only one season in the two sites or at only one site in both seasons were analysed solely from a spatial or a temporal perspective, with t-tests or non-parametric Mann–Whitney U-tests.

RESULTS

Organic matter sources

The C and N isotopic values of the POM significantly varied from the river to the lagoon (Table 1). The mean values of the marine POM were -21.72 ± 1.65‰ for $\delta^{13}C$ and 2.55 ± 0.31‰ for $\delta^{15}N$ on average, although varying according to season (Supplementary Table S1). In comparison, estuary POM values were significantly C-depleted (~ -28.5‰) and N-enriched (5‰) at both sites between which $\delta^{13}C$ differences were observed, as the mid-estuary site is significantly more C-depleted than the mouth site (Table 1, Supplementary Table S1). Overall, $\delta^{13}C$ values of POM also significantly varied over seasons (Table 1), especially river POM that showed strong fluctuations of both $\delta^{13}C$ and $\delta^{15}N$ ratios (Supplementary Table S1). Conversely, SOM is a pool of OM that did not much fluctuate between sites or over seasons, except for a significant variation of $\delta^{15}N$ at the mid-estuary site between April and August (Table 1, Supplementary Table S1).

Two mangrove species, i.e. Avicennia marina and Rhizophora stylosa, demonstrated similar $\delta^{13}C$ but different $\delta^{15}N$ values (Supplementary Table S1). In both cases, few significant isotopic variations occurred between sites or seasons (Table 1). In the estuary area, the water hyacinth Eichornia crassipes had significantly different isotopic values according to the season (Mann–Whitney U-test; $P = 0.032$ and $P = 0.021$ for $\delta^{13}C$ and $\delta^{15}N$ respectively), especially for $\delta^{15}N$, which reached 10.17 ± 0.12‰ in April (Table 1). In contrast, benthic detritus displayed similar values between April and August (Mann–Whitney U-test; $P = 0.064$ for $\delta^{13}C$ and $P = 0.256$ for $\delta^{15}N$).

Table 1. Summary of the significant variations of isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of the OM sources in the mangrove forest of La Foa, New Caledonia.

Source	Factors	$\delta^{13}C$	$\delta^{15}N$
POM	Site	***	***
	Season	***	ns
	Site × season	***	***
SOM	Season	ns	***
	Site × season	ns	*
Avicennia marina	Site	**	ns
Rhizophora stylosa	Site	ns	*
	Site × season	**	ns
Eichornia crassipes	Season	*	***

POM, particulate organic matter; SOM, sedimentary organic matter. Analyses were run with two-way ANOVAs or Kruskal–Wallis tests: site (i.e. mid-estuary *vs* mouth) × season (April *vs* August). ns = $P > 0.05$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Relative contributions of organic matter sources to POM pool

Overall, from mouth to mid-estuary, the influence of marine POM clearly decreased from about 50 to 40% respectively, whereas the influence of river POM increased from about 50 to 60% (Figure 2A). This general pattern however varied greatly according to the season, with, for instance, a strong decrease of river POM influence in August, i.e. in the dry season (Figure 2B). This was particularly obvious in the mouth site where the river influence dropped to ~30% in that season.

Relative contributions of organic matter sources to SOM pool

All selected OM sources influenced the SOM pool (Figure 3). In the mouth site, each OM source contributed to about 15–25% of the SOM isotopic composition. Proportions were more variable in the mid-estuary site; the river POM being the lowest contributor (~7%) and the water hyacinth and detritus being the highest (~20%) (Figure 3A). Overall, these patterns of relative contributions of OM sources to the SOM pool remained relatively stable at different seasons in both sites, except a higher contribution of river POM (~13%) and a lower contribution of water hyacinth (~7%) to the mid-estuary SOM isotopic composition in April, i.e. the wet season (Figure 3B).

Invertebrates and fish

Invertebrate $\delta^{13}C$ values ranged from -27.59 ± 0.10‰ for the most C-depleted (the oyster *Saccostrea cucullata tuberculata*) to -20.00 ± 0.54‰ for the most C-enriched (the crab *Uca tetragodon*) and $\delta^{15}N$ values ranged from 3.38 ± 0.14‰ for the most N-depleted (the gastropod *Terebralia palustris*) to 9.05 ± 0.08‰ for the most N-enriched (the mantis shrimp *Gonodactylus* sp.) (Supplementary Table S1).

Fish's $\delta^{13}C$ values ranged from -25.70 ± 0.04‰ (the gobiid *Oxyurichthys* sp.) to -17.54 ± 0.49‰ (*Caranx* sp.) and $\delta^{15}N$ values ranged from 6.43 ± 0.05‰ (*Valamugil* sp.) to 11.24 ± 0.20‰ (*Caranx* sp.) (Supplementary Table S1).

Overall, invertebrates and fish displayed relatively few significant spatial and/or temporal variations in their carbon and nitrogen isotopic signatures. These fluctuations mostly concerned $\delta^{13}C$ rather than $\delta^{15}N$ (Table 2).

Reconstruction of the mangrove food web structure

The major potential OM sources in these food webs (mangrove, detritus, water hyacinth, SOM and POM) had different isotopic ratios (Figure 4, Supplementary Table S1). Depending on the invertebrate and fish isotopic values, and based on an average enrichment of 1‰ for C and ~3–3.4‰ for N, the results overall suggest that the food webs in this estuarine mangrove are mainly based on mouth POM and mid-estuary SOM, marine POM and river POM, depending on the consumer species. Conversely, the direct use of mangrove, detritus, mouth SOM, mid-estuary POM and water hyacinth appeared to be of little importance (Figure 4). However, this apparently poor contribution of primary producers (mangrove, water hyacinth) to food web structure should be buffered considering that primary producers contribute to POM and SOM pools (Figures 2 and 3).

The position of *Pinctada* sp. within the trophic network suggested the use of marine POM rather than river POM (this species was found only at the mouth of the estuary). The position of the species *Anodonstoma chacunda* did not clearly support a use of detritus that is usually considered to be its main food. Regarding some end-members of the studied food webs, i.e. carnivorous carangids and gerrids, the former appeared mainly linked to marine POM whereas the latter appeared to mainly depend on estuarine POM and SOM and possibly to detritus (Figure 4).

DISCUSSION

Several studies have explored mangrove trophic pathways using stable isotope ratios (Sheaves & Molony, 2000; Kon et al., 2007; Abrantes & Sheaves, 2008, 2009, 2010; Faye et al., 2011; Abrantes et al., 2014, 2015; Sepúlveda-Lozada et al., 2015) and other works on mangroves have mainly focused on links between mangroves and adjacent ecosystems such as seagrass and coral reefs (Cocheret de la Morinière et al., 2003; Lugendo et al., 2006; Vaslet et al., 2015). Thus, although it concerned a simplified and incomplete food web in a New Caledonian estuarine mangrove, the present study constitutes an important contribution in filling the gap of assessing mangrove food webs using stable isotope analyses in the Pacific.

Primary producers

The isotopic ratios of the estuarine mangrove OM sources obtained in this study generally fit well within the typical ranges documented in New Caledonia and other parts of the world (Ostrom & Fry, 1993; Briand et al., 2015). Primary producers revealed a large range of $\delta^{15}N$ signatures; for instance, the maximal $\delta^{15}N$ values obtained for the invasive riverine water hyacinth were slightly above documented ranges of benthic macrophytes and the minimal detected $\delta^{15}N$ values of mangrove were below other documented ranges.
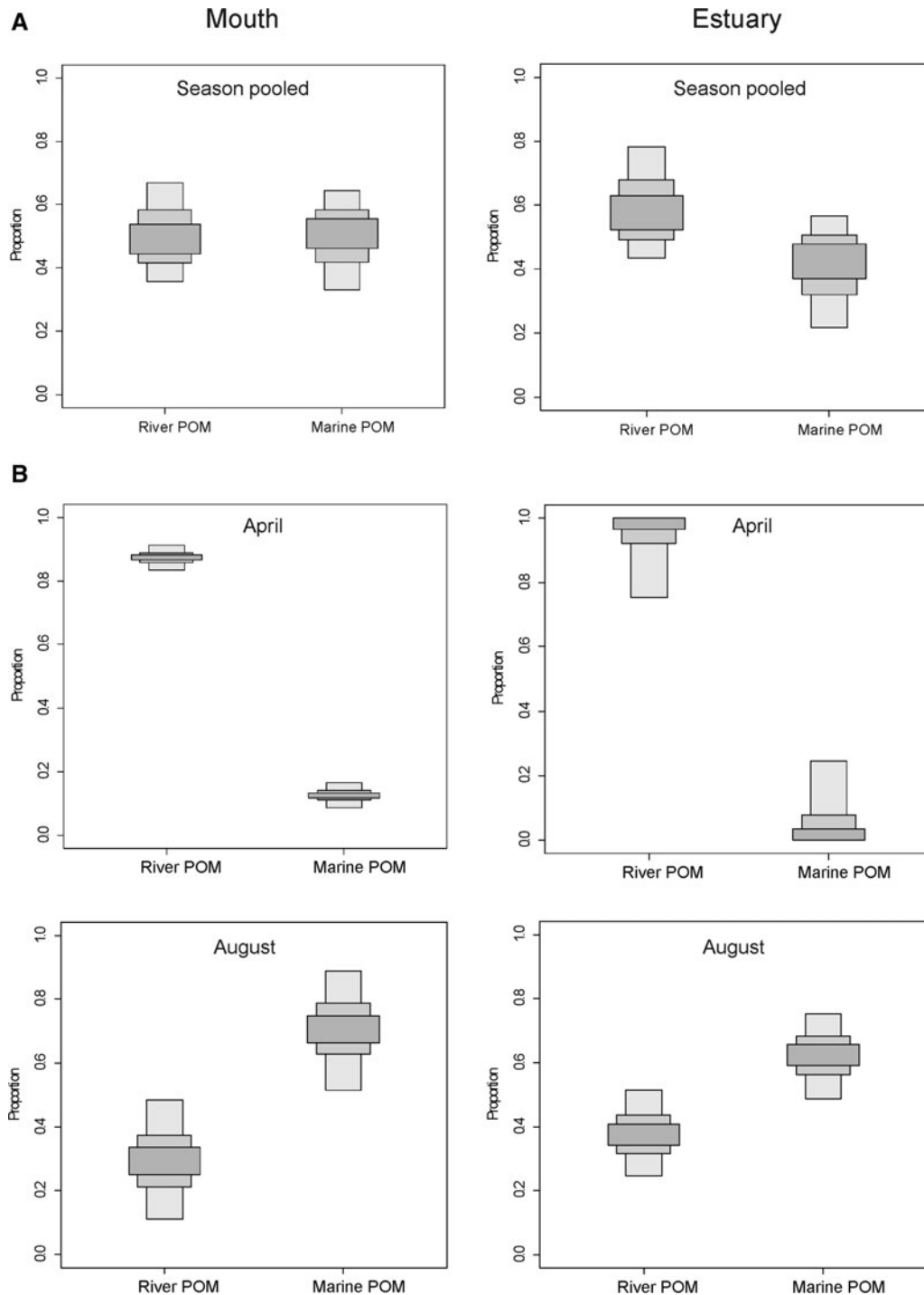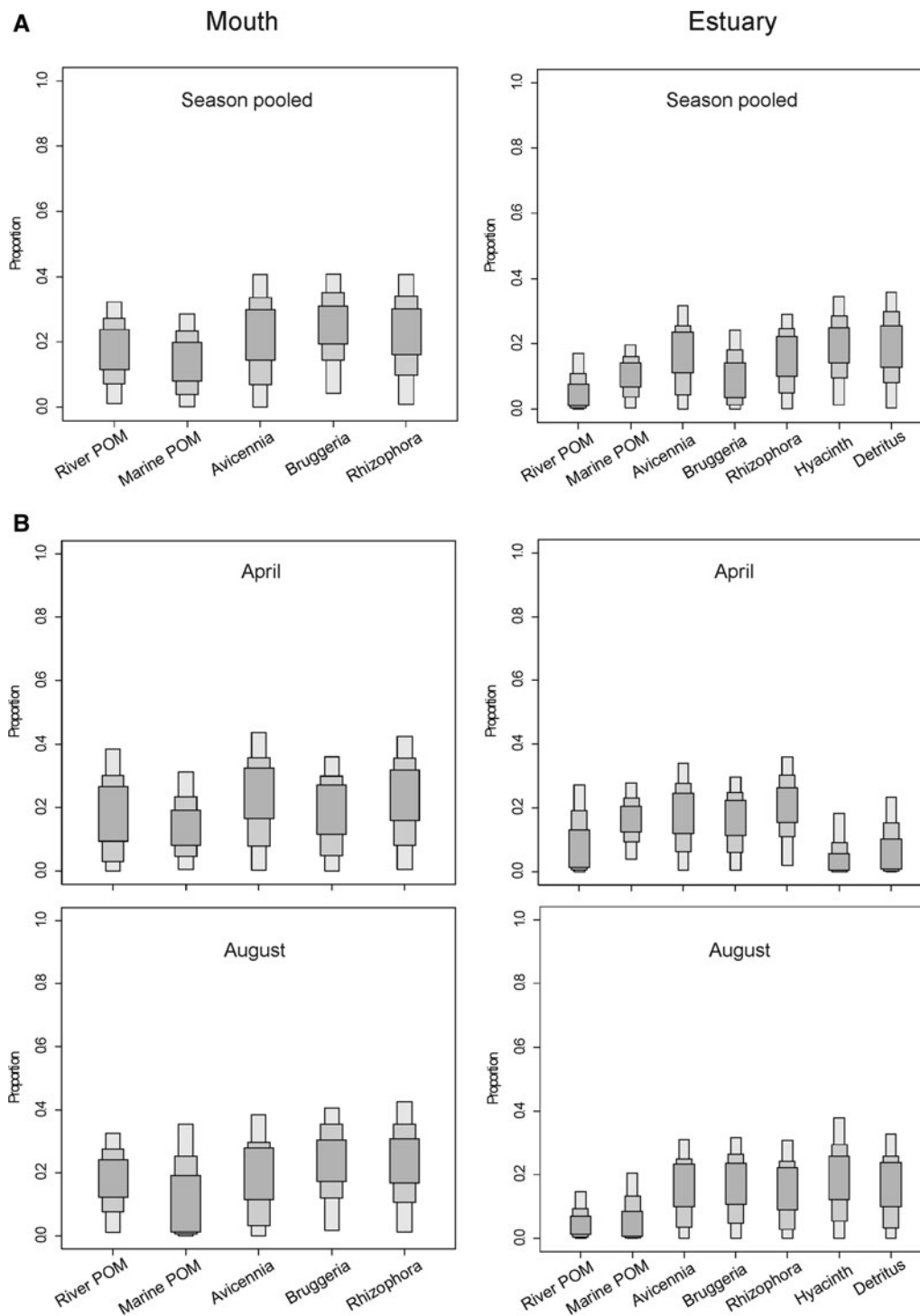
Fig. 2. Relative importance of river POM and marine POM in the isotopic composition of mouth POM (left panel) and estuary POM (right panel), both season pooled (A) and according to seasons, April (top) and August (down) (B). Shaded boxes represent, from dark to light grey, 50, 75 and 95% Bayesian credibility intervals.

Conversely, the primary producers showed a low variability in their $\delta^{13}C$ values. Thus, they cannot be discriminated as easily as the various sources from surrounding reef environments, e.g. macroalgae, epiphytes and seagrass (Briand et al., 2015).

Some OM sources displayed spatial and/or seasonal significant differences in their isotopic ratios, mainly river POM and water hyacinth. The freshwater masses are related to seasonal changes in hydrological regime, from a hot and wet season (December to April) towards a fresh and dry season (July to September), and thus might have contrasted isotopic characteristics during these two seasons. As proposed by Abrantes et al. (2015), it can be suggested that ^{13}C-enriched values for river POM in August (dry season) reflected a possible higher influence of material issued from C4 terrestrial plants that usually have higher $\delta^{13}C$ values compared with C3 plants. The case of water hyacinth still requires explanation. Although we do not have clear supporting data, we

Fig. 3. Relative importance of river POM, marine POM, *Avicennia*, *Bruguiera* and *Rhizophora* in the isotopic composition of mouth SOM (left panel) and river POM, marine POM, *Avicennia*, *Bruguiera*, *Rhizophora*, water hyacinth and detritus in the isotopic composition of estuary SOM (left panel), both season pooled (A) and according to seasons, April (top) and August (down) (B). Shaded boxes represent, from dark to light grey, 50, 75 and 95% Bayesian credibility intervals.

hypothesize the following assertion: the use of nitrogen-enriched fertilizers by farmers on the watershed during the wet season (agricultural activities are dropped in post-wet season due to water scarcity) could explain the strong δ^{15}N value of the freshwater plant, mainly in April. Indeed, the hyacinth might rapidly uptake the nitrogen inputs discharged into the river through groundwater, possibly to grow faster than native local species, representing an ability consistent with its invasive nature.

Origin of isotopic composition of OM pools

The Bayesian model showed that POM and SOM pools were influenced by various inputs, for which relative contributions varied little in space and from season to season, with the noticeable exception of POM, April *vs* August (Figure 3B).

Organic matter exchanges between riverine, estuarine and marine waters have been shown in large rivers with strong mean annual flows, such as the Rhône in the Mediterranean

Table 2. Summary of the significant variations of isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of invertebrates and fish in the mangrove forest of La Foa, New Caledonia.

| Species		Factors	$\delta^{13}C$	$\delta^{15}N$
Invertebrates	*Saccostrea cucullata tuberculata*	Site	***	ns
		Site × season	**	ns
	Terebralia palustris	Season	ns	**
Fish	*Anodonstoma chacunda*	Site	**	ns
		Season	*	ns
	Gerres filamentosus	Site	***	ns
	Gerres oyena	Site	***	ns
		Season	ns	*

Analyses were run with two-way ANOVAs or Kruskal–Wallis tests: site (i.e. mid-estuary *vs* mouth) × season (April *vs* August). ns = $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

(Bautista-Vega *et al.*, 2008; Harmelin-Vivien *et al.*, 2008), and in small rivers influencing some Pacific coral reefs (Letourneur *et al.*, 2013; Briand *et al.*, 2015). In the estuarine system studied, the relative roles of marine and river POM appeared negligible to highly dominant, depending on the site (i.e. mid-estuary or mouth) and season. However, our model is based on only two potential sources, and we cannot exclude the possibility that other sources and/or compounds may influence POM. For instance, we did not focus on mangrove root epiphytes because they were apparently not present at the sites studied, but this could be due to strong water turbidity preventing us from determining the presence or absence of such epiphytes. In addition, degradation of water hyacinth fragments emerging during low tides among mangrove roots might produce specific compounds that we were not able to take into account.

Regarding SOM, both potential sources constituted by water hyacinth and detritus were missing at the mouth site, preventing a rigorous comparison and a relevant interpretation of the relative influences of various sources between sites. However, it clearly appears that all OM sources present in both sites have an influence on SOM composition and that none of them strongly dominate, as the relative contributions fluctuated from ~7–20% in the estuary site and from ~14–24% in the mouth site. POM is known as a significant contributor to SOM, through sedimentation of dead phytoplankton and particulate matter (Letourneur *et al.*, 2013; Briand *et al.*, 2015). In New Caledonia, the residence time of marine waters on coastal sites can reach 3 months (Jouon *et al.*, 2006) and may explain the relative importance of marine POM in estuarine SOM isotopic composition. The residence time of estuarine waters (mouth or mid-estuary sites) at least partly depends on coastal characteristics and the circulation of water masses, and thus may explain the relatively high OM exchanges between mouth and estuary sites. The three mangrove species all demonstrated an equal contribution to SOM isotopic composition in both sites, probably through fragmentation, decomposition and incorporation of their leaves into sedimentary material. The relatively high contribution of macrophyte-derived OM to SOM might be a result of the integrative nature of this pool. On the contrary, POM is a much more highly variable pool. If water hyacinth is not directly consumed, detritus may accumulate in the
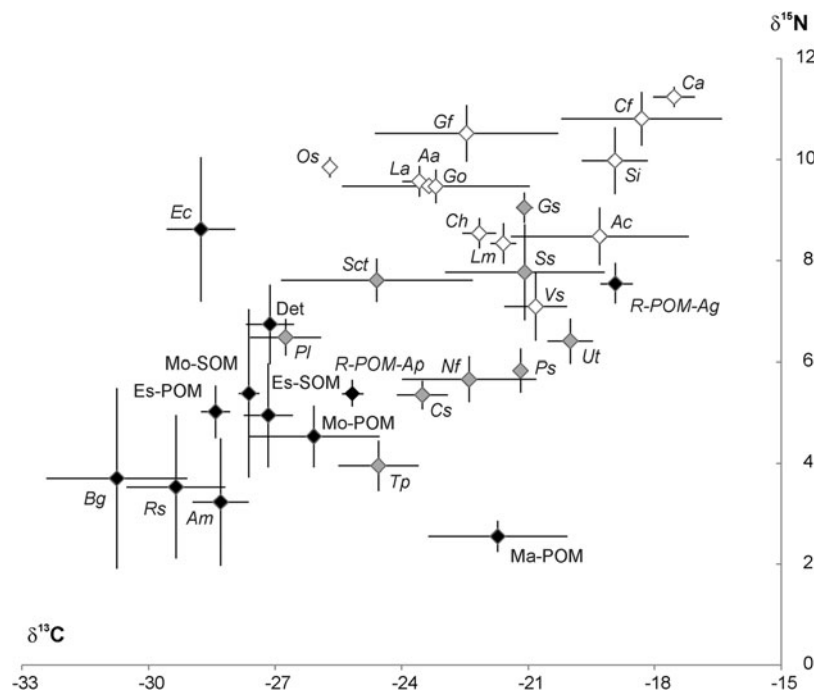
Fig. 4. Plot of $\delta^{13}C$ *vs* $\delta^{15}N$ (mean ± SD) of various compartments and taxa in the mangrove forest of La Foa. Codes of OM sources (black spots): Ma-POM, marine POM; Es-POM, estuary POM; Mo-POM, mouth POM; R-POM-Ap, river POM in April; R-POM-Ag, river POM in August; Det, Detritus; Es-SOM, estuary SOM; Mo-SOM, mouth SOM; Ec, *Eichornia crassipes*; Bg, *Bruguiera gymnorhiza*; Rs, *Rhizophora stylosa*; Am, *Avicennia marina*. Codes of invertebrates (grey spots): Sct, *Saccostrea cucullata tuberculata*; Tp, *Terebralia palustris*; Nf, *Neosarmatium* cf. *fourmanoiri*; Pl, *Perisesarma* cf. *lividum*; Ss, *Scylla serrata*; Ut, *Uca tetragodon*; Ps, *Pinctada* sp.; Cs, *Clibanarius* sp.; Gs, *Gonodactylus* sp. Codes of fish (white spots): Aa, *Acanthopagrus akazakii*; Ac, *Anodonstoma chacunda*; Ch, *Chelon* sp.; Gf, *Gerres filamentosus*; Go, *Gerres oyena*; Lm, *Liza macrolepis*; La, *Lutjanus argentimaculatus*; Vs, *Valamugil* sp.; Os, *Oxyurichthys* sp.; Ca, *Caranx* sp.; Cf, *Carangoides fulvoguttatus*; Si, *Sillago sahama*.

sediment. Such a conclusion, and the different time-resolution of POM and SOM, was reached by Cresson *et al.* (2012). Surprisingly, river POM was the lowest contributor to estuary SOM (∼7%), whereas the riverine water hyacinth and detritus were the highest (∼20%). This is possibly related to the low average river flow (from ∼ 0.3 to ∼ 1.4 m³ s⁻¹ in 'normal' years, Brunel, 1979) transporting relatively little particulate organic matter. Huge changes may nevertheless occur during sporadic and violent rainy episodes such as hurricanes and, at least over a short period of time, OM derived from freshwater flow (i.e. river POM, terrestrial detritus and plants, human waste etc.) may become a major contributor to the system (Abrantes & Sheaves, 2010). As we did not find the invasive water hyacinth in the mouth site, there is probably a rapid degradation and incorporation of fragments into detritus and sediments in the mid-estuary site. However, we cannot exclude that the water hyacinth influences SOM in the mouth site during strong rainy events, when the river flow peaks and transports river plants towards the mouth and even into the lagoon.

Use of OM by consumers

The 'semi-quantitative' picture of this estuarine food web allowed us to identify a number of features. One interesting point concerned the difference in $\delta^{15}N$ signature values between OM sources and species having the highest $\delta^{15}N$ ratios: approximately equal to 8.5 (see Figure 4). This difference broadly suggests, based on a commonly used average N-enrichment of 3.4‰ between two consecutive trophic levels (Post, 2002), that the food web studied comprised three trophic levels, i.e. two trophic steps. If we adopt the N-enrichment of 3‰ as proposed by Abrantes & Sheaves (2009) in an Australian mangrove, we then obtain a different picture, with a food web broadly comprising four trophic levels, i.e. three trophic steps. It remains, however, difficult to be certain that this studied food web has three (or four) trophic levels, because most species probably have opportunistic feeding behaviour and may consume primary producers as well as primary consumers in some cases, or may predate on primary and secondary consumers for some top predators, such as carangids or gerrids in this case. The relative trophic position of various carnivorous fish may suggest another picture. Indeed, carangids and to a lesser extent *Sillago* sp. apparently mostly depend on marine POM as a main source of OM, possibly with river POM. In such a case, the number of trophic levels might be four. If we are now looking at gerrids, plus *Lutjanus argentimaculatus* or *Acanthopagrus akazakii*, the difference in $\delta^{15}N$ values between OM sources (estuarine POM and SOM) and fish is lower and approximately equal to 6 (see Figure 4), suggesting only three trophic levels. Overall, the trophic networks in that estuarine mangrove appeared to present at least two major pathways of OM from sources to end-members, i.e. estuarine SOM and POM to gerrids, and marine POM to carrangids. Food chain lengths may also change with the season, possibly due to seasonal differences in fish species, densities and/or biomass composing the community, as observed in a Senegalese estuarine mangrove (Faye *et al.*, 2011).

Two OM sources, i.e. mangroves species and water hyacinth, were little directly used by organisms constituting the food web studied, although they indirectly enter the food web through OM pools (see above). The link with estuarine (mouth and mid-estuary) POM and SOM, detritus, *Avicennia*, *Bruggeria* or *Rhizophora* derived OM was not obvious for several consumer species, such as *Terebralia palustris*, hermit crabs *Clibanarius* sp., *Uca tetragodon*, *Anodonstoma chacunda* and carangids, among others. The position of those species in the reconstructed food web suggests that a potential important OM source could be missing: an OM source having more or less similar nitrogen signatures but characterized by less C-depleted signatures (around −25 to −22‰; see potential position on Figure 4). Microphytobenthos is a serious candidate, considering in particular the feeding behaviour of the mollusc *Terebralia palustris*, hermit crabs or the crab *Uca tetragodon*. This hypothesis is reinforced by studies from Australia (Abrantes & Sheaves, 2009) and Senegal (Faye *et al.*, 2011) highlighting the importance of this OM source. In a Mexican mangrove, Sepúlveda-Lozada *et al.* (2015) have found that consumers mostly depend on phytoplankton, macroalgae and OM derived from seagrass. The two latter potential sources are not present in the area studied, thus underlining the obvious role of local characteristics for understanding the food web structure. To some degree, phytoplankton can be broadly compared to POM (see Materials and methods section), and thus our results reinforce the role of POM as an important OM source that structures food webs in mangroves, although marine-, river- and estuarine-POM have different relative importance in such food webs.

The position of *Pinctada* sp. within the trophic network suggested the use of marine POM rather than river POM. This could also be due to bivalve abilities to sort out and exclude riverine derived matter of poor nutritional quality, an hypothesis already pointed out in a different marine context (Dubois & Colombo, 2014). On the other hand, the consumption of one source may not always be driven by its relative importance in the system, but also by biological variables such as nutritional interest, for instance. Such a process might partly explain the surprising position of *Anodonstoma chacunda* that did not support a use of detritus, usually considered to be its main food.

The place of top predators, i.e. *Caranx* sp. and *Carangoides fulvoguttatus*, in the mangrove system fitted well with the known average diet of these species on coral reefs: 88% fish, 4% crabs and 8% shrimps for *C. fulvoguttatus*, and ∼66% fish, ∼22% crabs and ∼12% shrimps for *Caranx* spp. (Kulbicki *et al.*, 2005). However, these fish are potentially highly mobile species and it is thus still unclear whether these fish move from mangroves to coral reefs, or whether they spend most of their time within the estuary or close to its mouth. Other fish species (and possibly some invertebrates) sampled in this study have the potential to move in or out of the estuary seasonally or even for short-term periods (days or weeks) from or towards adjacent ecosystems. Thus it is not surprising that the position of some species on the reconstructed food webs remains partly unclear as it integrated such movements and the possible use of OM sources belonging to these adjacent ecosystems.

CONCLUSION

Several important points about food webs in a New Caledonian mangrove forest have been made in this study, despite

its non-exhaustive view on the environment. Inputs of terrestrial material as well as marine influence were demonstrated, with important seasonal variations of river POM *vs* marine POM influence probably due to overall low freshwater flow particularly during the dry season and long seawater residence time (i.e. slow renewal), respectively. The importance of both POM and SOM pools of various origins as key sources of OM driving the food webs was shown. The role of mangrove species appeared indirect, i.e. through integration within SOM, as we found no evidence for its direct consumption by invertebrates or fish. An additional likely missing source of OM, i.e. microphytobenthos, was also suggested thus calling for future investigation.

Overall, most of the invertebrates and fish studied, from primary consumers to top predators, fitted well with the 'semi-quantitative' picture of the reconstructed food web, although some questions arose in certain cases. It is also clear that a better knowledge of feeding, behavioural and/or home-range characteristics of each species at the spatial scale studied would greatly improve our understanding of the functioning of this mangrove forest.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/S0025315417001412.

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