Trophic opportunism of central Amazon floodplain fish

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SUMMARY

1. The food web of the central Amazon basin displays one of the largest discrepancies in food source utilisation versus availability for consumers. While C₄ macrophytes dominate the primary producing biomass in floodplains, the food web is dominated by the use of C₃ carbon sources. Amazon fish species have wide-ranging diets and show feeding flexibility in response to spatial and temporal patterns in food source availability. Fish are therefore expected to use a range of available resources. Fatty acids and stable carbon and nitrogen isotopic compositions were studied to investigate their trophic behaviour and provide a better assessment of food source utilisation by nine fish species from two Amazon floodplains.

2. Although nitrogen stable isotopes positioned detritivores at the base of the food chain, their large proportions of polyunsaturated fatty acids (FAs) suggest selection of a high-quality food source, such as microalgae. Omnivores and insectivores displayed a wide range of food source utilisation, indicating opportunist feeding behaviour. Piscivores displayed the most ¹⁵N-enriched signature (up to 10.6‰), concomitant with their predator position in the studied food web.

3. C₃ carbon was the dominant source for most species, which is a finding consistent with current classical knowledge. However, consumption of C₄ macrophytes was detected for the herbivore Schizodon fasciatus, in line with the spatial availability of this food source in the floodplain system. Large amounts of polyunsaturated and essential FAs in these C₄ macrophytes indicate their high nutritive value. Our results suggest that this food source is rather neglected by fish due to low digestibility, with the exception of the herbivore that may possess modification of its digestive system that allows the use of C₄ plants.

Keywords: Amazon, fatty acids, fish, floodplains, stable isotopes

Introduction

Primary production is considered a main structuring factor of food webs in aquatic systems. Both terrestrial and aquatic sources of production are involved. However, the relationship between source production and use by consumers is not always clear. Evaluation of organic matter (OM) sources and transfer pathways through the food web is essential to understand ecosystem functioning. Fish production results from a series of transformations of organic carbon through the food web, beginning with carbon dioxide fixation by primary producers, such as plants and phytoplankton (Forsberg et al., 1993).

In the Amazon system, primary production is dominated by aquatic macrophytes (52–64%), followed by flooded forest trees (28–32%), periphyton (5–8%) and phytoplankton (2–8%) (Junk, 1985; Melack et al., 1999). Among macrophytes, the perennial grasses Echinochloa polystachya, Paspalum fasciculatum and Paspalum repens can reach cumulative biomasses of 160 t ha⁻¹ (Piedade, Junk & Long, 1991; Junk & Piedade, 1993). These species, which convert carbon dioxide into
biodiversity through a C₄ pathway, can form floating meadows (Junk & Howard-Williams, 1984) in which macrophytes using the C₃ photosynthetic pathway, such as *Eichhornia* sp., *Pistia stratiotes* and *Salvinia auriculata*, are also found. However, the total biomass of C₃ macrophytes is lower than that of C₄ plants (3 to 15 t ha⁻¹; Furch & Junk, 1992). If ecosystem functioning involved consumption of the most available source of carbon, a dominant contribution of C₃ aquatic macrophytes to the organic matter of upper trophic levels would be expected. However, various studies characterising the food web of Amazon floodplains have reported a dominance of C₃ carbon sources, including macrophytes, microalgae and trees (Araujo-Lima et al., 1986; Forsberg et al., 1993; Oliveira et al., 2006). Moreover, recent studies suggest a stronger than expected contribution of phytoplankton to particulate organic matter (POM) primary production in the central Amazon *Várzea* (Mortillaro et al., 2011). There remains, therefore, uncertainties about the fate of the C₄ carbon in the Amazon ecosystem, which might relate to neglect by consumers, although some studies have suggested that bacterial degradation could be the main driver (Quay et al., 1992; Marshall, Forsberg & Thome-Souza, 2008; J. M. Mortillaro unpubl. data).

In the central Amazon basin, many studies use carbon stable isotopes (SI, δ¹³C) to determine fish autotrophic food sources (Araujo-Lima et al., 1986; Forsberg et al., 1993; Benedito-Cecílio & Araujo-Lima, 2002; Oliveira et al., 2006; Marshall et al., 2008). Carbon isotopic ratios can be useful in distinguishing terrestrial from aquatic producers. Isotopic signatures are not always easy to distinguish in freshwater ecosystems, however, particularly when organisms receive OM contributions from various origins, such as phytoplankton or aquatic, semi-aquatic and terrestrial C₃ primary producers (Hedges et al., 1986; Townsend-Small, McClain & Brandes, 2005). Thus, studies in freshwater ecosystems often use both SI and fatty acids (FAs; Canuel et al., 1995; Alfaro et al., 2006). FAs are carbon-rich compounds ubiquitous in all organisms and relatively easy to metabolise and store (Alfaro et al., 2006). Some FAs are only biosynthesised by specific organisms and transferred without modification from primary producers towards higher trophic levels (Parrish et al., 2000; Dalsgaard et al., 2003). Thus, according to the tissue analysed, FAs may provide taxonomic information (Kwetegyeka et al., 2011) or may help characterise food sources and quality within trophic webs (Ahlgren et al., 1994; Koussoroplis et al., 2011).

In the Amazon basin, food source production is modulated by the hydrological cycle and local inputs (e.g. water, OM, nutrients) result from landscape variations (i.e. upland basin area, maximum floodable area and vegetation cover; Junk, 1997). Also, due to the large variability and ephemeral character of habitats and resources of riverine ecosystems, fish species are generally considered as mostly opportunistic in their feeding habits (Lowe-McConnell, 1987; Araujo-Lima, Agostinho & Fabre, 1995; Mérona & Mérone, 2004). Within this context, the objectives of this study were to provide an assessment of food sources for nine fish species, as well as spatial variations in their utilisation. FAs and SI (δ¹³C, δ¹⁵N) compositions of fish were compared in order to depict the trophic structure and function of two Amazon floodplains and to evaluate the fate of the C₄ carbon in upper trophic levels.

**Methods**

**Study sites**

Samples were collected in two central Amazon floodplains, Cabaiá and Janauacá, adjacent to the Solimões River, near the confluence of the Solimões and Negro rivers, upstream of Manaus city (Fig. 1a). These floodplains are mainly supplied by white water from the Solimões River, which is characterised by high concentrations of sedimentary material and dissolved and POM (Sioli, 1984). A large diversity of vegetation typical of the central Amazon floodplain, including flooded forest and shrubs, floating macrophytes and phytoplankton in open waters, is present in these floodplains (Hess et al., 2003). Two sampling programmes occurred during a similar hydrological period: the beginning of the low water period (c. 4 months after the flood peak) in October 2009 and during the period of falling water level (c. 3 months after the flood peak) in August 2010 (Fig. 1b, Table 1).

**Sampling**

Fish were captured using 2.5 m by 25 m gillnets with a wide range of mesh size (20, 25, 30, 35, 40 and 50 mm). Major habitats of each floodplain were sampled, including open waters, non-vegetated banks, floating meadows and flooded forests. Gillnets were left fishing perpendicular to the bank for 2 h in the evening (17:00–19:00 hours) and for 2 h in the morning (5:00–7:00 hours). Captured fish were immediately identified to the species level, and non-selected living fish were returned to the water. For selected individuals, fish were sacrificed rapidly after capture to minimise suffering.
Fish were photographed and measured (standard length), and a 3 to 5 g of antero-dorsal muscle was sampled. Nine fish species were selected, based on the frequency of capture. According to the literature, five dietary groups are found in the nine selected species (Table 2): detritivores, herbivores, insectivores, omnivores and piscivores. Trophic groups used in this study represent general tendencies and not strict diets based exclusively on one food source. Differences in diet are commonly observed according to developmental stage and fish size (Merigoux & Ponton, 1998). Consequently, for each species, only large adult individuals were selected.

Potential food sources were also sampled, including POM (Whatman GF/F filters burned at 450 °C for 12 h), surface sediments, plankton net contents (63 μm mesh size) and aquatic macrophytes.

### Samples analysis

Fish and food source samples were immediately frozen and freeze-dried after collection for FA and SI analyses. FA composition of samples was obtained according to a modification of the method of Bligh & Dyer (1959) previously described in Mortillaro et al. (2011). FA analyses were performed in the Resaqua Laboratory (MNHN, Paris), using gas chromatography coupled either to a flame ionisation detector (Varian GC 3800CP, Varian, Inc., Walnut Creek, California, USA) or a mass spectrometer (Varian 200MS, Varian, Inc., Walnut Creek, California, USA). Carbon (δ¹³C, ¹³C/¹²C) and nitrogen (δ¹⁵N, ¹⁵N/¹⁴N) isotopic ratios were calculated in parts per thousand (‰) in relation to an international standard (Vienna PeeDee Belemnite for δ¹³C and atmospheric nitrogen for δ¹⁵N; Peterson & Fry, 1987). Isotopic results were determined at the Davis Stable Isotope Facility, U.S.A., using a Europe Hydra 20/20 spectrometer. Nylon (G-11, n = 59, SD = 0.058 and 0.131 for δ¹³C and δ¹⁵N, respectively), enriched glutamic acid (G-12, n = 8, SD = 0.212 and 0.297 for δ¹³C and δ¹⁵N, respectively), bovine liver (G-13, n = 4, SD = 0.164 and 0.07 for δ¹³C and δ¹⁵N, respectively), peach leaves (G-7, n = 32, SD = 0.119 and 0.131 for δ¹³C and δ¹⁵N, respectively) and non-enriched glutamic acid (G-9, n = 2, SD = 0.012 and 0.3 for δ¹³C and δ¹⁵N, respectively) were used as internal isotope standards.

### Data analysis

The FA composition and isotopic signatures of fish species were compared by species and trophic groups to highlight spatial variations (differences between the two floodplains).

All identified FAs were used in these analyses without transformation, and individual FAs are represented by their relative proportions. Dissimilarity in FA composition (%) between two individuals was evaluated using the Bray–Curtis coefficient. A dissimilarity matrix between each pair of individuals was created and used as a basis to evaluate the statistical differences in FA composition.
proportions. Distances between individuals were graphically represented using nMDS (non-metric multidimensional scaling; Zuur, Ieno & Smith, 2007). Between-group differences were analysed with similarity tests (ANOSIM, with 5000 permutations; Oksanen et al., 2010). When there were significant differences, a similarity tests (ANOSIM, with 5000 permutations; Oksanen et al., 2010) was used to determine the relative contribution of each FA to between-groups differences.

The differences in δ\(^{13}\)C and δ\(^{15}\)N isotopic signatures between species (n = 9) and floodplains (n = 2) were tested using a nonparametric Kruskal–Wallis test (KW). A nonparametric Mann–Whitney–Wilcoxon (MWW) post hoc test was then used to identify differences between independent groups, after correction following a Benjamini and Hochberg (BH) correction procedure (Benjamini & Hochberg, 1995) for multiple comparisons. All statistical analyses were implemented in the R programming environment (R Development Core Team 2010, package Vegan; Oksanen et al., 2010), with the probability α set at 0.05.

Results
Characterisation of trophic variability

Forty-five FAs were identified in the fish samples (Fig. 2), among which eight represented a cumulative contribution of 68.4 to 85.1% of the total FAs of each species. Fish species displayed significant differences in their global FA composition (ANOSIM, R = 0.55, p < 0.001). Similarity in the FA composition within trophic groups was higher than 78% (Table 3), whereas intergroup similarities ranged from 59.7 to 81.3% (Table 4). The FA composition of the frugivore *M. aureum* was dominated by 18:1\(_0\), 18:2\(_0\) and 20:4\(_0\) and had intergroup similarity (from 59.7 to 73.9%, Table 4). Differences among the other diet groups were lower, and several species from different groups could not be differentiated; for example, both herbivores *H. microlepis* and *S. fasciatus* (R = 0.12, p = 0.13) and also *H. microlepis* were indistinguishable from the piscivore *P. nattereri* (R = 0.07, p = 0.21). Moreover, no significant differences were found between *S. fasciatus* and *P. nattereri* (R = −0.03, p = 0.56), or between the omnivore *L. friderici* and the insectivore *T. angulatus* (R = 0.07, p = 0.24). Global patterns of FA composition were observed (Fig. 2, Table 3) with a stronger proportion of 20:4\(_0\) and 22:6\(_0\) in piscivores and detritivores; a stronger proportion of 18:1\(_0\) and 18:2\(_0\) in frugivores, insectivores and omnivores; and a stronger proportion of 16:1\(_0\) in detritivores and algivores. Herbivore feeding predominantly on roots (*S. fasciatus*) contained a stronger proportion of 18:3\(_0\) and 20:4\(_0\). The FA composition of the sampled food sources is summarised in Tables S1 and S2.

Carbon isotope signatures of the sampled food sources ranged from −41 to −29‰ with the exception of C\(_4\) macrophytes, which were 13C enriched (−13.1 ± 5.4‰). Food source nitrogen isotope signatures ranged between
0.5 and 6% (Fig. 3). Fish isotope signatures ranged from –37 to –21‰ for δ¹³C and 5 to 11‰ for δ¹⁵N. Detritivores and frugivores were the most ¹⁵N-depleted species and piscivores the most ¹⁵N enriched. Additionally, isotopic signatures revealed interspecific differences. The carbon isotope signature of *M. aureum* differed significantly from all other species (MWW, *p* < 0.05) except *S. fasciatus*. However, the nitrogen isotope signature of *M. aureum* was not significantly different from the omnivore and detritivores. The δ¹⁵N signature from two detritivores, *S. insignis* and *P. multiradiatus*, was significantly different from all other species (except *L. friderici*). However, the carbon isotope signatures of both detritivores were not significantly different from other species (*p* > 0.05), with the exception of *H. microlepis* (*p* = 0.04, *P. multiradiatus* and *H. microlepis*). The algivore, *H. microlepis*, also displayed significant differences in δ¹³C from other species (except *C. monoculus*), but only with piscivores and insectivores for δ¹⁵N. All remaining species (*C. monoculus, P. nattereri, T. angulatus, L. friderici* and *S. fasciatus*) displayed significant differences among them for δ¹⁵N, with the exception of *C. monoculus and L. friderici* (*p* > 0.05) as well as *L. friderici* and *S. fasciatus* (*p* > 0.05). However, no difference in carbon isotopic signature was found for these species.

**Spatial variability**

Significant differences were observed in FA composition between the two floodplains (ANOSIM, *R* = 0.07, *p* = 0.03). The large intragroup variability (*R* close to 0) may be a result of differences between species. A spatial difference between the two sampled floodplains was recorded for *S. fasciatus* (*R* = 0.28, *p* = 0.01, Figs 2 & 4).
and for piscivores ($R = 0.32$, $p = 0.02$, sampled in 2010). In contrast, no spatial difference was recorded for any of the other species: detritivores ($R = 0.04$, $p = 0.23$), algivores ($R = 0.43$, $p = 0.06$), frugivores ($R = 0.03$, $p = 0.29$) and insectivores ($R = -0.14$, $p = 0.70$).

The isotopic composition of fish between the two floodplains also differed significantly (Fig. 3). Spatial differences in $\delta^{13}C$ and $\delta^{15}N$ composition were observed for S. fasciatus, P. nattereri and M. aureum. In addition, M. aureum was $^{15}N$ depleted in Cabaliana in comparison with Janaucá (MWW, $p = 0.02$), and samples of S. fasciatus from Cabaliana were $^{15}N$ ($p = 0.002$) and $^{13}C$ ($p = 0.0004$, Figs 3 & 4) enriched in comparison with those from Janaucá. Furthermore, samples of P. nattereri from Cabaliana were $^{13}C$ depleted in comparison with those from Janaucá ($p = 0.04$).

**Discussion**

In the nine studied species, 45 FAs were identified, a large proportion being mono- and polyunsaturated. Mono- and polyunsaturated FAs (with the exception of the $\omega3$ series, e.g. 20:5$\omega3$ and 22:6$\omega3$) are primarily catabolised during starvation (Koven, Kissil & Tandler, 1989; Izquierdo, 1996; Rainuzzo, Reitan & Olsen, 1997), suggesting that fish in our study were not starved. Of the eight major FAs present in fish samples, six were essential fatty acids (EFAs) or EFA precursors, which cannot be synthesised by fish but must be obtained through feeding (Holman, 1998; Arts, Ackman & Holub, 2001). Additional FAs each represented less than 1% of the total, but their global diversity is in accord with other Amazon fish assemblages (Inhamuns & Franco, 2001; Inhamuns, Franco & Batista, 2009). Our aquatic ecosystem can thus be considered to be in an equilibrium state, without major limiting food resources (Wetzel, 2001). Isotopic results also correspond to the classical notion of food-web organisation. In agreement with other Amazon studies, $\delta^{15}N$ enrichment was observed among the successive trophic levels and $\delta^{13}C$ indicated a predominance of $C_3$ food sources (Forsberg et al., 1993; Oliveira et al., 2006).
Food source utilisation

The predominance of detritus in gut contents means *P. multiradiatus* is considered a detritivore (Mérona & Mérona, 2004). This species displayed one of the most $15^N$-depleted signatures (6.7 ± 0.8‰), positioning it at the base of the food chain. Similarly, *S. insignis* preferentially consumes detritus aggregates of algae and microorganisms (Goulding, Carvalho & Ferreira, 1988); its $\delta^{15}N$ signature closely resembles that of *P. multiradiatus* (6.2 ± 0.8‰). These two species usually display an affinity for C$_4$ macrophytes (*P. multiradiatus*; Araujo-Lima et al., 1986; Forsberg et al., 1993) and for phytoplankton (*S. insignis*; Araujo-Lima et al., 1986). Our isotopic composition of POM and *S. insignis* confirms a preference for phytoplankton. However, $^{13}C$-depleted signatures ($-31.8 \pm 2.3\%_{\text{oo}}$ and $-33.0 \pm 3.0\%_{\text{oo}}$ for *P. multiradiatus* and *S. insignis*, respectively) suggest that both species avoid C$_4$ macrophytes. Such $^{13}C$-depleted signatures contradict results from Forsberg et al. (1993; $-23.8\%_{\text{oo}}$ for *P. multiradiatus*), where the dietary contribution of carbon from C$_4$ macrophytes was estimated to range from 10.4 to 41.5%. Instead, our results suggest a greater contribution of microalgae to the diet of these detritivores. This finding is further supported by the greater proportion in these species of 16:1ω7, 18:1ω9 and 22:6ω3, FAs associated with cyanobacteria and microalgae in freshwater ecosystems (Napolitano, 1999; Mortillaro et al., 2011). These species do not have anatomical adaptations to filter-feed on phytoplankton (Goulding et al., 1988). Forsberg et al. (1993) assumed that OM consumed by these fish is either derived from (1) the phytoplankton layer decomposing on sediments or (2) from the selective assimilation of phytoplankton in detritus. The former hypothesis is unlikely, due to slight differences between POM and sediment isotopic compositions. The second hypothesis appears more plausible and is supported by the occurrence of morphological adaptations in the digestive system of *Prochilodus platensis*, another Neotropical detritivore (Bowen, 1983). Morphological adaptations, such as long coiled intestines, are also found in Loricariidae and presumably enhance diatom digestibility (Power, 1983). The presence of such morphological adaptations would explain the large proportion of monounsaturated and polyunsaturated FAs (16:1ω7, 18:1ω9, 18:2ω6, 20:4ω6 and 22:6ω3) in the muscles of *P. multiradiatus* when only small amounts of these FAs were recorded in the sediment of these floodplains (Mortillaro et al., 2011).

The herbivores can be divided in three subgroups. Within these subgroups, *M. aureum* has been described as feeding principally on fruits. Among fish inhabiting

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**Fig. 4** Summary of $\delta^{13}C$ composition, total fatty acid (FA) concentration (mg g$^{-1}$) and FA marker proportion in *S. fasciatus* muscles sampled in Cabaliana and Janauacá.

central Amazon Várzea, fruit feeders are common (Goulding, 1980). However, trees are not always accessible, particularly during the drought when the forest is disconnected from the lakes, and thus fruit consumption is seasonal. When fruits are inaccessible, the diet of these fish can be supplemented by plankton, detritus, macrophytes and insects (Mérona & Mérona, 2004; Oliveira et al., 2006). The 13C-enriched composition of M. aureum (−27.6 ± 0.8‰) and its strong proportions of 18:1ω9 and 18:2ω6ω9 separate this species from other herbivores, suggesting different feeding behaviour in the months preceding sampling (i.e. the flood season). The two other herbivores (H. microlepis and S. fasciatus) are believed to prefer algae and roots, respectively (Soares, Almeida & Junk, 1986; Silva, Ferreira & Deus, 2008). However, FA composition and stable isotope signatures suggest that they have similar diets. Previous gut content studies of S. fasciatus found its diet to be rich in plant remains (Mérona & Mérona, 2004; Oliveira et al., 2006) and roots (Soares et al., 1986). With large variability in the FA and δ13C isotopic compositions of this species (−30.3 ± 4.1‰), a preference for C3 and C4 macrophytes cannot be discriminated. While S. fasciatus has been described as one of the rare species capable of feeding on C4 macrophytes (Forsberg et al., 1993), large proportions of 16:1ω7, 18:1ω9 and 22:6ω3, markers of microalgae (Napolitano, 1999; Mortillaro et al., 2011), suggest that this species unintentionally feeds on macrophyte roots while focusing on microalgae and microfauna (such as Gammaridae and Oligochaeta; Bell, Ghioni & Sargent, 1994) inhabiting the floating meadows (Engle & Melack, 1993).

In a study by Mérona & Mérona (2004), gut contents of Hemiodopsis microlepis (synonym for H. microlepis) collected in Várzea do Rei, a floodplain at the junction between the Amazon and Negro rivers, were composed of 50% eggs and scales. However, various studies have described this species as an omnivore (Mérona & Mérona, 2004), algivore and detritivore (Forsberg et al., 1993; Silva et al., 2008). In the samples collected in our study, FA composition of H. microlepis was indistinguishable from those of the herbivore S. fasciatus and the piscivore P. nattereri. The isotopic signature of H. microlepis suggests a 15N-enriched diet, comparable to an omnivore’s diet. As a result, H. microlepis can be considered as an opportunist, like many other Amazon fish species, adapting its diet based on food availability.

Mérona & Mérona (2004) described L. friderici as an omnivore, with large proportions of plant remains in its gut contents. Consequently, L. friderici has also been reported to be a herbivore (Manetta, Benedetto-Cecilio & Martinelli, 2003), dependent upon environmental conditions (Albrecht & Caramaschi, 2003; Pouilly et al., 2003). Such herbivorous tendencies are supported by the 15N-depleted composition of L. friderici samples (6.8 ± 0.5‰), whose isotopic signature resembles those of detritivores and frugivores. However, similar FA composition was found in L. friderici and T. angulatus, an insectivore (Pouilly et al., 2003) or omnivore (Mérona & Mérona, 2004). Nevertheless, in contrast to L. friderici, the 15N-enriched composition of T. angulatus (8.9 ± 0.5‰) confirms it to be a secondary consumer. Also, as previously suggested for H. microlepis and L. friderici, the presence of terrestrial and aquatic insects, as well as fruits and flowers, in the gut contents of T. angulatus (Pouilly et al., 2003; Mérona & Mérona, 2004), indicates opportunist behaviour in these three species (M. Pouilly, pers. obs.).

Lastly, C. monoculus and P. nattereri have been reported to be piscivores (Pouilly et al., 2003; Mérona & Mérona, 2004). The 15N-enriched composition of C. monoculus and P. nattereri (9.2 ± 0.7 and 9.9 ± 0.4‰, respectively) places them as predators in the studied food web. Polyunsaturated FA composition and δ13C signatures of these fish resemble those of detritivores. Strong proportions of 20:4ω6 and 22:6ω3 were also observed for C. monoculus by Inhamuns et al. (2009). Assuming a δ15N trophic enrichment factor of 2.8‰ for Neotropical fish (Jepsen & Winemiller, 2007), P. multiradiatus and S. insignis, and other non-sampled species with similar isotopic signatures, may thus be considered as preferred prey for both piscivores. The pectoral spines and osseous plates of adult armoured catfish, P. multiradiatus, makes predation by C. monoculus unlikely (Nico, 2010), suggesting a stronger predation of C. monoculus on S. insignis. However, while C. monoculus is described as an exclusive piscivore (Goulding, 1980), P. nattereri may also feed on macrophytes, crabs and insects (Sazima & Machado, 1990; Pouilly et al., 2003).

**Trophic structure and functioning**

Our data confirm that the food web of the studied central Amazon Várzea is 13C depleted and mainly centred on a C3 carbon source, with δ13C composition ranging between −25‰ (−30‰ for C3 macrophytes) and −40‰ (phytoplankton). Within this pool of primary producers, C3 macrophytes are considered as the main carbon source for fish of Amazon floodplains (Oliveira et al., 2006). For species sampled in this study, SI analyses did not detect a stronger dietary contribution of C3 macrophytes than POM (>0.7 and 63 μm) or sediments. The
contribution of $C_4$ macrophytes to Amazon aquatic food webs needs to be weighted by the number of sources with similar $\delta^{13}C$ compositions (Oliveira et al., 2006). Forsberg et al. (1993) reported that $C_4$ macrophytes contributed 82.4 to 97.5% for adult fish. This discrepancy may be explained by the similar $\delta^{13}C$ compositions of terrestrial plants and periphyton pooled in the analysis by these authors. In contrast, the FA composition of species from low trophic levels, such as $S$. insignis, $P$. multi-radiatus and $H$. microlepis, indicates a stronger contribution of POM with markers characteristic of microalgal.

A weak contribution of $C_4$ macrophytes and their associated macro- and microfauna to fish diets has been previously observed (Forsberg et al., 1993; Oliveira et al., 2006). However, $C_4$ macrophytes may account for up to 65% of Várzea primary production (Melack et al., 1999) and constitute the dominant proportion of the region’s biomass (Junk & Piedade, 1997). Such differences between biomass production and utilisation in the food web have been tentatively attributed to low nutritional value, as well as lower digestibility due to strong fibres in $C_4$ macrophytes (Forsberg et al., 1993). Comparisons of the nutritional quality of $C_3$ and $C_4$ plants have produced inconsistent results (Scheirs, De Bruyn & Verhaegen, 2001), which may be due to high interspecific variability. However, in the central Amazon Várzea, FA composition of the $C_4$ P. repens displayed higher concentrations of 18:2$\omega$6 and 18:3$\omega$3 than $C_3$ macrophyte species (Mortillaro et al., 2011). Such FAs, along with overall polyunsaturated FAs, are indicators of good organic matter quality, as they are precursors of 20:4$\omega$6, 20:5$\omega$3 and 22:6$\omega$3 (Cunnane, 1996). These three FAs are essential for the metabolism and function of tissues and organs (Holman, 1998; Arts et al., 2001). In Várzea, low consumption of $C_4$ macrophytes may therefore be attributed to lower digestibility rather than lower nutritional value.

A spatial difference in food source utilisation is apparent for one species, $S$. fasciatus, in our studied food web. The $\delta^{13}C$ composition of $S$. fasciatus was enriched in Cabaliana ($-26.8 \pm 3.1\%o$) relative to Janaucacá ($-33.2 \pm 2.1\%o$). This may be due to a larger contribution of $C_4$ macrophytes to the diet of $S$. fasciatus in Cabaliana. Consumption of $C_4$ carbon by species in the genus Schizodon has been previously observed (Forsberg et al., 1993; Jepsen, 1999; Manetta et al., 2003). This spatial pattern is supported by a shift in the FA composition of $S$. fasciatus within the floodplains, with a stronger proportion of 18:2$\omega$6 and 18:3$\omega$3 in Cabaliana. Digestive enzymes, microorganisms or digestive system modifications may allow the use of $C_4$ plants, despite their low digestibility for herbivores (Caswell et al., 1973). However, among the nine studied species, only $S$. fasciatus from Cabaliana appears to feed on $C_4$ macrophytes. During the sampling period, Cabaliana had greater vegetation cover (111–464 km$^2$ for flooded forest and 26–45 km$^2$ for macrophytes) than Janauacá (1–13 km$^2$ for flooded forest and 3–7 km$^2$ for macrophytes). The higher availability of flooded or aquatic vegetation in Cabaliana may explain the larger consumption of $C_4$ macrophytes. Therefore, the use of this carbon source may be associated with both particular environmental conditions and availability. In addition, greater total FA concentration in $S$. fasciatus muscles from Cabaliana suggests that these fish have a higher fat content. This finding corroborates the selection by $S$. fasciatus of $C_4$ macrophytes, as they have high nutritional value and are widely available.

Within the Amazon Várzea system, oscillation of the hydrological cycle leads to spatial and temporal variability in trophic resources (Junk, 1997), necessitating species adaptability and flexibility in diet and habitat. Species consuming seasonal resources are thought to adopt the strategy ‘half a loaf is better than none’. Observations confirm the use of this strategy, as species adapt their feeding behaviours during food shortages by increasing animal food consumption (e.g. fish and invertebrates for omnivores and insectivores species; Soares et al., 1986; Wantzen et al., 2002; Ménora & Mérona, 2004). Other species, such as $S$. fasciatus, focus on neglected food sources, such as $C_4$ macrophytes, which predominate in terms of biomass. The paradox of low $C_4$ macrophyte consumption in the Amazon food web, however, remains largely unexplained. Our results indicate that digestibility rather than nutritional value may explain their low contribution to aquatic food webs. However, further investigation is needed to explain the fate of this predominant resource. While digestibility may be the main reason for underuse, nothing yet explains why these macrophytes are not integrated in the food web after degradation. We suggest that degradation experiments be implemented to understand the processes behind this discrepancy.

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Table S1.** FAs composition of leaves and roots of 4 macrophytes species.

**Table S2.** FAs composition of POM (>0.7 and 63 $\mu$m) and sediment samples.

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