

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

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biomass through a C₄ pathway, can form floating meadows (Junk & Howard-Williams, 1984) in which macrophytes using the C₃ photosynthetic pathway, such as *Eichornia* 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 C₄ 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-Cecilio & 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 & Mérona, 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, Cabaliana 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

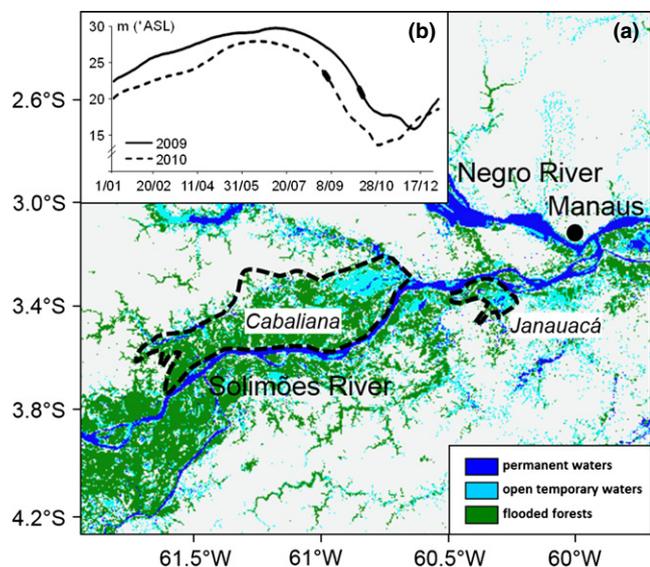


Fig. 1 (a) Sampling sites on the Solimões River upstream of Manaus city (Brazil). Dashed lines delineate the Cabaliana and Janauacá floodplains (Abril *et al.*, 2014). (b) Hydrograph at the Manaus gauging station of the Amazon River. Solid line is for the 2009 hydrograph and dashed line for 2010, with bold areas highlighting the sampling periods.

Table 1 Surface and proportional area of floodplain vegetation in Cabaliana and Janauacá during October 2009 and August 2010 (Abril *et al.*, 2014)

Surface in km ²	Cabaliana (%)	Janauacá (%)
Low water, October 2009		
Open waters	139 (50.4)	48 (92.3)
Flooded forest	111 (40.2)	1 (1.9)
Floating vegetation	26 (9.4)	3 (5.8)
Total floodplain	276	52
Falling water, August–September 2010		
Open waters	210 (29.2)	62 (75.6)
Flooded forest	464 (64.5)	13 (15.9)
Floating vegetation	45 (6.3)	7 (8.5)
Total floodplain	719	82

(by stunning or freezing). Fish were photographed and measured (standard length), and a 3 to 5 g of anterodorsal 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. The herbivores were separated into three subgroups: consuming mainly algae, mainly macrophytes or mainly fruits. 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 ($\delta^{13}\text{C}$, $^{13}\text{C}/^{12}\text{C}$) and nitrogen ($\delta^{15}\text{N}$, $^{15}\text{N}/^{14}\text{N}$) isotopic ratios were calculated in parts per thousand (‰) in relation to an international standard (Vienna PeeDee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$; 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), enriched glutamic acid (G-12, $n = 8$, SD = 0.212 and 0.297 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), bovine liver (G-13, $n = 4$, SD = 0.164 and 0.07 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), peach leaves (G-7, $n = 32$, SD = 0.119 and 0.131 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) and non-enriched glutamic acid (G-9, $n = 2$, SD = 0.012 and 0.3 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, 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

Table 2 Classification and trophic groups of the nine fish species sampled

Order	Family	Species	Common name (Brazil)	N	Size range (mm)	Trophic group	Reference
Silur	Loricariidae	<i>Pterygoplichthys multiradiatus</i>	Bodó	11	225–363	Detritivore	Mérona & Mérona (2004)
Chara	Prochilodontidae	<i>Semaprochilodus insignis</i>	Jaraqui	9	150–180	Detritivore	Benedito-Cecilio & Araujo-Lima (2002)
Chara	Hemiodontidae	<i>Hemiodus microlepis</i>	Orana	7	160–220	Herbivore (algae)	Silva <i>et al.</i> (2008)
Chara	Characidae–Serrasalminae	<i>Mylossoma aureum</i>	Pacu	12	122–180	Herbivore (fruits)	Mérona & Mérona (2004)
Chara	Anostomidae	<i>Schizodon fasciatus</i>	Aracu	20	190–283	Herbivore (roots)	Soares <i>et al.</i> (1986)
Chara	Characidae–Triportheinae	<i>Triportheus angulatus</i>	Sardinha	8	155–180	Insectivore	Yamamoto, Soares & Freitas (2004)
Chara	Anostomidae	<i>Leporinus friderici</i>	Aracu cabeça gorda	5	155–230	Omnivore	Goulding (1980)
Chara	Characidae–Serrasalminae	<i>Pygocentrus nattereri</i>	Piranha	11	130–145	Piscivore	Mérona & Mérona (2004)
Perci	Cichlidae	<i>Cichla monoculus</i>	Tucunare	8	155–320	Piscivore	Oliveira <i>et al.</i> (2006)

Silur, Siluriformes; Chara, Characiformes; Perci, Perciformes.

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 of percentage analysis (SIMPER; Oksanen *et al.*, 2010) was used to determine the relative contribution of each FA to between-groups differences.

The differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 ω 9, 18:2 ω 6 and 20:0 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 ω 6 and 22:6 ω 3 in piscivores and detritivores; a stronger proportion of 18:1 ω 9 and 18:2 ω 6 in frugivores, insectivores and omnivores; and a stronger proportion of 16:1 ω 7 in detritivores and algivores. Herbivore feeding predominantly on roots (*S. fasciatus*) contained a stronger proportion of 18:3 ω 3 and 20:4 ω 6. 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 ^{13}C enriched ($-13.1 \pm 5.4\text{‰}$). Food source nitrogen isotope signatures ranged between

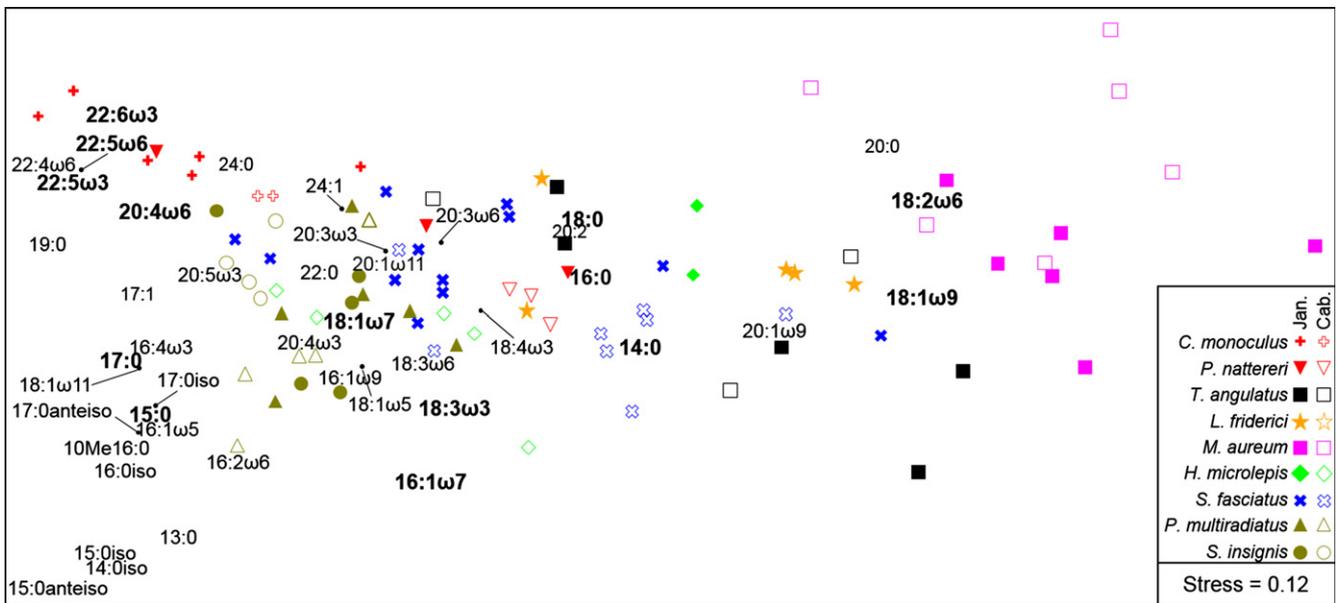


Fig. 2 Non-metric MDS of individual fatty acid (FA) proportion (%) in fish with different diets. Each point represents a sample collected in Janauacá (Jan., filled symbol) or Cabaliana (Cab., open symbol), with piscivores in red, insectivores in black, omnivores in orange, detritivores in brown and herbivores (fruits – pink; algae – green; roots – blue). FAs in bold displayed an average proportion greater than 1% of total FAs.

Table 3 Summary of SIMPER procedure for mean fatty acid compositions and intragroup similarity for each trophic group

Trophic group (intragroup similarity)	16:0	18:0	16:1 ω 7	18:1 ω 9	18:2 ω 6	18:3 ω 3	20:4 ω 6	22:6 ω 3	Σ (%)
Detritivores (85.6%)	22.3	10.5	5.9	9.9	4.4	2.2	8.1	5.1	68.4
Herbivore roots (82.4%)	27.6	8.8	3.1	15.3	5.3	3.7	7.2	3.7	74.7
Herbivore fruits (78.7%)	28.0	14.3	2.0	25.9	11.3	1.0	1.4	1.2	85.1
Herbivore algae (82.9%)	28.0	9.4	5.3	14.1	2.5	2.9	6.1	5.0	73.3
Insectivores (80.1%)	23.9	9.7	4.6	25.9	6.9	2.1	4.9	4.8	82.8
Omnivores (84.8%)	28.3	10.4	3.2	25.1	4.0	1.0	5.8	5.3	83.1
Piscivores (82.7%)	22.9	12.1	2.5	10.9	3.8	2.0	9.4	10.0	73.6

0.5 and 6‰ (Fig. 3). Fish isotope signatures ranged from -37 to -21 ‰ for $\delta^{13}\text{C}$ and 5 to 11‰ for $\delta^{15}\text{N}$. Detritivores and frugivores were the most ^{15}N -depleted species and piscivores the most ^{15}N 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 $\delta^{15}\text{N}$ 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 differ-

ences in $\delta^{13}\text{C}$ from other species (except *C. monoculus*), but only with piscivores and insectivores for $\delta^{15}\text{N}$. All remaining species (*C. monoculus*, *P. nattereri*, *T. angulatus*, *L. friderici* and *S. fasciatus*) displayed significant differences among them for $\delta^{15}\text{N}$, 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)

Table 4 Summary of SIMPER procedure for intergroup similarity for each trophic group

Intergroup similarity (%)	Detritivores	Herbivore-roots	Herbivore-fruits	Herbivore-algae	Insectivores	Omnivores
Herbivore-roots	78.9					
Herbivore-fruits	59.7	66.7				
Herbivore-algae	79.8	81.3	64.8			
Insectivores	73.4	76.4	73	75.8		
Omnivores	73.7	79.6	73.9	79	80.4	
Piscivores	80.4	77.1	60.7	76.9	72.4	74.5

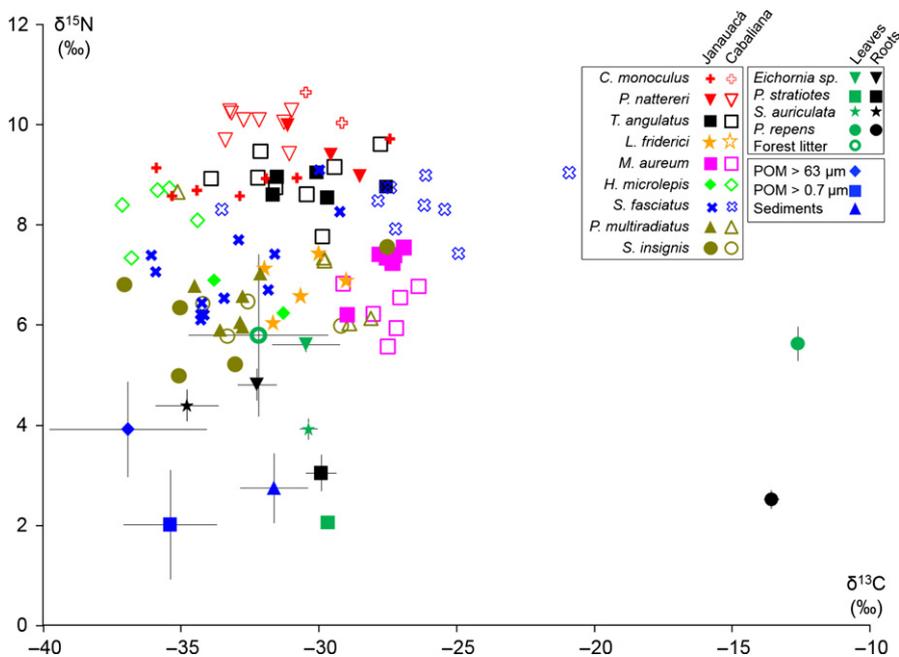


Fig. 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) biplot of sampled fish and potential food sources. For fish, each point represents a sample collected in Janauacá (filled symbol) or Cabaliana (open symbol), with piscivores in red, insectivores in black, omnivores in orange, detritivores in brown and herbivores (fruits – pink; algae – green; roots – blue). For sources, each point highlights the mean value and standard deviation from both floodplains, with leaves in green, roots in black, particulate organic matter and sediments in blue.

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition were observed for *S. fasciatus*, *P. nattereri* and *M. aureum*. In addition, *M. aureum* was ^{15}N depleted in Cabaliana in comparison with Janauacá (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 Janauacá. Furthermore, samples of *P. nattereri* from Cabaliana were ^{13}C depleted in comparison with those from Janauacá ($p = 0.04$).

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 $\omega 3$ series, e.g. 20:5 $\omega 3$ and 22:6 $\omega 3$) 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, $\delta^{15}\text{N}$ enrichment was observed among the successive trophic levels and $\delta^{13}\text{C}$ indicated a predominance of C_3 food sources (Forsberg et al., 1993; Oliveira et al., 2006).

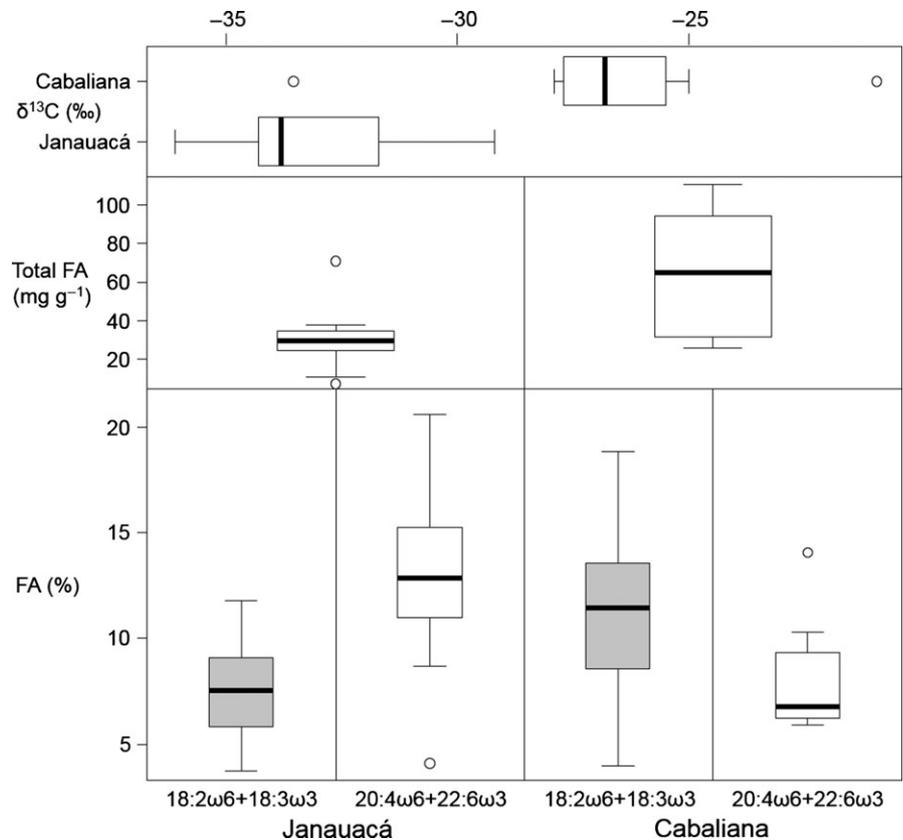


Fig. 4 Summary of $\delta^{13}\text{C}$ composition, total fatty acid (FA) concentration (mg g^{-1}) and FA marker proportion in *S. fasciatus* muscles sampled in Cabaliana and Janauacá.

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 ($6.7 \pm 0.8\text{‰}$), 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 $\delta^{15}\text{N}$ signature closely resembles that of *P. multiradiatus* ($6.2 \pm 0.8\text{‰}$). 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 ($-31.8 \pm 2.3\text{‰}$ and $-33.0 \pm 3.0\text{‰}$ 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‰ 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 16:1 ω 7, 18:1 ω 9 and 22:6 ω 3, 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 (16:1 ω 7, 18:1 ω 9, 18:2 ω 6, 20:4 ω 6 and 22:6 ω 3) 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

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 ^{13}C -enriched composition of *M. aureum* ($-27.6 \pm 0.8\text{‰}$) and its strong proportions of 18:1 ω 9 and 18:2 ω 6 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 $\delta^{13}\text{C}$ isotopic compositions of this species ($-30.3 \pm 4.1\text{‰}$), a preference for C_3 and C_4 macrophytes cannot be discriminated. While *S. fasciatus* has been described as one of the rare species capable of feeding on C_4 macrophytes (Forsberg *et al.*, 1993), large proportions of 16:1 ω 7, 18:1 ω 9 and 22:6 ω 3, 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 ^{15}N -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 of 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, Benedito-Cecilio &

Martinelli, 2003), dependent upon environmental conditions (Albrecht & Caramaschi, 2003; Pouilly *et al.*, 2003). Such herbivorous tendencies are supported by the ^{15}N -depleted composition of *L. friderici* samples ($6.8 \pm 0.5\text{‰}$), 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 ^{15}N -enriched composition of *T. angulatus* ($8.9 \pm 0.5\text{‰}$) 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 ^{15}N -enriched composition of *C. monoculus* and *P. nattereri* (9.2 ± 0.7 and $9.9 \pm 0.4\text{‰}$, respectively) places them as predators in the studied food web. Polyunsaturated FA composition and $\delta^{13}\text{C}$ signatures of these fish resemble those of detritivores. Strong proportions of 20:4 ω 6 and 22:6 ω 3 were also observed for *C. monoculus* by Inhamuns *et al.* (2009). Assuming a $\delta^{15}\text{N}$ 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 ^{13}C depleted and mainly centred on a C_3 carbon source, with $\delta^{13}\text{C}$ composition ranging between -25‰ (-30‰ for C_3 macrophytes) and -40‰ (phytoplankton). Within this pool of primary producers, C_3 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 C_3 macrophytes than POM (>0.7 and $63 \mu\text{m}$) or sediments. The

contribution of C₃ macrophytes to Amazon aquatic food webs needs to be weighted by the number of sources with similar $\delta^{13}\text{C}$ compositions (Oliveira *et al.*, 2006). Forsberg *et al.* (1993) reported that C₃ macrophytes contributed 82.4 to 97.5 % for adult fish. This discrepancy may be explained by the similar $\delta^{13}\text{C}$ 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 microalgae.

A weak contribution of C₄ macrophytes and their associated macro- and microfauna to fish diets has been previously observed (Forsberg *et al.*, 1993; Oliveira *et al.*, 2006). However, C₄ 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 C₄ macrophytes (Forsberg *et al.*, 1993). Comparisons of the nutritional quality of C₃ and C₄ plants have produced inconsistent results (Scheirs, De Bruyn & Verhagen, 2001), which may be due to high interspecific variability. However, in the central Amazon *Várzea*, FA composition of the C₄ *P. repens* displayed higher concentrations of 18:2 ω 6 and 18:3 ω 3 than C₃ 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 ω 6, 20:5 ω 3 and 22:6 ω 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 C₄ 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 $\delta^{13}\text{C}$ composition of *S. fasciatus* was enriched in Cabaliana ($-26.8 \pm 3.1\text{‰}$) relative to Janauacá ($-33.2 \pm 2.1\text{‰}$). This may be due to a larger contribution of C₄ macrophytes to the diet of *S. fasciatus* in Cabaliana. Consumption of C₄ 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 ω 6 and 18:3 ω 3 in Cabaliana. Digestive enzymes, microorganisms or digestive system modifications may

allow the use of C₄ 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 C₄ macrophytes. During the sampling period, Cabaliana had greater vegetation cover (111–464 km² for flooded forest and 26–45 km² for macrophytes) than Janauacá (1–13 km² for flooded forest and 3–7 km² for macrophytes). The higher availability of flooded or aquatic vegetation in Cabaliana may explain the larger consumption of C₄ 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 C₄ 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; Mérona & Mérona, 2004). Other species, such as *S. fasciatus*, focus on neglected food sources, such as C₄ macrophytes, which predominate in terms of biomass. The paradox of low C₄ 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 μm) and sediment samples.

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