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ECOSYSTEMS

Can species guilds act as hubs for energy transfer in macrophyte meadows of Amazonian floodplain lakes?

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Abstract: Aquatic macrophytes are the main autochthonous component of primary production in the Amazon Basin. Floating meadows of these plants support habitats with highly diverse animal communities. Fishes inhabiting these habitats have been assumed to use a broad range of food items and compose a particular food web. We employed carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analysis to draw the trophic structure of these habitats and to trace the energy flow by its trophic levels. Fishes and other animals from 18 independent macrophyte meadows of a floodplain lake of the Solimões River (Amazonia, Brazil) were analyzed. The food web of macrophyte meadows consists of four trophic levels above autotrophic sources. In general, primary consumers exhibited a broader range of food sources than the upper trophic levels. Some fish species depended on a large number of food sources and at the same time are consumed by several predators. The energy transfer from one trophic level to the next was then mainly accomplished by these species concentrating a high-energy flux and acting as hubs in the food web. The broad range of δ^{13}C values observed indicates that the organisms living in the macrophyte meadows utilize a great diversity of autotrophic sources.

Key words: fish, food webs, energy flow, stable isotopes, invertebrates, Amazonian floodplains.

INTRODUCTION

Aquatic macrophytes are the main component of primary production in the Amazon basin, accounting for 52-65% of the total aquatic primary production in floodplain areas (Melack & Forsberg 2001). According to Piedade et al. (2010), floating macrophytes reached a biomass of 30 t.ha^{-1} in a 9.5 month period. Considering a monthly loss of biomass by decomposition and consumption between 10 and 25%, net primary production (NPP) varies between 37-48 t.ha^{-1}. They mainly develop in whitewater floodplains, locally known as *várzea*, which are supplied with nutrients by the rivers draining the Andean and pre-Andean areas of the Western Amazon (Sioli 1984, Meade et al. 1985, Junk et al. 2011). While more than 100 species of aquatic macrophytes are found in the Amazon basin (Junk & Piedade 1997), less than 10 species are dominant in floodplain lakes. The most abundant grasses *Echinochloa polystachya, Paspalum repens* and *P. fasciculatum,* all following a C$_4$ pathway to convert carbon dioxide into biomass, produce a biomass of up to 160 t.ha^{-1} (Junk

& Howard-Williams 1984). Species such as *Ludwigia elegans*, *L. helminthorrhiza* and *Pistia estratiotes* utilizing a C_3 pathway are less abundant, with a total production yielding just 3 to 15 t.ha^{-1} (Furch & Junk 1992). Previous studies on Amazon have shown that while C_4 vegetation is dominant in biomass, it is poorly incorporated in the aquatic food webs in comparison to the C_3 photosynthetic plants (Araújo-Lima et al. 1986, Forsberg et al. 1993, Oliveira et al. 2006, Mortillaro et al. 2015). Nevertheless, these studies were performed on samples collected in open water and flooded forest habitats and were conducted almost exclusively on adult fish.

Located primarily in the inshore zone of the floodplain lakes, floating meadows are composed of a high density of mono- or multispecific aquatic macrophytes and support a large number of fish species and other aquatic and semi-aquatic animals (Sánchez-Botero & Araújo-Lima 2001, Petry et al. 2003, Correa et al. 2008, Sánchez-Botero et al. 2008, Prado et al. 2010, Soares et al. 2014). Fish living herein find favorable habitats for shelter (Henderson & Hamilton 1995, Araújo-Lima et al. 1986), nursery (Sánchez-Botero & Araújo-Lima 2001, Petry et al. 2003, Sánchez-Botero et al. 2008) and foraging (Casatti et al. 2003). This high fish diversity has been associated to structural complexity provided by the dominant plants (Correa et al. 2008, Sánchez-Botero et al. 2008, Dibble & Pelicice 2010). Prado et al. (2010) compared fish assemblages associated to different type of macrophyte meadow and observed a highest diversity in meadows dominated by *Paspalum* spp., which provide the highest structural complexity of roots, branches, and leaves. Dias et al. (2011) observed that the correlation between fish assemblage composition and macrophyte meadow structure is dependent on meadow size. Other studies have also documented a strong relationship between macrophyte habitat structure and fish species richness (Petry et al. 2003, Soares et al. 2014). However, we still know little about the food web structure associated with this important whitewater resource.

Traditionally, energy and organic matter flux is considered directional within food webs, moving from primary producers to herbivores, and then through a number of trophic levels containing carnivores and parasites. MacArthur (1955) proposed that the ability of a food web to persist (by a higher stability) would be higher in communities composed of many species with restricted diets. More species would represent more alternate pathways for energy transfer among trophic levels, whereas restricted diets are expected to increase transfer efficiency. Modern considerations have focused on nodes (Borer et al. 2002, Jordán et al. 2019), which are either individual species connected to their diet and predators, or groups of species within the same trophic niche (constituting a guild *sensu* Root 1967). Nodes with a higher number of connections, typified as species dependent on a large number of food sources and at the same time consumed by several predators, may be ecologically more important than those with fewer connections, as they concentrate a higher energy flux, and their loss may have disproportionate effects on the web structure as a whole (Solé & Montoya 2001). Theoretical considerations of complex systems look for whether most of the nodes of a community have about the same number of connections (exponential model), or whether they are scale-free, where most of the nodes have few links, but few nodes have many links (Albert et al. 2000). These highly connected nodes could be considered as a kind of 'hub'. If such a hub is composed of a single species, this would be analogous to the keystone species concept of Paine (1955).

Stable Isotope Analysis (SIA) is nowadays commonly used to untangle food web relationships, through the measurement of the isotopic signature of chemical elements assimilated by the consumers (especially $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$) over a period of time estimated to be 2 and 8 weeks in the case of fish muscle (Boecklen et al. 2011). However, there is no consensus on the replacement rate of white muscle tissue in freshwater fish. Some authors reported 13.9 days to 85 days for tissues to equilibrate with dietary isotopic signatures (Sacramento et al. 2016). SIA can be useful to track the basal sources of energy and matter, to estimate the trophic position of broad-ranging sources, consumers and predators (deHart & Strand 2012, Wise et al. 2006) and the food chain length (Post et al. 2000). Species isotopic composition can be included in mixing models, which could provide precise insight into the relative importance and contribution of potential sources/prey items that a consumer/predator consumes (Phillips et al. 2005, 2014, Parnell et al. 2013).

In this study, we identified the principal carbon sources used by fish and other animals inhabiting aquatic macrophytes meadows of whitewater Amazonian floodplain lakes and we estimated the main carbon pathways through the trophic food web of these habitats. We therefore identified species acting as hubs due to their highest importance on the energy flux among the food web levels.

MATERIALS AND METHODS

Study area

The study was conducted in the Central Lake of the Marchantaria Island located on the whitewater Solimões River (Amazon Basin, Brazil), 15 km upriver from the confluence with the Negro River (Fig. 1). Central Lake is a typical *várzea* lake, connected year-round with the main river channel by a narrow and short canal. During the rising, high and receding water a broad swath of macrophyte meadows, dominated by *Paspalum repens, Eichhornia crassipes* and *Echinochloa polystachya,* colonize the inshore part of the lake.

Data sampling

Samples were done in macrophyte meadows during the receding water season, from August through September 2012. Samplings were conducted daily between 0700h and 1130h, in 18 randomly selected sites of the Central Lake. Each site was isolated from surrounding open water by a purse seine measuring 20m(length) x 3m(height), and mesh size of 5mm between opposite knots. Sampling sites were at least 100m apart, and each covered a total area of approximately 10 m^2. Sampling was performed under the license 30052-1 (ICMBio – SISBIO). All material collected in the nets was transferred to the boat. Non-fish animals were identified to the lowest taxonomic level. All individuals were counted and individuals of each class (Insects, crustaceans, mollusks and other vertebrates' taxa) were frozen for SIA analyses.

Captured fish were identified to species level and counted. Living fishes were euthanized by thermal shock in a cooler with ice and water to minimize suffering. Sampled fish assemblages did not include endangered or protected species. After measurement (total length), a small part (3-5g) of the dorsal muscle of each individual was immediately frozen for SIA analyses.

At the laboratory of the Federal University of Amazonas, muscle samples were washed with sterile water and dried in an oven with air circulation at 55 °C for 24 hours. Dried samples were then finely ground and stored in plastic tubes. Samples were subsequently processed for future analyses of their stable isotope

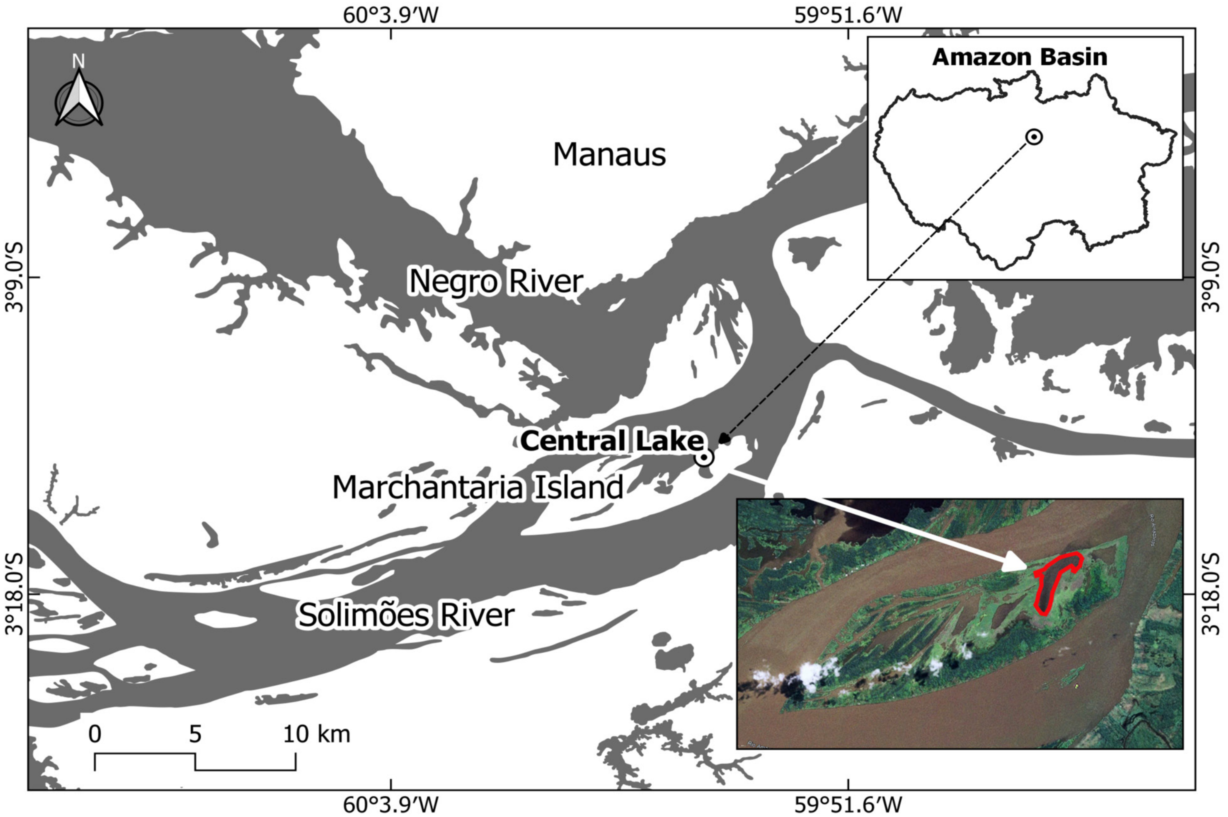

Figure 1. Map of floodplain area showing the position of the Central Lake, near the confluence between Negro and Solimões Rivers, where samplings were done.

signatures using the procedure developed at the Laboratory of the Environmental Sciences (Center of Biosciences and Biotechnology – Universidade Estadual do Norte Fluminense). The isotopic concentrations were obtained from 1 mg of the original sample using a Delta V Advantage Isotope Ratio Mass Spectrometer (Thermo Scientific, Bremen, Germany) coupled with an interface with Conflo IV linked to an Elemental Analyzer Flash 2000 (Thermo Scientific). Analytical accuracy was validated against internal laboratory standards and cross-calibrated against the Elemental Microanalysis Protein Standard and wheat flour Standard. Analytical precision was estimated at ~0.1‰ and ~0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, determined by repeated analysis of duplicates (one in ten). Stable isotope ratios were expressed as $\delta^{15}N$, or $\delta^{13}C = [(R_{sample}/R_{standard})-1] \times 1{,}000$ where *R represents* the ratio of $^{15}N/^{14}N$ and $^{13}C/^{12}C$, respectively. All measurements were expressed in parts per thousand (‰) with respect to the international reference standards. Standards used were carbonate rock from the Peedee Belemnite formation for $\delta^{13}C$ (Craig 1957) and atmospheric air for $\delta^{15}N$ (Mariotti 1983).

Data analysis

Relative individual trophic position (TP) was calculated by the formula (modified from Post et al. 2000):

$$TP = \lambda + \left(\delta^{15}N_{organism} - \delta^{15}N_{base\ of\ food\ web}\right)/Nfrac$$

Where: λ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$. It was estimated using mean $\delta^{15}N$ of the Baetidae (Insecta, Ephemeroptera) and then was set to 2.

N_{frac} is the N isotopic fractionation that occurs between each trophic level. It was set to 2.3‰ as proposed by Molina et al. (2011) for aquatic environments of the Bolivian Amazon.

Food chain length was estimated following Post (2002) with the equation: Food Chain Length = Maximum Trophic Position -1.

Taxa's mean trophic position was used to classify it in five trophic levels: plant groups (δ^{13}C: -39.69 to -11.29; and $\delta^{15}N$: -0.59 to 8.51), primary consumers (δ^{13}C: -39.45 to -11.91; and $\delta^{15}N$: 2.11 to 5.68), secondary consumers (δ^{13}C: -30.82. to -20.51; and $\delta^{15}N$: 6.51 to 8.20), tertiary consumers (δ^{13}C: -35.04 to -25.98; and $\delta^{15}N$: 8.81 to 10.31) and quaternary consumers (δ^{13}C: -35.52 to -30.33; and $\delta^{15}N$: 10.83 to 11.69). Inside each trophic level, taxa were ordered by a Linear Discriminant Analysis (LDA), using isotopic ratios δ^{13}C and $\delta^{15}N$ as response variables. Mahalanobis distance was employed as post hoc criteria to cluster species in subgroups. LDAs were performed using the package WMDB (Wu 2012) of the R Statistical Software (R Development Core Team 2012).

We ran three Bayesian mixing models using SIAR Package (Parnell et al. 2010) of the R Statistical Software (R Development Core Team 2012) in order to estimate the relative contribution of the different sources/prey in the diet of each consumer/predator. Fractionation factors were estimated as 1.0 ± 1.1‰ δ^{13}C and 2.3 ± 1.3‰ for δ^{15}N (Molina et al. 2011). Model 1 included secondary consumers as predators and primary consumers as potential prey (sources). Model 2 considered tertiary consumers as predators and secondary consumers as potential prey (sources). And Model 3 considered quaternary consumers as predators and tertiary consumers as potential prey (sources). All models unambiguously converged. The results of these models were used to estimate the carbon pathway along the food webs from autotrophic producers to top piscivorous predators. This modeling approach addresses the uncertainties inherent to biological systems, using a concomitant assessment of several potential sources.

RESULTS

Fauna of macrophyte meadows

A total of 30 species of six orders: Characiformes, Siluriformes, Perciformes, Beloniformes, Gymnotiformes and Synbranchiformes were caught in the 18 sampled sites (Table I). The dominant group was Characiformes, encompassing 48.55% of the total abundance and 17 species, followed by Perciformes with 31.60% of the individuals and seven species. The other orders all together reach less than 20% of abundance and five species. The three most abundant species were *Mesonauta festivus* (Perciformes), *Synbranchus marmoratus* (Synbranchiformes) and *Hoplias malabaricus* (Characiformes) (Table I). There was a marked dominance of young individuals of several species that reach large body size, as *Acestrorhynchus falcirostris*, *Hoplias malabaricus*, *Cichla monoculus* and *Serrasalmus rhombeus* (Table I). Individuals of only five species (*Rhytiodus microlepis*, *Brachyhypopomus brevirostris*, *Hypselecara temporalis* and *Trachelyopterus galeatus* - Table I) were large enough to be considered adults, considering the size at first sexual maturity. We also caught 32 species groups of non-fish animals living in the macrophyte meadows, including invertebrates such as insects, mollusks and crustaceans, and vertebrates such as frogs.

Consumers: groups by trophic level and isotopic ratios

The food chain of macrophyte meadows was composed of four trophic levels above autotrophic sources (Appendix SI – Tables II to V, Fig. 2). The primary consumers level was

Table I. Average estimates and standard deviation of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰), mean standard length (cm) and feeding behavior of fish species associated with macrophyte meadows.

Order/Family/Species	N	$\delta^{13}C$ (‰)±SD	$\delta^{15}N$(‰)±SD	Length(cm)	Feeding Behavior	Reference
BELONIFORMES						
Belonidae						
Potamorrhaphis guianensis	3	-28.9±0.4	10.6±0.7	1.6	Carnivorous	Abelha et al. 2001
CHARACIFORMES						
Acestrorhynchidae						
Acestrorhynchus falcirostris	2	-33.0±1.9	11.46±0.5	6.1	Piscivorous	Merona & Rankin-de-Merona 2004
Anostomidae						
Rhytiodus microlepis	22	-30.9±0.9	7.6±0.4	18.9	Omnivorous	Petry et al. 2003
Characidae						
Moenkhausia intermedia	12	-31.7±1.2	10.5±0.5	4.0	Omnivorous	Petry et al. 2003
Ctenobrycon hauxwellianus	35	-31.3±4.5	10.0±1.0	2.3	Omnivorous	Petry et al. 2003
Roeboides myersii	5	-30.8±0.4	10.2±0.1	3.6	Lepidofagous	Petry et al. 2003
Serrapinnus sp.	6	-29.6±0.7	8.9±0.9	1.9		
Hyphessobrycon eques	12	-31.6±1.4	10.6±0.4	1.9	Omnivorous	Petry et al. 2003
Hemigrammus ocellifer	7	-28.0±1.2	10.3±0.1	1.6	Invertivorous	Mills & Vevers 1989
Moenkhausia collettii	22	-28.2±2.3	9.9±0.49	2.3	Insectivorous	Abelha et al. 2001
Odontostilbe fugitiva	5	-32.1±1.0	10.8±0.6	2.0	Omnivorous	Petry et al. 2003
Erythrinidae						
Hoplias malabaricus	83	-26.4±1.5	9.9±0.5	5.1	Piscivorous	Petry et al. 2003
Serrasalmidae						
Mylossoma duriventre	5	-26.4±1.9	8.4±0.6	7.4	Omnivorous	Petry et al. 2003
Serrasalmus maculatus	40	-33.8±0.5	9.9±0.6	1.9	Piscivorous	Villares Junior et al. 2008
Pygocentrus nattereri	44	-35.2±0.6	11.0±0.3	1.8	Omnivorous	Petry et al. 2003
Serrasalmus rhombeus	6	-30.2±1.0	10.9±0.1	2.2	Omnivorous	Petry et al. 2003
Serrasalmus elongatus	6	-34.9±0.5	10.8±0.1	1.8	Piscivorous	Merona & Rankin-de-Merona 2004
Serrasalmus sp.	1	-34.9	10.7	1.9	Carnivorous	Merona & Rankin-de-Merona 2004
Triportheidae						
Triportheus albus	5	-30.8±0.1	9.1±1.1	2.2	Omnivorous	Petry et al. 2003
GYMNOTIFORMES						
Hypopomidae						
Brachyhypopomus brevirostris	13	-30.7±1.6	8.7±0.9	11.8	Omnivorous	Crampton et al. 2016
Sternopygidae						
Eigenmannia trilineata	2	-26.2±1.6	10.5±0.5	8.8	Carnivorous	Giora et al. 2005

Table I. Continuation.

Order/Family/Species	N	δ^{13}C (‰)±SD	δ^{15}N(‰)±SD	Length(cm)	Feeding Behavior	Reference
PERCIFORMES						
Cichlidae						
Mesonauta festivus	160	-27.1±1.1	9.2±0.3	4.5	Herbivorous	Crampton et al. 2016
Pterophyllum scalare	11	-29.5±2.1	10.0±0.4	4.9	Omnivorous	Crampton et al. 2016
Heros sp.	5	-33.4±1.5	10.5±0.5	1.6	Omnivorous	Merona & Rankin-de-Merona 2004
Cichla monoculus	19	-35.5±0.3	11.7±0.4	3.6	Piscivorous	Merona & Rankin-de-Merona 2004
Cichlasoma amazonarum	8	-24.6±1.7	9.4±0.3	4.2	Omnivorous	Petry et al. 2003
Crenicichla cincta	2	-30.3±1.6	11.2±0.2	6.8	Carnivorous	Crampton et al. 2016
Hypselecara temporalis	2	-27.7±2.0	9.9±0.8	9.4	Carnivorous	Crampton et al. 2016
SILURIFORMES						
Auchenipteridae						
Trachelyopterus galeatus	3	-24.8±3.7	8.7±0.8	9.6	Piscivorous	Petry et al. 2003
SYNBRANCHIFORMES						
Synbranchidae						
Synbranchus marmoratus	109	-23.7±1.7	8.0±0.8	18.2	Piscivorous	Petry et al. 2003

composed exclusively of invertebrates (Table II). Mean isotopic ratios by species showed a wide variation for δ^{13}C and δ^{15}N with values ranging from -39.45 to -11.91 and between 2.11 and 5.68, respectively (Table II). LDA analysis on both δ^{13}C and δ^{15}N revealed significant differences between these primary consumers (λ = 0.00019, F-approximate (22, 24) = 77.205, $p < 0.001$). The post-hoc paired comparison clustered them into five groups (Table II; Fig. 2). The most depleted group δ^{13}C (PC1) was composed exclusively of individuals from the Baetidae family. The highest δ^{15}N also was found in group PC5 which is composed of individuals of just one family – Curculionidae.

The secondary consumers level was mainly composed of invertebrates, but also included two omnivores *Mylossoma duriventre* and *Rhytiodus microlepis*, one piscivore *Synbranchus marmoratus*; and two frogs: *Dendropsuphus nanus* (tadpole and adults) and adults of *Pseudis limellum* (Table III). Estimated isotopic ratios showed a smaller variation for δ^{13}C and δ^{15}N than autotrophic sources and primary consumers groups, with values ranging from -30.82 to -20.51 and between 6.51 and 8.20, respectively (Table III; Fig. 2). The LDA revealed the existence of significant difference between taxa (λ = 0.049, F-approximate (38, 108) = 9.968, $p < 0.001$) that could be clustered into five main groups (post-hoc paired comparison, Table III; Fig. 2). The most depleted group δ^{13}C was composed by individuals belonging to the families Salticidae and Tetigonidae (Table III). And the higher δ^{15}N was obtained for the group 5 composed by *Mylossoma duriventre* and Therididae (Table III).

The tertiary consumer level was composed almost exclusively of fish species apart from

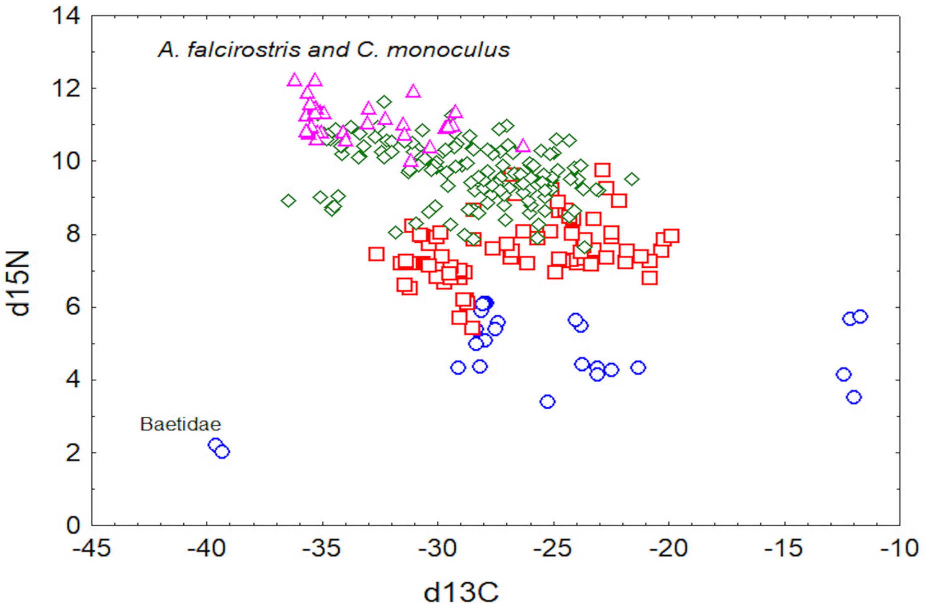

Figure 2. Scatter-plot of consumers by their estimates of $\delta^{13}C$ and $\delta^{15}N$, where: blue circles = primary consumers, red squares = secondary consumers, green diamonds = tertiary consumers, and pink triangles = quaternary consumers.

Table II. Average of $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and respective standard deviation (±SD) of the five groups of primary consumers clustered by the Discriminant Analysis and their isotopic values.

GROUP	Average $\delta^{13}C$ (‰)	(±SD)	Average $\delta^{15}N$ (‰)	(±SD)
Family/Species*				
PC1	-39.4	0.2	2.1	0.1
Baetidae				
PC2	-12.2	0.3	3.8	0.5
Pyralidae				
PC3	-23.3	1.2	4.5	0.7
Dilocarcinus pagei, *D. septemdentatus*, Moluscos, Polymitarcyidae				
PC4	-28.1	<0.1	5.4	0.7
Acrididae, Dytiscidae, Hydrophilidae Orthoptera, Naucoridae				
PC5	-11.9	0.3	5.7	<0.1
Curculionidae				

invertebrate individuals belonging to Aranaidae, Pisauridae, and Scirtidae (Table IV). Taxa of this trophic level exhibited narrower intervals of $\delta^{13}C$ and $\delta^{15}N$, ranging from -35.57 to -25.98 and from 8.81 to 10.31, respectively (Table IV). However, LDA showed the existence of significant differences among taxa (λ = 0.136, F-approximate (44, 214) = 8.33, $p < 0.001$) that could be clustered into five groups (post-hoc paired comparison, Table IV; Fig. 2). The most depleted group $\delta^{13}C$ (TC3) was composed by the individuals from the families Pisauridae and Scirtidae. The highest values of $\delta^{15}N$ were estimated for a group (TC5) composed by seven fish species: *Ctenobrycon hauxwellianus,*

Table III. **Average of $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and respective standard deviation (±SD) of the five groups of secondary consumers clustered by the Discriminant Analysis and their isotopic values.**

GROUP	**Average $\delta^{13}C$(‰)**	**(±SD)**	**Average $\delta^{15}N$(‰)**	**(±SD)**
Family/Species*				
SC1	-29.4	0.9	6.5	0.5
Gerridae, *Dendropsuphus nanus* (tadpole), *Dendropsophus nanus* (adult) Corixidae, Belostomatidae, Chrysomelidae, Libellulidae				
SC2	-24.0	1.7	7.9	0.8
Hydrometridae, Coleoptera, *Synbranchus marmoratus*, Trechaleidae, *Pseudis limellum*,				
SC3 Salticidae, Tetigonidae	-20.5	0.6	7.6	0.3
SC4	-30.8	0.7	7.6	0.4
Rhytiodus microlepis, Lycosidae Nepidae, Lestidae				
SC5	-26.6	1.7	8.2	0.6
Mylossoma duriventre, Therididae				

Roeboides myersii, Potamorhaphis guianensis, Pterophillum scalare, Hemigrammus ocellifer, Moenkhausia colleti and *Eigenmannia trilineata* (Table IV; Fig. 2).

Finally, the quaternary consumers level was composed exclusively of fish species (Table V; Fig. 2). Species of this level showed the narrowest interval of $\delta^{13}C$ and $\delta^{15}N$, ranging from -35.52 to -30.33 and 10.83 to 11.69, respectively (Table V; Fig. 2). The LDA detected significant differences among species (λ = 0.067, F-approximate (12, 48) = 11.471, $p < 0.001$) that could be clustered into four groups (post-hoc paired comparison, Table V; Fig. 2). The most depleted group $\delta^{13}C$ was composed by *Cichla monoculus*, which also showed the highest $\delta^{15}N$ (Table V; Fig. 2).

Carbon sources and the energy transference

The energy transfer from primary to secondary consumers was dominated by one important pathway, represented by the primary group PC4, with a high contribution for the energy transferred for almost all secondary consumer groups (Fig. 3a). The high contribution of the PC4 group, composed of invertebrates of the families Acrididae, Dytiscidae, Hydrophilidae, Orthoptera and Naucoridae, was notable for the secondary consumers group SC2 (> 60% of contribution). It was between 25% and 50% of contribution for the other secondary consumers groups SC1, SC3, SC4 and SC5 (Fig. 3a). SC2 group includes a fish species *Synbranchus marmoratus,* the Anura *Pseudis limellum*, the spider family Trechaleidae and the insect groups Hydrometridae and Coleoptera (Table IV).

The energy transfer from secondary to tertiary consumers also showed a noticeable pathway stronger than others. The secondary consumers that composed the group SC4, which includes a fish species *Rhytiodus microlepis* and insect families Lycosidae, Nepidae and Lestidae were the major sources of energy for the tertiary groups TC4 and TC5 (more than 60% and around 50% of contribution, respectively) (Fig. 3b). These two groups are composed exclusively by fish species (Table

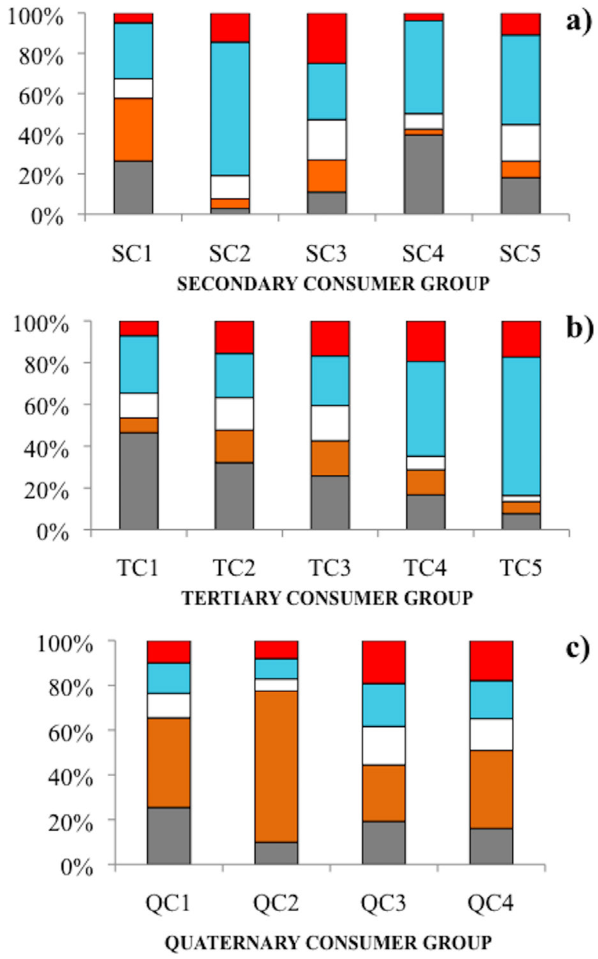

Figure 3. SIAR mixing model relative contribution (%) of Carbon from one trophic level for the next immediately above. (a) primary consumers to the secondary consumers, where the groups into trophic levels were discriminated as gray = PC1, orange = PC2, white = PC3, blue = PC4, and red = PC5 (Table II); (b) secondary consumers to the tertiary consumers, where the groups into trophic levels were discriminated as gray = SC1, orange = SC2, white = SC3, blue = SC4, and red = SC5 (Table III); and, (c) tertiary consumers to the quaternary consumers, where the groups into trophic levels were discriminated as gray = TC1, orange = TC2, white = TC3, blue = TC4, and red = TC5 (Table IV).

V). A second important energy pathway was from SC1 to TC1, (> 40% of contribution), which corresponded to a diverse group encompassing Aranaiedae, *Macrobrachium amazonicum* and five fish species (Table V, Fig. 3b). The groups SC2 (orange), SC3(whit) and SC5 (red) presented a low contribution (<20%?) for all the tertiary consumers groups.

Finally, the same pattern showing an important energy transfer pathway was observed between tertiary and quaternary consumers QC2 group. The TC2 group, composed by two insect families Pisauridae and Scirtidae, was the highest contributor of energy for all quaternary groups, but mainly for QC2, composed by two piranha species *Serrasalmus elongatus* and *Pygocentrus nattereri*. The quaternary groups QC3, composed exclusively by *Acestrorhyncus falcirostris*, and QC4 with *Cichla monoculus* showed the feed on a high variety of sources (Fig. 3c). TC3 (white), TC4 (blue) and TC5 (red) presented a low contribution (<20%?) for all the quaternary consumers groups.

DISCUSSION

Biota of the macrophyte meadows

As evidenced in previous studies on macrophyte meadows of Amazonian floodplains (Sánchez-Botero et al. 2008, Dias et al. 2011, Soares et al. 2014), we found that *P. repens* was one of the dominant macrophyte species in these habitats. The fish assemblage was composed of 30 species from 12 families and was dominated by small-bodied species and young individuals of large-bodied species, which spend part of their life cycle in these habitats (Casatti et al. 2003, Dibble & Pelicice 2010). The prevalence of Characiformes was similar to what was observed in previous studies examining these habitats in the Amazon Basin (Sánchez-Botero et al. 2003, Petry et al. 2003, Prado et al. 2010, Soares et al. 2014). The macrophyte meadows act as environmental filters, influencing the colonization of species within these habitats. Consequently, the composition of assemblages inhabiting macrophyte meadows is composed of species that are locally restricted to specific

Table IV. Average and standard deviation (±SD) of the isotopic composition for six groups of tertiary consumers clustered by the Discriminant Analysis and their isotopic values.

GROUP Family/Species*	Average $\delta^{13}C$ (‰)	(±SD)	Average $\delta^{15}N$(‰)	(±SD)
TC1	-27.6	2.2	9.0	0.5
Aranaiedae, *Trachaelopterus galeatus*, *Triportheus albus*, *Serrapinus* sp., *Mesonauta festivus*, *Macrobrachium amazonicum*, *Brachyhypopomus brevirostris*				
TC2	-35.0	0.8	8.8	0.1
Pisauridae, Scirtidae				
TC3	-26.0	1.8	9.7	0.5
Hoplias malabaricus, Cichlasoma amazonarum, Hypselacaria temporalis				
TC4	-30.2	4.0	10.0	0.9
Serrasalmus maculatus, Heros sp., Moenkhausia intermedia, Hyphessobrycon eques				
TC5	-30.6	2.4	10.3	0.5
Ctenobrycon hauxwellianus, Roeboides myersii, Potamorhaphis guianensis, Pterophillum scalare, Hemigrammus ocellifer, Moenkhausia colleti, Eigenmannia trilineata				

favorable segments of environmental gradients (Ganaça et al. 2021).

Isotopic values

The non-fish fauna (i.e., other consumers) was composed of several taxa that showed a broad range of $\delta^{13}C$ values, and $\delta^{15}N$ values spanning at least four trophic levels (Tables III, IV and V). These isotopic variations could be an indication of different trophic strategies to exploit autotrophic sources and primary consumers available in the macrophyte meadows. The more depleted values of $\delta^{13}C$ and $\delta^{15}N$ (-39.45 ‰ and -2.11 ‰ respectively) were obtained from insects of the family Baetidae. These animals are filterers of fine organic material, whilst also consuming periphytic and epiphytic algae (Shimano et al. 2012). At the opposite end of the isotopic spectrum, the most $\delta^{13}C$ enriched primary consumers were the insects of the Pyralidae family, which are mainly shredders associated with coarse organic substrates (Da-Silva & Salles 2012) and snout beetles of the Curculionidade family. In general, the isotopic signatures estimated in our studies for invertebrates matched estimates obtained by Molina et al. (2011), although our limits were broader than those observed in their study conducted in the floodplain lakes of the Beni River (Bolivian Amazon).

As expected, fish showed a narrower range of $\delta^{13}C$ (-35.3 to -29.8) and $\delta^{13}N$ (7.3 to 12.2) in comparison to the other consumers. This narrow variation of $\delta^{15}N$ is an indication that the fish assemblages exploit a smaller spectrum of prey items in the macrophyte meadows than in the general floodplain system. This could be an indication of the prevalence of invertivory predicted to dominate in tropical areas (González-Bergonzoni et al. 2012), including lakes (Thompson et al. 2012). Nevertheless, this higher level of omnivory at the macrophyte meadows is accentuated by the composition of fish assemblage dominated by small (juveniles) individuals of large piscivorous species (i.e. *Acestrorhynchus falcirostris* and

Table V. **Average of $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and respective standard deviation (±SD) of the four groups of quaternary consumers, clustered by Discriminant Analysis.**

GROUP **Family/Species***	**Average $\delta^{13}C$ (‰)**	**(±SD)**	**Average $\delta^{15}N$(‰)**	**(±SD)**
QC1	-30.3	1.8	10.8	0.4
Odontostibe fugitiva, Serrasalmus rhombeus, Crenicichla cincta				
QC2	-35.1	0.6	10.9	0.3
Serrasalmus elongatus, Pygocentrus nattereri				
QC3	-33.0	1.9	11.6	0.3
Acestrorhynchus falcirostris				
QC4	-35.5	0.3	11.7	0.4
Cichla monoculus				

Cichla monoculus). Aguiar-Santos et al. (2018) observed diet and trophic position of young and adults of *Cichla temensis* are similar but larger individuals displayed higher $\delta^{13}C$ than smaller individuals. In lakes associated with large rivers, *Cichla temensis* juveniles were observed feeding on detritivorous fish and shifted to omnivorous fish as they increased in size (Aguiar-Santos et al. 2022).

Additionally, the absence of typical detritivorous species (also highly specialized like species the families Curimatidae and Prochilodontidae), which are abundant in open water areas of these lakes (Siqueira-Souza & Freitas 2004, Siqueira-Souza et al. 2016) may have accentuated those results. This absence of species might also explain the low contribution of phytoplankton to the food web of the macrophyte meadows compared to previous studies conducted on fish caught in the open waters of the lakes and rivers (Forsberg et al. 1993). In comparison with other Amazonian floodplain habitats, the contribution of C_4 plants to the food web seems to be higher in these herbaceous banks, mainly for juveniles' fish diet (Silva-Prado et al. 2019).

Food chain length and energy transfer

Our study showed that the macrophyte meadow food web of the Amazonian floodplains is organized into four levels above the autotrophic sources and is the first to document such organization in the freshwater habitats of the Amazonian floodplain lakes. Other studies on wetland trophic structure are scarce; nevertheless, they accordingly concluded that the food web is organized with few trophic levels (Kwak & Zedler 1997, Jepsen & Winemiller 2002, Mendoza-Carranza et al. 2010). Nevertheless, we can argue that macrophyte meadows support young fish (as growth habitats) with a specific food web different from the other floodplain habitats.

The length of the chains within a food web is related to nutrient cycling and primary productivity (Pace et al. 1999, Post 2002). The energy transfer from one trophic level to the next seems to not be homogenous among each prey/consumers links. Some prey groups are privileged and concentrate on high contribution of energy transfer, acting as a 'hub or highly connected 'nodes' (Fig. 4). At the primary consumer level, the very diverse group PC4 (hub), composed of several insect taxa, seems to be the most important hub to the upper

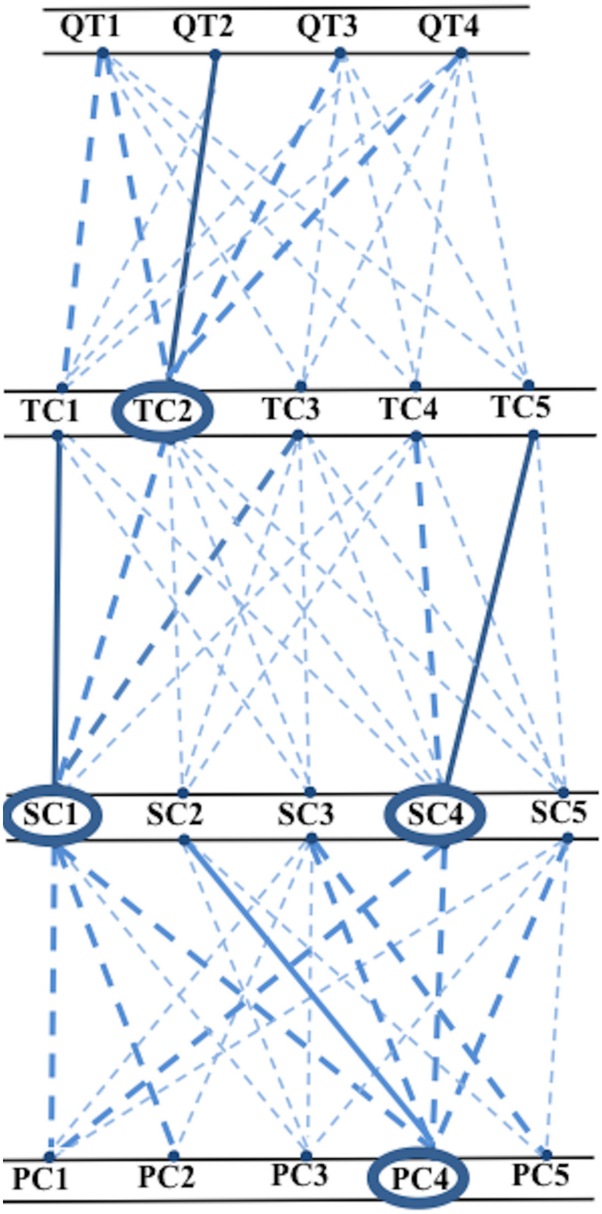

Figure 4. **Schematic model of energy transfer (for one trophic level to upper one) on the macrophyte meadows of Amazonian floodplain lakes. Light doted line = 10 to 24% of Carbon transfer, heavy doted line = 25 to 50% of Carbon transfer, and full line = higher 50% of Carbon transfer. Linkages with Carbon transfer smaller than 10% were not plotted. Blue circles indicated species or groups those act as hubs of energy transference.**

trophic levels. At the secondary consumer level, we identified two hubs: the very diverse group SC1 and SC4 (composed of one fish species *Rhytiodus microlepis* and three insect families). Finally, the energy transfer from the tertiary trophic level to the quaternary trophic level was also by one preferential node, the TC2 composed of two insect families. The existence of 'hub' species in food webs has already been modeled (Gaichas & Francis 2008) and some studies have indicated that these species or species groups could be essential to community stability (Solé & Montoya 2001). It is noticeable that the hubs in the macrophyte food chain of the Amazonian floodplain lakes belonged to a high variety of taxa, predominantly from insect families. This diversity may be considered a factor of stability and resilience.

Species such as peacock bass (*Cichla monoculus*) and dogfish (*Acestrorhyncus falcirostris*) are, in general, described as predominantly piscivorous for adult fish (Lubich et al. 2004). As changes in the diet of Cichla sp. were already associated with body size (Aguiar-Santos et al. 2018), it is possible that the dominance of young individuals of these large piscivorous species is a key factor to explain the dominance of invertivory as the feeding strategy in the macrophyte meadows. Then macrophytes meadows constitute a particular habitat, with a fish assemblage not dominated by detritivorous or herbivorous species but by young individuals of large piscivorous and small size species. These species, which are mainly invertivores, are attracted by the high invertebrate abundance and the refuge against predation procured by C_4 macrophytes structure. The young fish find here an optimal habitat for growth. Our results then confirm that these habitats are valorized by fish for the feeding resources they support and those macrophytes themselves appeared valorized for their structure and the physical support they gave to the fauna rather than by their biological productivity, even if it is one of the most important in the Amazonian system. In addition, the predominant use of the macrophyte meadows by juvenile individuals of highly mobile fish species illustrates the importance of these temporary habitats and the connectivity among floodplain environments to the maintenance of regional biodiversity (Hurd et al. 2016).

We recognize that the landscape and functioning of the floodplains adjacent to large rivers, like the Amazon, are strongly influenced by the flood pulse. As consequence, these results are limited because they are based on a unique sample performed exclusively during the receding water season. Nevertheless, we believe that the pattern of hub species determinant to the energy flow by the food web present in the macrophyte meadows was demonstrated.

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SUPPLEMENTARY MATERIAL

Appendix SI.

How to cite

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Author contributions

ACBO and CECF conceived and designed the experiments. ACBO and KCY collected data and prepared the samples. ACBO, MGA and CER developed laboratorial analyses. CECF analyzed the data. ACBO, CECF, FKSS, LEH and PDH wrote the manuscript; and MP and JAS provided editorial advice.