PRIMARY RESEARCH PAPER

Macroinvertebrate food web structure in a floodplain lake of the Bolivian Amazon

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Abstract Two stable isotopes $\delta^{13}C$ and $\delta^{15}N$ were used to identify the energy sources and trophic relationships of the main freshwater macroinvertebrates in a floodplain lake of the Beni River (Bolivian Amazonia). Four energy sources (seston, bottom sediment, periphyton, and aquatic macrophytes) and macroinvertebrate communities were collected during three periods of the river hydrological cycle. Macroinvertebrates showed greater temporal variation in isotope values than their food sources. Six trophic chains were identified: four were based on seston, periphyton, C_3 macrophytes, and bottom sediments, and the last two chains on a combination of two carbon sources. One mixed seston and periphyton sources during the wet season while the other mixed periphyton and macrophytes sources during the wet and dry seasons. Periphyton was the most important energy source supporting the highest number of trophic levels and consumers. The macrophytic contribution was only significant during the dry season. Bottom sediments constituted a marginal energy source. As each season is associated with different physical and chemical conditions, processes organizing macroinvertebrate food web structure in the Beni floodplain seem strongly linked to hydrological seasonality.

Keywords Stable isotopes · Floodplain lake · Freshwater macroinvertebrates · Energy sources · Trophic chains

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Introduction

In the Amazon floodplains, four major primary producers are recognized: phytoplankton, herbaceous macrophytes (C_3 and C_4 types), flooded forest (C_3 type), and periphytic algae (Melack & Forsberg, 2001; Leite et al., 2002). Their relative contribution depends on local conditions (forest, lake, swamps, etc.). According to many studies in Brazil, macrophytes generally constitute the greatest primary biomass and are assumed to be important food sources for herbivorous and detritivorous macroinvertebrates (Junk &

Piedade, 1997; Junk & Robertson, 1997; Melack & Forsberg, 2001; Leite et al., 2002). However, it is also possible that many macroinvertebrates simply use the floating plants as shelter, feeding on other sources such as periphyton and phytoplankton. The phytoplankton is generally recognized as the main carbon source for fishes in the Amazon and Orinoco River systems (Araujo-Lima et al., 1986; Hamilton et al., 1992; Forsberg et al., 1993; Benedicto-Cecilio et al., 2000; Lewis et al., 2001). This is surprising since, for example, phytoplankton represents only 2% of the net primary production of the Amazon River system, which is quite low compared to macrophytes (65%) or periphytic algae (10%) (Melack & Forsberg, 2001). However, macrophytes could also be a significant source sustaining fish productivity in the Amazon River systems (Benedicto-Cecilio et al., 2000; Benedicto-Cecilio & Araujo-Lima, 2002; Wantzen et al., 2002; Manetta et al., 2003; Oliveira et al., 2006), even if their direct consumption by fish seems unusual (Forsberg et al., 1993; Winemiller, 2004). Recently, Oliveira et al. (2006) have suggested that macrophytes might serve as an indirect carbon source for fish through the consumption of invertebrates that live in the floodplain. Despite the importance of these issues, the trophic foundations of flooded ecosystems, the relative importance of various energy sources and the paths taken to reach the terminal links remain partly hypothetical.

In this study, our main objectives were to (1) identify the major sources supporting macroinvertebrate communities in a floodplain lake of the Bolivian Amazon, and (2) analyze the resulting trophic chains. Given the important hydrological seasonality in this type of aquatic system, a secondary objective was to compare three hydrological periods (wet, dry, and transition periods) to highlight potential seasonal changes in energy sources and feeding links.

Methods

Study area

Our study was carried out in La Granja Lake (lat. 14°15′52″S, long. 67°28′97″W) situated in the Beni River floodplain, a few kilometers downstream from the city of Rurrenabaque (Fig. 1). The Beni River, a tributary of the Rio Madeira, originates in the

Cordillera Real. It drains the waters from the Andean summits and the Yungas region and enters the floodplain at Rurrenabaque. The Beni River waters are considered "white waters", characterized by heavy sediments loads, high nutrient concentrations and moderate pH (Guyot et al., 1999). The rapid evolution of the main channel, resulting from the depositing of coarse sediments at the exit of the Andes, leads to the formation of numerous abandoned or weakly connected oxbow lakes (Gautier et al., 2007). These lakes are important components of the floodplain as they include open water but also flooded or floating vegetation areas. During the dry season, lakes may be reduced to shallow turbid pools and, occasionally, may dry up completely. During the wet and intermediate seasons, the lakes expand, invading riverine forests or savannas and allowing the seasonal growth of emergent aquatic macrophytes in areas locally known as *Pantanal*.

In this region, the flooding period coincides with the rainy season. The water level starts to rise in September or October and peaks in late February. During this peak, the Beni River may connect to the La Granja Lake and may even inundate the adjacent floodplain and riverine forest. During this period the lake reaches a mean depth of 2.5 m. During the dry season, the water level recedes from April to May and the lake is restricted to its central basin with an average depth of 1–1.5 m. There are small temperature variations in this region, and the highest temperatures generally coincide with the highest precipitations (Fig. 2a, b). An organic layer is restricted to the macrophytic belt along the lake margin, including some closed channels containing large fragments of wood that are used as shelter by invertebrates and fish. Marginal vegetation consists mainly of C_3 macrophytes (mostly *Eichhornia crassipes*, *Polygonum densiflorum*, and *Salvinia auriculata*) and C_4 grasses (*Paspalum repens* and *Hymenachne donacifolia*).

Field collection

Samples were collected in 2004 and 2005, during three periods: wet season (high water), dry season (low water) and one transition season (rising water) (Fig. 2a). Sampling was carried out in open water ("pelagic") and in the vegetation belt ("littoral"). In open water, two types of sources were collected: seston and bottom sediment. Seston (i.e.,

Fig. 1 Geographical location of the study area: **a** map of the Amazon basin in South America and the Beni River showing a classic meandering course, **b** geomorphological features of the floodplain, and **c** schematic cross-section of the sampled habitat of La Granja Lake
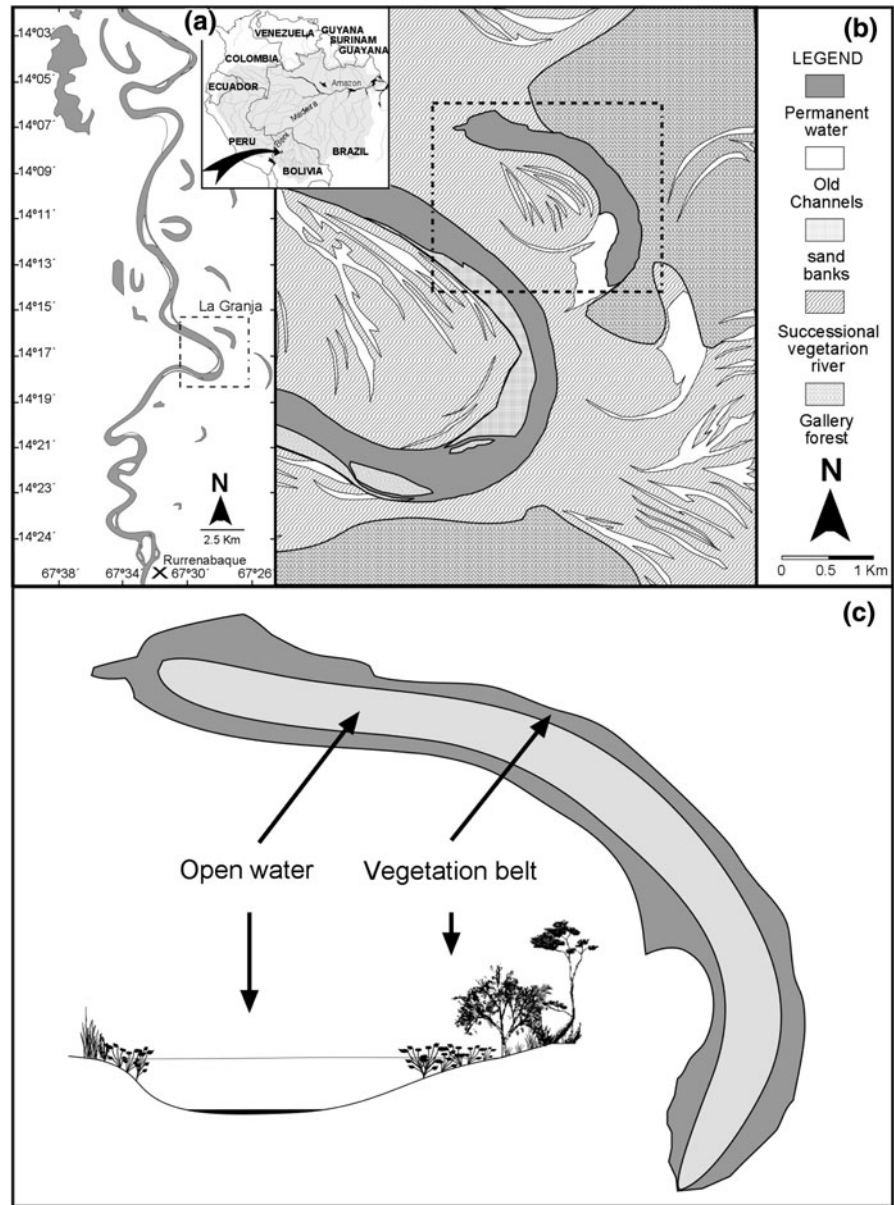
zooplankton, phytoplankton, organic detritus, and bacteria) was chosen due to difficulties in acquiring pure samples of plankton, and was collected by filtering water through a 63-µm mesh net, washing with ultra-pure water and filtering through GF/C filters. Bottom sediment samples were taken using a PVC pipe (30 cm long with an internal diameter of 4 cm). The upper 2 cm of each pipe were immediately transferred into a plastic bag. In this area, macroinvertebrates were collected using a Ponar grab sampler. In the vegetation belt, we collected two

sources that were absent from open waters: macrophytes (free floating and emergent plants) and periphyton (heterotrophic and autotrophic organisms, as well as adhering particles of detritus). Macrophytes were collected by hand, washed several times to remove detrital matter, placed into plastic bags and frozen. Intact roots from the most abundant macrophytes were also collected and frozen. Macroinvertebrates were collected in macrophytic belts using a hand net. Each specimen was washed, identified to family or genus levels, kept alive for approximately
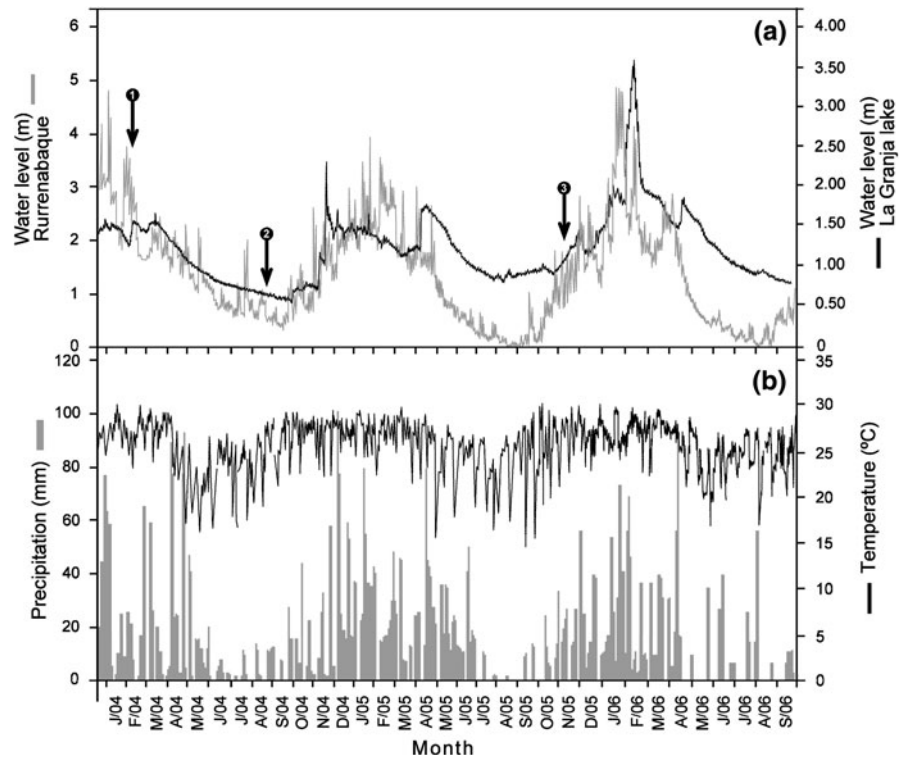
3 h in order to clear guts, and then frozen. At the laboratory, periphyton was separated from the roots by using the centrifugation process described by Roulet et al. 2000. Finally, all samples were lyophilized for 72 h and later ground into a homogeneous powder. All invertebrates were used for isotopic analyses and small organisms were pooled by species.

Stable isotope analyses

All the analyses were done at the University of California (Davis Stable Isotope Facility, Department of plant Sciences), using a Europa Hydra 20/20 stable isotope ratio mass spectrometer IRMS, which determines the $\delta^{13}C$ and $\delta^{15}N$ values as well as the carbon:nitrogen ratios. Isotopic compositions were quantified using international standard reference materials (i.e., Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen). The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were expressed as the relative difference between the sample and the conventional standard $\delta^{15}N$ or $\delta^{13}C$ (‰ = $[(R_{sample} - R_{standard})/R_{standard}] \times 10^3$) (Peterson & Fry, 1987; Vander Zanden & Rasmussen, 1999). Standards were run in

duplicate every 12 measurements within a run of 100 samples. The analytical precision of these measurements was 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$.

Data processing and analyses

We first investigated the relationships between sources or association of sources and primary consumers or potential predators. These relationships were established using a K Nearest-Neighbors randomization test proposed by Rosing et al. (1998). This analysis computes the lowest Euclidian distance between two bivariant samples $\delta^{13}C$ and $\delta^{15}N$, based on the assumption that a shorter distance between a food item and the consumer's isotopic ratio implies a greater contribution of this food item to the diet (Ben-David & Schell, 2001). The robustness of this analysis is based on a multivariate extension of ranks with small sample sizes (Conover, 1999). Probability values were corrected using a Bonferroni algorithm (Rice, 1989). These computations were performed using a Pascal simulation program available from M.N. Rosing. When isotope values did not show any relationship between sources and consumers, we compared differences in mean $\delta^{13}C$ signatures using Student's *t* tests.

If the δ^{13}C signatures of a consumer overlapped two sources, we examined the relative contributions of the two sources through a linear mixing model, using the equations: % $C_{consumer\ mixed} = [1 - \delta^{13}C_{consumers} - \delta^{13}C_{source1}/\delta^{13}C_{source1} - \delta^{13}C_{source2}] \times 100$, where $\delta^{13}C_{consumers}$ is the δ^{13}C values of the invertebrates, and $\delta^{13}C_{source1}$ and $\delta^{13}C_{source2}$ are the average δ^{13}C values of the sources (Peterson & Fry, 1987). Using this methodology, taxa are automatically grouped according to the most probable trophic level and sources.

We then assessed the trophic fractionation f of δ^{15}N, i.e., the relative difference between consumers and their sources (Peterson & Fry, 1987). The nitrogen fractionation values allow the estimation of trophic positions.

The estimation of trophic positions (TP) was based on the δ^{15}N fractionation between consumers and sources (Vander Zanden & Rasmussen, 1999; Post, 2002). Calculations were performed using the equation: TP = $[\delta^{15}N_{consumer} - \delta^{15}N_{baseline}]/f + \lambda$, where $\delta^{15}N_{consumer}$ is the mean of consumers, $\delta^{15}N_{baseline}$ is the mean of baseline organisms, f is the mean trophic fractionation and λ is the trophic position expected. For consumers mixing two sources, we used the equation: TP = $\lambda + (\delta^{15}N_{consumer} - [\delta^{15}N_{baseline1} \times \alpha + \delta^{15}N_{baseline2} \times (1 - \alpha)])/f$, where α is the relative proportion of consumers ultimately derived from the mixing model (Post, 2002). The statistical validation of the trophic positions was established using a one-way ANOVA, and differences between seasons and types of trophic chains using a Tukey's multiple comparisons test.

Results

Sources

We collected 96 samples: 48 during the wet season, 29 during the dry season, and 19 during the transition season. Seston showed the lowest δ^{13}C (-34.2‰ $\pm$ 1.6) and the highest δ^{15}N values (6.8‰ $\pm$ 1.01). Bottom sediments showed low δ^{13}C (-28.7‰ $\pm$ 0.8) and low δ^{15}N values (-0.2‰ $\pm$ 0.94). The values of C_3 macrophytes and periphyton were usually found between seston and sediments values. C_3 macrophyte δ^{13}C values varied from -26.1‰ $\pm$ 0.1 during the wet season to -28.8‰ $\pm$ 0.8 and -30.0‰ $\pm$ 0.4

during the dry and transition seasons; their δ^{15}N values showed a slight increase during the wet season (4.5 $\pm$ 0.4), compared to the dry and transition seasons (4.1‰ $\pm$ 0.4 and 3.9‰ $\pm$ 0.01, respectively). Periphyton values presented more variations than the other sources; δ^{13}C values were generally more depleted than those of C_3 macrophytes and bottom sediments, except for the transition season during which C_3 macrophyte values became slightly more depleted than those of periphyton. Periphyton δ^{15}N values were less enriched than those of C_3 macrophytes. Bottom sediment values of δ^{13}C fell between those of C_3 macrophytes and periphyton, whereas the δ^{15}N values were the least enriched of all sources, mostly during the transition season (Table 1; Fig. 3). It is important to note that terrestrial vegetation (type C_3) was found in some cases during the wet and transition seasons, but its isotopic values was not statistically different from those of type C_3 aquatic macrophytes (K Nearest-Neighbors test, $P < 0.05$). In contrast, C_4 macrophytes (*Paspalum repens*), only present during the wet and dry seasons, had signatures well separated from those of other sources (δ^{13}C = -12.7‰ $\pm$ 1.4 and δ^{15}N = 7.2‰ $\pm$ 1.0, Table 1; Fig. 3).

Macroinvertebrate consumers

We analyzed 243 macroinvertebrate samples representing 38 taxa (Table 1; Fig. 3). Macroinvertebrate fauna was rich, varied and variable. Although sampling efforts were intensive in all seasons, some taxa were not found during the dry and transition seasons. The dominant taxa were a water bug *Belostoma* sp. (Insecta, Hemiptera), dragonflies *Dythemis* sp. and *Limnetron* sp. (Insecta Odonata), aquatic beetles *Hydrophilus* spp. (Insecta Coleoptera), a freshwater shrimp *Palaemonetes ivonicus* (Crustacea, Decapoda) and a snail *Pomacea scalaris* (Mollusca, Gasteropoda). The isotopic compositions of invertebrates showed greater seasonal variations of δ^{13}C and δ^{15}N than their trophic sources. The δ^{13}C values ranged from -35.2 ‰ $\pm$ 0.6 for the snail *Eupera* sp. during the dry season to -22.8 ‰ $\pm$ 3.5 for the aquatic beetle *Tropisternus* sp. during the dry season. The δ^{15}N values ranged from 10.1‰ $\pm$ 0.6 for *Palaemonetes invonicus* during the dry season to 2.0‰ $\pm$ 0.1 in shell (*Biomphalaria* sp.) during the wet season.

Table 1 Seasonal dual isotope signatures (δ^{13}C and δ^{15}N, mean ± SD), carbon sources and aquatic invertebrates

Type of sample	Wet					Dry					Transition				
	n	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N	n	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N	n	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N
Primary producers															
Seston	9	−35.1	2.2	6.7	1.3	11	−33.8	0.6	6.7	0.9	3	−33.5	1.2	7.3	0.2
Terrestrial plant C$_3$	3	−28.1	0.8	4.1	1.1	–	–	–	–	–	2	−29.5	0.5	3.3	0.3
C$_3$ macrophytes	8	−26.1	0.1	4.5	0.4	6	−28.8	0.8	4.1	0.4	3	−30.0	0.4	3.9	0.0
C$_4$ macrophytes	3	−12.3	1.6	7.3	0.6	3	−13.6	1.3	7.3	0.6	–	–	–	–	–
Periphyton	20	−28.8	1.5	3.6	1.4	6	−30.5	1.0	2.1	0.5	5	−29.3	1.3	3.1	0.7
Bottom sediment	5	−28.1	0.6	1.0	0.5	3	−29.8	0.5	−0.9	0.4	6	−28.6	0.4	−0.7	0.2
Consumers															
Bivalvia															
Hyriidae															
Castalia sp.	1	−34.5	–	7.0	–	–	–	–	–	–	–	–	–	–	–
Pisidiidae															
Eupera sp.	–	–	–	–	–	3	−35.2	0.6	6.8	0.5	–	–	–	–	–
Gastropoda															
Ampullariidae															
Pomacea scalaris	1	−25.3	–	6.0	–	6	−28.7	1.7	4.0	0.6	4	−29.2	0.3	5.8	1.3
Ancylidae															
Hebetancylus sp.	–	–	–	–	–	3	−30.1	3.7	4.8	0.4	3	−25.6	0.0	5.2	0.3
Planorbidae															
Acrorbis sp.	1	−28.4	–	5.5	–	–	–	–	–	–	3	−29.0	0.6	5.2	0.4
Biomphalaria sp.	3	−27.7	1.5	2.0	0.1	–	–	–	–	–	–	–	–	–	–
Crustacea															
Decapoda															
Palaemonidae															
Palaemonetes invonicuos	1	−32.4	–	8.9	–	17	−31.0	1.2	10.1	0.6	3	−29.8	0.7	9.5	0.9
Trichodactylidae															
Dilocarcinus pagei	7	−28.4	2.9	5.9	0.9	–	–	–	–	–	–	–	–	–	–
Insecta															

Table 1 continued

Type of sample	Wet					Dry					Transition				
	n	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N	n	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N	n	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N
Ephemeroptera															
Baetidae															
Callibaetis sp.	1	−31.9	–	6.3	–	–	–	–	–	–	3	−28.9	1.0	5.5	0.3
Polymitarcydae															
Campsurus violaceus	7	−35.7	0.8	7.0	0.3	10	−34.4	0.8	6.2	0.7	4	−34.7	0.3	6.1	0.4
Trichoptera															
Leptoceridae															
Nectoopsyche sp.		−29.8	0.7	5.0	0.3	3	−30.2	0.9	6.3	0.1	–	–	–	–	–
Oecetis sp.	–	–	–	–	–	1	−33.8	–	7.0	–	–	–	–	–	–
Odonata															
Anisoptera															
Aeshnidae															
Limnetron sp.	6	−33.0	1.0	8.3	1.1	4	−29.3	0.9	6.1	1.5					
Libellulidae															
Dythemis sp.	3	−33.4	0.2	6.9	0.9	11	−31.1	1.0	6.1	1.2	1	−28.7	–	4.5	–
Erythemis sp.	1	−31.1	–	7.8	–						1	−36.9	–	8.2	–
Libellula sp.	3	−34.0	0.5	6.7	0.2	3	−32.7	1.1	9.4	0.1	1	−30.9	–	6.9	–
Sympetrum sp.	1	−35.6	–	9.7	–	–	–	–	–	–	–	–	–	–	–
Tramea sp.	5	−34.4	1.1	7.4	0.8	9	−31.5	1.5	8.1	1.2	3	−31.0	1.1	7.0	0.4
Zygoptera															
Coenagrionidae															
Acanthagrion sp.	3	−34.0	0.2	7.2	0.2	4	−30.2	1.5	6.4	0.8	3	−32.0	01	7.0	0.1
Homeoura sp.	–	–	–	–	–	1	−32.1	–	7.7	–	–	–	–	–	–
Oxyagrion sp.	–	–	–	–	–	3	−30.5	1.9	6.8	0.9	–	–	–	–	–
Protoneuridae															
Pronuera sp.	3	−32.2	2.0	8.3	1.0	1	−32.0	–	8.1	–	–	–	–	–	–
Hemiptera															
Belostomatidae															

Table 1 continued

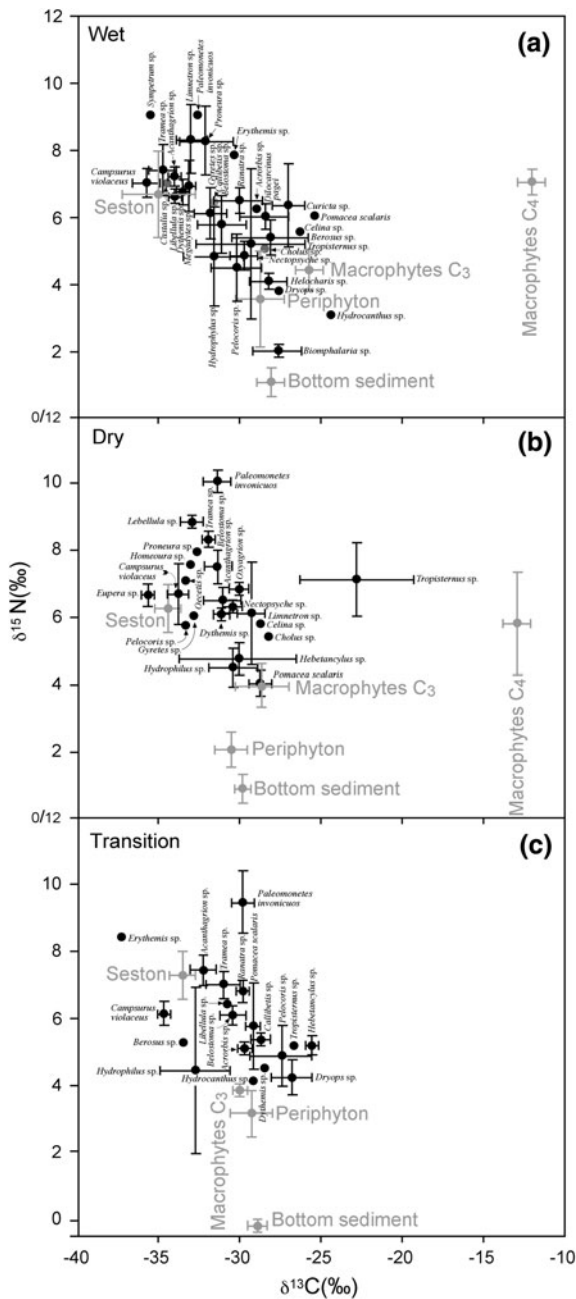| Type of sample	Wet					Dry					Transition				
	n	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$	n	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$	n	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$
Belostoma spp.	6	−31.1	1.6	5.8	0.8	4	−30.8	1.7	7.3	0.7	16	−30.4	1.6	6.1	0.7
Naucoridae															
Pelocoris sp.	3	−30.2	1.5	4.5	1.0	1	−32.1	–	6.0	–	3	−27.4	1.9	4.9	0.9
Nepidae															
Curicta sp.	3	−27.0	0.9	6.3	1.3	–		–	–	–	–	–	–	–	–
Ranatra sp.	3	−30.6	2.8	7.4	1.3	–		–	–	–	3	−29.8	0.2	6.9	0.2
Coleoptera															
Curculiomidae															
Cholus sp.	1	−28.8	–	5.3	–	1	−28.7	–	5.1	–	–	–	–	–	–
Dryopidae															
Dryops sp.	1	−27.6	–	3.7	–	–		–	–	–	3	−26.8	1.3	4.2	0.5
Dytiscidae															
Celina sp.	1	−28.3	–	5.4	–	1	−29.3	–	6.9	–	–		–	–	–
Megadytes sp.	3	−33.5	1.0	6.7	1.5	–		–	–	–	–		–	–	–
Gyrinidae															
Gyretes sp.	3	−31.4	2.2	6.3	1.8	1	−32.5	–	6.0	–					
Hydrophilidae															
Berosus sp.	3	−28.2	2.3	5.4	0.5	–		–	–	–	1	−33.3	–	5.5	–
Helocharis sp.	3	−31.5	1.2	3.8	0.2	–		–	–	–	–	–	–	–	–
Hydrophilus spp.	5	−31.1	3.4	5.1	2.1	3	−30.4	1.5	4.5	0.6	3	−32.8	2.2	4.4	2.5
Tropisternus sp.	4	−29.4	3.4	5.2	2.3	3	−22.8	3.4	7.1	1.1	1	−26.4	–	5.3	–
Noteridae															
Hydrocanthus sp.	1	−24.9	–	3.5	–	–		–	–	–	1	−29.4	–	4.3	–
Total	138					122					79				339

Fig. 3 Dual plots of $\delta^{13}C$ and $\delta^{15}N$ (mean $\pm$ SD) for sources and consumers sampled during **a** wet season, **b** dry season, and **c** transitions season. Sources are represented by *solid symbols* and consumer groups by *shaded symbols*

Trophic position and associations

Three main trophic chains were consistently identified throughout the analysis. They were based on seston, periphyton and C_3 macrophytes, respectively. Their

detailed zoological compositions are given in Table 2 and Fig. 4. A fourth one, limited to *Biomphalaria*, was based on bottom sediments and was only found during the wet season. The last two trophic chains were based on a combination of two carbon sources. A mix of seston and periphyton sources was found during the wet season for the aquatic beetles: *Gerytes* sp., *Hydrophilus* sp. and *Megadytes* sp., a water bug (*Belostoma* sp.) and a Baetidae mayfly (*Callibaetis* sp.). Using the mixing model, we observed a greater contribution of the periphyton (>60%). The mix of periphyton and macrophyte sources was found during the wet and dry seasons. During the wet season, we observed a similar contribution of macrophytes and periphyton as carbon sources to the populations of a beetle (*Berosus* sp.) and a bug (*Curicta* sp.). During the dry season, this combination has been observed in a limpet (*Hebetancylus* sp.) and a dragonfly (*Limnetron* sp.) with a major contribution of periphyton (66 and 78%, respectively).

When comparing the lower trophic levels of each chain, it should be emphasized that the lowest values of $\delta^{15}N$ belonged to the sediment-based chain (2.0 $\pm$ 0.1) and the highest values were observed in the seston chain (6.7 $\pm$ 0. 4), while the values of periphyton and macrophyte-based chains were intermediate (4.8 $\pm$ 0.6 and 3.6 $\pm$ 0.3, respectively). We assessed trophic fractionation of nitrogen and carbon between consumers and predators for each trophic chain and each season. The average $\delta^{15}N$ fractionation was 2.3‰ (SD = 1.30, n = 208). The average $\delta^{13}C$ trophic fractionation was 1‰ (SD = 1.1, n = 208). The seasons had no significant effect on positions of the different food chain (one-way ANOVA, F = 8.7, P > 0.001). The trophic levels (consumers, primary and secondary predators) significantly differed between trophic chains (one-way ANOVA, F = 3.05, P < 0.001) (Table 3).

Discussion

This exploratory work has some limitations, due to the fact that the potential sources used by consumers are heterogeneous and probably comprise several trophic levels. It was indeed impossible to clearly separate sources on the base of isotope values alone. However, our approach which takes into account the biological traits of taxa is increasingly used when addressing

Table 2 Food chain and trophic level of the macroinvertebrates

Type of chains	Trophic level	Season					
		Wet		Dry		Transition	
		$\delta^{13}C \pm SD$ $\delta^{15}N \pm SD$	Species	$\delta^{13}C \pm SD$ $\delta^{15}N \pm SD$	Species	$\delta^{13}C \pm SD$ $\delta^{15}N \pm SD$	Species
Sestonic	Primary predator	−31.5 ± 0.4 9.0 ± 0.5	Odonata: *Limnetrum* sp., *Proneura* sp. and *Sympetrum* sp.* Decapoda: *Palaemonetes invonicuos**	−33.0 ± 0.9 9.2 ± 0.7	Odonata: *Homeoura* sp.* *Libellula* sp. and *Proneura* sp.*	–	–
	Primary consumer	−34.2 ± 1.3 7.0 ± 0.6	Bivalvia: *Castalia* sp.* Odonata: *Acanthagrion* sp., *Dythemis* sp, *Libellula* sp. and *Tramea* sp. Ephemeroptera: *Campsurus violaceus* Coleoptera: *Megadytes* sp.	−34.1 ± 1.1 7.0 ± 0.3	Bivalvia: *Eypera* sp. Ephemeroptera: *Campsurus violaceus* Trichoptera: *Oecetis* sp.* Hemiptera: *Pelocoris* sp.* Coleoptera: *Gyretes* sp.*	−34.3 ± 1.1 7.4 ± 0.3	Ephemeroptra: *Campsurus violaceus* Odonata: *Acanthagrion* sp. Coleoptera: *Besorus* sp.*
Mixed between sestonic and periphytic	Primary consumer	−31.6 ± 0.5 7.0 ± 0.7	Ephemeroptera: *Callibaetis* sp.* Hemiptera: *Belostoma* spp. Coleoptera: *Gerytes* sp.	–	–	–	–
	Secondary predator	−31.5 9.0	Odonata: *Erytemis* sp.	−31.0 ± 1.2 10.1 ± 0.6	Decapoda: *Palaemonetes invonicuos*	−29.8 ± 0.7 9.4 ± 1.0	Decapoda: *Palaemonetes invonicuos*
Periphytic	Primary predator	−28.1 ± 2.3 7.0 ± 0.8	Gastropoda: *Acrorbis* sp.* Decapoda: *Dilocarcinus pagei* Coleoptera: *Tropisternus* sp. and *Cholus* sp.* Hemiptera: *Ranatra* sp.	−30.9 ± 0.9 7.4 ± 0.9	Odonata: *Dythemis* sp. and *Tramea* sp. Hemiptera: *Belostoma* spp.	−30.3 ± 0.6 7.0 ± 0.2	Gastropoda: *Acrorbis* sp. *Pomacea scalaris* Ephemereoptera: *Callibaetis* sp. Odonata: *Libellula* sp.* Hemiptera: *Belostoma* spp. and *Ranatra* sp.
	Primary consumer	−30.0 ± 1.4 4.3 ± 0.5	Coleoptera: *Dryops* sp.* and *Helocharis* sp.* Tricoptera: *Nectopsyche* sp. Hemiptera: *Pelocoris* sp.	−31.2 ± 0.7 4.5 ± 0.8	Gastropoda: *Hebetancylus* sp. Odonata: *Acanthagrion* sp. and *Oxyagrion* sp.	−28.4 ± 2.6 5.1 ± 0.6	Odonata: *Dythemis* sp.* Hemiptera: *Pelocoris* sp. Coleoptera: *Dryops* sp. *Hydrocanthus* sp.* and *Tropisternus* sp.*
Mixed between periphytic and macrophytic	Primary predator	–	–	−29.3 ± 0.9 7.0 ± 1.5	Tricoptera: *Nectopyche* sp. Odonata: *Limnetrom* sp.	–	–

Table 2 continued

Type of chains	Trophic level	Season					
		Wet		**Dry**		**Transition**	
		δ13C ± SD / δ15N ± SD	Species	δ13C ± SD / δ15N ± SD	Species	δ13C ± SD / δ15N ± SD	Species
	Primary consumer	−29.0 ± 1.7 / 6.7 ± 0.4	Hemiptera: *Curicta* sp. Coleoptera: *Hydrophylus* spp. and *Berosus* sp.	−29.4 ± 0.6 / 4.7 ± 0.6	Coleoptera: *Hydrophylus* spp.	− / −	−
Macrophytic	Primary predator	−26.1 ± 0.6 / 6.5 ± 0.5	Gastropoda: *Pomacea scalaris* Coleoptera: *Celina* sp.	−29.5 ± 1.2 / 5.9 ± 0.9	Coleoptera: *Celina* sp.* and *Cholus* sp.*	− / −	−
	Primary consumer			−28.9 ± 1.21 / 3.6 ± 0.3	Gastropoda: *Hebetancylus* sp. *Pomacae scalaris*	− / −	−
Sediment	Primary consumer	−27.7 ± 1.5 / 2.0 ± 0.1	Gastropoda: *Biomphalaria* sp.	−	−	−	−

* Limited data, confirmation needed

complex systems, since "There is no a priori reason to prefer one solution over another on a strictly isotopic basis. But in a real food web with various food sources, factors such as availability, palatability, and productivity will vary strongly among organic matter sources and these inequalities will determine the unique solution of what gets eaten and assimilated" (Benstead et al., 2006). Most of our taxa were small and their movements restricted. For a large number of specimens, the real choice was thus reduced. Moreover, the diet of most invertebrates can be inferred from the morphology of mouthparts and, for a given species, the range of possibilities is reduced. Then, in most cases, the choice of the source was between seston and periphyton and the use of the basic mixing model was therefore effective.

Sources

We found clearly distinct baseline values of dual isotopes between sources. Seston was more $\delta^{13}C$ depleted and more $\delta^{15}N$ enriched while the opposite was true for sediment values. The C_3 macrophytes and periphyton values were intermediate. A similar phenomenon was observed in Lake Baikal (Yoshii, 1999) and in temperate Canadian lakes (France, 1995). This is due to the differential uptake of isotopes by pelagic and littoral zone primary producers (Gannes et al., 1998; Jones et al., 2004; Finlay & Kendall, 2007).

The microscopic examination of seston revealed the dominance of phytoplankton (Chlorophyta and Chromophyta) and, to a lesser extent, the presence of zooplankton (Rotifera, Cladocera and Copepoda) and fine organo-mineral matter. The seston $\delta^{13}C$ values observed here are within the range of values observed on other sites in the Amazon Basin (Table 4). These variations are of low amplitude and there are almost no differences between seston and phytoplankton, probably because phytoplankton is the only food source of the zooplankton. Seston $\delta^{15}N$ values are scarce but remarkably close to the ones obtained in the present study (Oliveira et al., 2006).

$\delta^{13}C$ from bottom sediments had signatures intermediate between those of periphyton and C_3-macrophytes, possibly because both sources are deposited as detritus (fine and coarse particulate organic matter) in the superficial part of the lake. They are similar to those reported in other Amazonian studies (Table 4) and differ little from those of C_3 macrophytes. $\delta^{15}N$ values
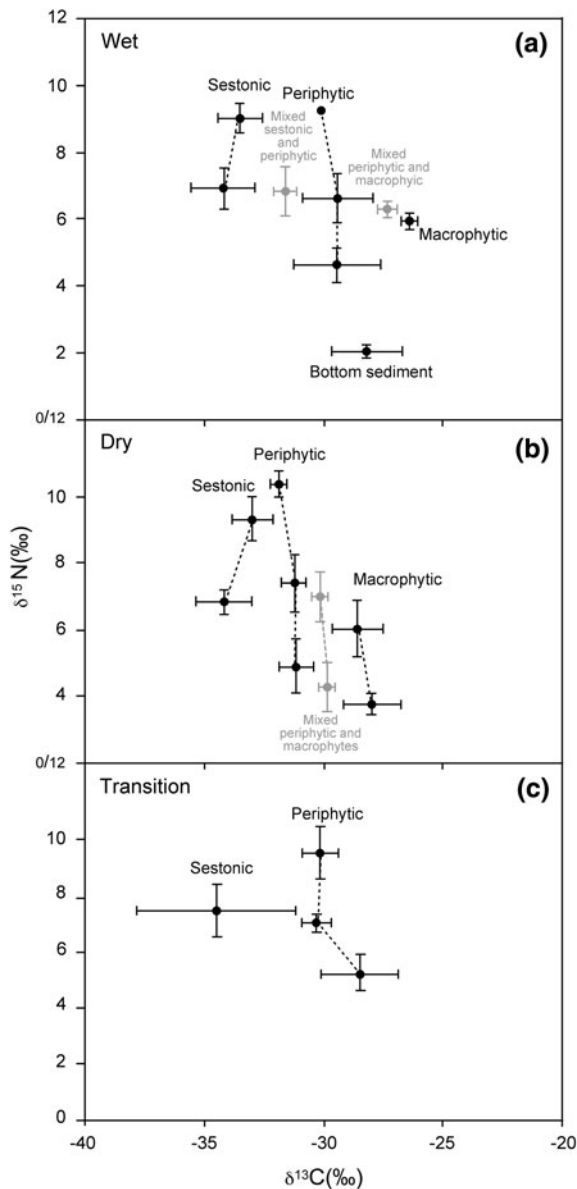
Fig. 4 Mean consumer $\delta^{13}C$ and $\delta^{15}N$ values associated with sources isotope signature during **a** wet season, **b** dry season, and **c** transitions season. The main trophic chains are represented by *solid symbols* and mixed trophic chains by *shaded symbols*

were strongly depleted, probably due to the denitrification process induced by bacterial activity (Jones et al., 2004; Finlay & Kendall, 2007).

Finally, we found that C_4 macrophytes had $\delta^{13}C$ and $\delta^{15}N$ signatures well separated from the other sources (−12.6 ± 1.6, 7.3 ± 0.6, respectively). These values were similar to those found by other

stable isotope studies in the Amazonian aquatic system (Araujo-Lima et al., 1986; Benedicto-Cecilio et al., 2000; Leite et al., 2002; Benedicto-Cecilio & Araujo-Lima, 2002; Oliveira et al., 2006), and other neotropical aquatic systems (Hamilton et al., 1992; Lewis et al., 2001; Jepsen & Winemiller, 2007). The $\delta^{13}C$ values of C_3 macrophytes and periphyton samples were also within the range of those published in previous studies (Benedicto-Cecilio et al.. 2000; Benedicto-Cecilio & Araujo-Lima, 2002; Manetta et al., 2003) (Table 4).

Relative importance of sources

The snail *Biomphalaria* was the only taxon exhibiting a strong dependence on bottom sediments as an energy source. *Campsurus violaceus* is a burrowing mayfly generally considered as a sediment feeder (Nolte, 1987), but was, in this study, clearly a seston feeder. It is probable that these mayflies live within bottom sediments during the day in order to avoid predation, but return to the water column at night in order to feed on seston. This poor contribution of sediments to the trophic chain may be due to anoxic conditions near the bottom, caused by the decomposition of plants and detritus under the floating vegetation (Enrich-Prast et al., 2004).

Throughout the year, periphyton was the most important carbon source for invertebrates in vegetation areas, while seston was the most important carbon source in open waters. These results are similar to those previously published by Thorp & Delong (1994); Thorp et al. (1998, 2006); Benedicto-Cecilio et al. (2000); Leite et al. (2002). Although the contribution of periphyton to the net primary production of the Amazon River floodplains is estimated at only 5% compared to the 65% of herbaceous macrophytes (Melack & Forsberg, 2001), it constitutes a much more important carbon source for aquatic macroinvertebrates. Floating vegetation roots certainly provide a good shelter for invertebrates (Junk, 1973; Junk & Piedade, 1997; Heckman, 1998), but the periphyton offers a significantly higher nutritive value than the plant matter itself (Enrich-Prast et al., 2004). C_3 macrophytes were only identified as a feeding source during the dry season, mostly for *Pomacea scalaris*. This result is consistent with observations made by Leady & Gottgens (2001) and Carlsson & Brönmarck (2006).

Table 3 Result of K nearest-neighbors randomization test between primary producers and taxonomic aquatic invertebrates

K - n e a r e s t   n e i g h b o r   p (<0.05)

Wet	Seston	C₃ macrophytes	C₄ macrophytes	Periphyton	Bottom sediment	Acanthagrion sp.	Acrobis sp.	Belostoma spp.	Berosus sp.	Biomphalaria sp.	Callibaetis sp.	C. violaceus	Curicta sp.	D. pagei	Dryops sp.	Dythemis sp.	Eupera sp.	Gyretes sp.	Hebetancylus sp.	Hylocharis sp.	Hydrophilus spp.	Libellula sp.	Limnetron sp.	Megadytes sp.	Nectopsyche sp.	Oxyagrion sp.	Pelocoris sp.	P. ivonicus	P. scalaris	Pronuera sp.	Ranatra sp.	Tramea sp.
Seston		< 0.001	< 0.001	< 0.001	< 0.001	0.2		< 0.001				0.12																				
C₃ macrophytes	< 0.001		< 0.001	< 0.001	< 0.001	< 0.001		< 0.001				0.05																				
C₄ macrophytes	< 0.001	< 0.001		< 0.001	< 0.001	< 0.001		< 0.001				< 0.001																				
Periphyton	< 0.001	< 0.001	< 0.001		< 0.001	< 0.001		< 0.001				0.14																				
Bottom sediment	< 0.001	< 0.001	< 0.001	< 0.001		< 0.001		< 0.001				< 0.001																				

Number of similarities (Wet row): 9 3 0 5 1 1 — 3 3 0 — 1 1 2 — 2 1 1 1 — 1 1 1 0 2 — 1 — — 0 1 0

Dry	C₃ macrophytes	C₄ macrophytes	Periphyton	Bottom sediment	Acanthagrion sp.	Belostoma spp.	C. violaceus	Dythemis sp.	Eupera sp.	Hebetancylus sp.	Hylocharis sp.	Hydrophilus spp.	Libellula sp.	Limnetron sp.	Nectopsyche sp.	Oxyagrion sp.	P. ivonicus	P. scalaris	Tramea sp.	Tropisternus sp.
C₃ macrophytes		< 0.001	< 0.001	< 0.001																

Number of similarities (Dry row): 2 4 0 2 0 3 — 0 — 1 0 1 1 0 1 2 0 0 0 0

Table 3 continued

Transition		
C₃ macrophytes	< 0.001	
Periphyton	< 0.001 **0.05**	
Bottom sediment	< 0.001 **0.05**	< 0.001
Acanthagrion sp.	**0.21** < 0.001	< 0.001 < 0.001
Acrobis sp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001
Belostoma spp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 **0.23**
Callibaetis sp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 < 0.001
C. violaceus	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 **0.08** < 0.001
Dryops sp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 < 0.001 < 0.001
Hebetancylus sp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 **0.05** **0.05**
Hydrophilus spp.	**0.05** < 0.001	< 0.001 < 0.001 < 0.001 < 0.001 < 0.001
P. ivonicus	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 < 0.001 < 0.001
Pelocoris sp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 **0.05** **0.08**
P. scalaris	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 **0.05** **0.08**
Ranatra sp.	< 0.001 < 0.001	< 0.001 < 0.001 < 0.001 < 0.001 < 0.001
Tramea sp.	< 0.001 < 0.001	**0.22** < 0.001 < 0.001 < 0.001 < 0.001
Number of similarities	2 1	0 0 1 4 2

P values were adjusted using the Bonferroni correction, $\alpha_{\text{adjusted}} = 0.025$

Bold values indicated a high similarity

Diet and seasonal changes

The diet of Amazonian aquatic invertebrates is very poorly known, generally extrapolated from knowledge obtained on related taxa from temperate zones. The morphology, in particular that of the mouthparts, gives us a good indication of the mode of acquisition but little information on the food itself. Although the present work is not a study of invertebrate diets, the identification of carbon sources and the determination of trophic levels can contribute to the subject. Some of our results are surprising given the generally accepted knowledge. The mayfly *Campsurus violaceus* is a good example (cf. Relative importance of the sources). Another one is *Dilocarcinus pagei*, a common crab. Species belonging to this genus prefer semi-aquatic habitats and are usually assumed to feed on detritus or terrestrial resources (Collins et al., 2007). Our results show, however, that *D. pagei* feeds preferentially on periphyton during the dry season and is a predator of smaller invertebrates consuming periphyton during the wet season. The Ancylidae, a group of limpets (small freshwater snails that have a simple shell conical in shape), are usually considered as microorganism and detritus feeders (Heckman, 1998). This family is represented in our study by the genus *Hebetoncylus*, which seems to depend both on periphyton and C₃ macrophytes during the dry and transition seasons. *Nectopsyche* (Trichoptera, Leptoceridae) and *Callibaetis* (Ephemeroptera, Baetidae) are both known as consumer of particulate organic matter (Wiggins, 2004; Dominguez et al., 2006). Our results indicate that they belong, as primary consumers, to the periphyton and macrophyte-based chains during the wet season. Unexpectedly, during the dry and transition season, *Nectopsyche* and *Callibaetis* appear to be first-level predators feeding on small, still unidentified, consumers of periphyton. *Oecetis* (Trichoptera, Leptoceridae) was found to belong to the seston-based chain as a consumer and this also represents a new perspective for the biology of this genus.

Some other seasonal changes in the sources are interesting to note. During the dry and transition seasons, the water bugs *Belostoma*, *Pelocoris*, and *Ranatra* all belong to the periphyton-based chain, but *Belostoma* also depends on the periphyton-seston mixed chain during the wet season. However, they occupy primary consumer and predator positions as

Table 4 $\delta^{13}C$ and $\delta^{15}N$ signatures (mean $\pm$ SD), bibliographic data on carbon sources and invertebrates of the Amazon floodplain system

Locality	Sources	Mean $\delta^{13}C \pm$ SD	Mean $\delta^{15}N \pm$ SD	Study
Central Amazon River, Manaus, Brazil	Phytoplankton	−33.3	–	Araujo-Lima et al. (1986)
	Periphyton	−26.8	–	
	C_3 Macrophytes	−27.6	–	
	C_4 Macrophytes	−12.9	–	
	Tree leaves	−27.6	–	
Central Amazon River, Manaus, Brazil	Phytoplankton	−33.3	–	Forsberg et al. (1993)
	Periphyton	−26.2	–	
	C_3 Macrophytes	−27.6	–	
	C_4 Macrophytes	−12.8	–	
	Tree leaves	−28.8	–	
Tapajós River basin, Pará State, Brazil	C_3 Trees	−29.7	–	Magnusson et al. (1999)
	C_4 Grasses	−13.4 ± 0.27	–	
Amazon River, Manaus and Pará State, Brazil	Phytoplankton	−37.2	–	Benedito-Cecilio et al. (2000)
	Zooplankton	−36.2	–	
	Periphyton	−28.3	–	
	C_3 Macrophytes	−30.0	–	
	Forest leaves	−30.0	–	
Amazon River, Manaus and Pará State, Brazil	C_3 Macrophytes	−28.9 ± 0.8	–	Adis & Victoria (2001)
	C_4 Macrophytes	−12.9 ± 1.1	–	
Several Amazonian rivers (white water), Brazil	Phytoplankton	−37.4 ± 3.8	–	Benedito-Cecilio & Araujo-Lima (2002)
	Periphyton	−28.8 ± 3.7	–	
	C_3 Macrophytes	−28.1 ± 1.8	–	
	C_4 Macrophytes	−13.0 ± 0.6	–	
	Forest leaves	−30.8 ± 1.6	–	
	Detrital aggregate	−29.2 ± 3.5	–	
Cuiabá River, Pantanal State, Brazil	Particulate organic matter	−26 to −32	–	Wantzen et al. (2002)
	C_3 Macrophytes	−27 to −31	−4 to −9.5	
	C_4 Macrophytes	−13.4 to −11.4	–	
	Organic sediments	−29.2 ± 1.6	–	
	Forest leaves	−28 to −31	−0.5 to −3	
Paranã River, Mato Grosso State, Brazil	Phytoplankton	−36.6 ± 2.33	3.1 ± 2.15	Manetta et al. (2003)
	Periphyton	−28.7 ± 2.70	2.7 ± 1.38	
	C_3 Macrophytes	−28.9 ± 1.21	1.2 ± 2.32	
	C_4 Macrophytes	−12.6 ± 0.62	1.2 ± 2.32	
	Riparian vegetation	−29.5 ± 0.87	1.3 ± 1.31	
Ichilo River, Cochamaba State, Bolivia	Particulate organic matter	−37.1 ± 06	5.2 ± 1.0	Rejas (2004)
	C_3 Macrophytes	−27.9 ± 0.2	6.8 ± 1.0	
	C_4 Macrochytes	−12.6 ± 0.3	7.1 ± 2.1	
	Leaf litter	−32.1 ± 0.7	3.4 ± 0.7	
Solimões River, Amazonas State, Brazil	Seston	−36.1 ± 02	6.6 ± 0.2	Oliviera et al. (2006)
	C_3 Macrophytes	−29.5 ± 0.87	1.3 ± 1.31	
	C_4 Macrophytes	−12.9	6.6	
	Terrestrial plants	−29.1 ± 1.2	4.5 ± 2	

Table 4 continued

Locality	Sources	Mean $\delta^{13}C \pm$ SD	Mean $\delta^{15}N \pm$ SD	Study
Macroinvertebrates				
Amazon River, Manaus and Pará State, Brazil	Grasshopper (*Stenacris* f. *fissicanda*)	−11.9	–	
	Terrestrial millipedes (*Mestosoma hylaeicum*)	−14.1 to −13.1	–	Adis & Victoria (2001)
Cuiabá River, Pantanal State, Brazil	Aquatic insects (*Campsurus*, mayflies)	−27.3 to −31.4	−3.3 to −5.3	Wantzen et al. (2002)
	Crustacea (shrimps and crabs)	−26.8 to −23.5	9.5 to 10.0	
Ichilo River, Cochamaba State, Bolivia	Diptera (*Chaoborus*)	−35.8	7.7	Rejas (2004)
	Benthos (Chironomidae, Ephemeroptera)	−39.7 ± 0.1	1.0 ± 0.2	
	Littoral insects (Odonata, Orthoptera)	−31.3 ± 0.8	6.5 ± 0.1	
Solimões River, Amazonas State, Brazil	C_3 Insects	−28.8	1.3	Oliviera et al. (2006)
	C_4 Insects	−15.0	6.0	
	Mollucs	−24	9.5	
	Shrimps	−24	4.5	

previously noticed (Bachmann & Mazzucconi, 1995; Pereira & Melo, 1998). A similar pattern is observed for the freshwater shrimp *Palaemonetes ivonicus.* Palaemonids are omnivores and belong to different trophic levels in the floodplain lakes of the Paraná River (Collins, 1999; Collins et al., 2007). In the Granja Lake, this shrimp occupies the highest trophic position in the invertebrate community, belonging to the seston-based chain during the wet season and to the periphyton-based chain during the dry and transition seasons. At the same time, $\delta^{15}N$ values of Palaemonids increase from wet to dry seasons.

The Coleoptera exhibit wide variation regarding trophic position and sources. During the wet and dry seasons adult Hydrophilids (*Berosus*, *Hydrophylus*, *Helocharis*, and *Tropisternus*) depend on periphyton and C_3 macrophytic sources. However, during the dry season, *Tropisternus* presents unclear trends towards C_4 macrophytes. For these reasons, they were not considered in our trophic association models. Spangler (1982) describes a similar position and considers them to be herbivores feeding preferentially on algae.

Many Odonata larvae present a high dependence on the seston source, with various trophic positions throughout the year. *Acanthagrion* is a primary consumer, but other genera vary from consumer to primary

and secondary predator, such as *Dythemis*, *Erythemis*, *Libellula*, *Limnetron*, *Proneura*, and *Tramea*. For this reason, many authors have considered the Odonata to be generalists (De Marco & Latini, 1998).

Baseline indicators

Finding an adequate baseline indicator can be difficult because the $\delta^{15}N$ values of aquatic consumers are affected by factors such as taxonomic level and life stage (Zah et al., 2001; Vanderklift & Ponsard, 2003; Anderson & Cabana, 2007). Primary consumers, such as snails and mussels, are usually chosen as baseline indicators because their larger body size and greater longevity compared to other candidates result in less seasonality in $\delta^{15}N$ values (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999). In the Bolivian Amazon, we could have proposed *Campsurus violaceus* and *Pomacea scalaris* as primary consumers for open water and vegetation areas, respectively. But if *Pomacea scalaris* feeds on C_3 macrophytes during the wet and dry seasons, it also feeds on periphyton during the transition season. For this reason, we have used the sources of each identified food chain as baselines.

Trophic chain length

The maximum length of trophic chains through all seasons was three trophic levels for the periphytic chain and two trophic levels for the sestonic chain. The macrophytic chain was variable, ranging from one trophic level during the dry season to two trophic levels during the wet season.

From consumers to top predators, we evaluated the trophic fractionation of the two isotopes. Concerning $\delta^{15}N$, we found an average of 2.3‰ per trophic level. This is less than the generally accepted value of 3.4‰ (Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 1999; Adams & Sterner, 2000; Post, 2002). In the meantime Minagawa & Wada (1984), Adams & Sterner (2000), and Vanderklift & Ponsard (2003) have reported a wide range of $\delta^{15}N$ trophic enrichment values across taxa and diets. Such variations could be due either to incomplete knowledge of food resources or to dynamic biogeochemical and environmental conditions. The most recent studies have revealed that trophic fractionation in invertebrates is smaller and more variable than usually assumed. McCutchan et al. (2003) reported 2.0‰, Vanderklift & Ponsard (2003) 2.5‰, Herwing et al. (2004) 2.3‰; values close to the one presently observed. The causes of these variations in fractionation are still debated, but they are often attributed to modifications of the balance of nitrogen isotopes during the deamination or transamination physiological processes (Karasov & Martínez del Rio, 2007; Koch, 2007).

Conclusion

To conclude, six trophic chains were identified. The three most important were based on seston, periphyton and C_3 macrophytes. A fourth one, marginal, was based on bottom sediments and appeared only during the wet season. The last two were based on a combination of two carbon sources: one mixed seston and periphyton sources during the wet season while the other mixed periphyton and macrophyte sources during the wet and dry seasons. The role of superficial sediments as an energy source was remarkably low and that of the C_3 macrophytes not as important as assumed. In summary, during the wet season, when the water level increases, macroinvertebrates show a stronger preference for seston as a carbon source. In contrast, during the dry season, when environmental conditions are more stable, macroinvertebrates show stronger preferences for periphyton and macrophyte sources. The main processes organizing food web structure in the Beni floodplain seem therefore to be linked to the hydrological seasonality, which determines changes in trophic levels and sources observed throughout the year.

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