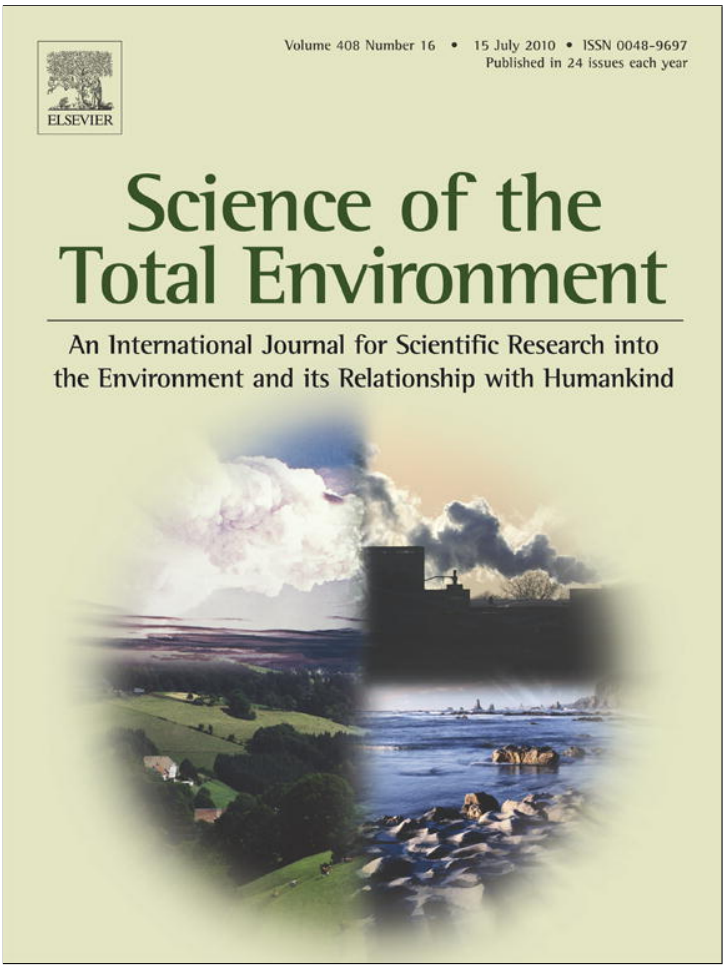

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Transfer of mercury and methylmercury along macroinvertebrate food chains in a floodplain lake of the Beni River, Bolivian Amazonia

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ABSTRACT

We have evaluated the mercury and methylmercury transfers to and within the macroinvertebrate communities of a floodplain lake of the Beni River basin, Bolivia, during three hydrological seasons and in two habitats (open water and vegetation belt). Using the stable isotopes $\delta^{13}C$ and $\delta^{15}N$, six trophic chains were identified during a previous study. Four are based on only one source: seston, organic matter from the bottom sediment, periphyton and macrophytes. Two are based on mixed sources (seston and periphyton in one case, periphyton and macrophytes in the other). During sampling, we found only one taxon that had surface sediment organic matter as food source and very few taxa whose trophic source was constituted by macrophytes. The periphyton was the most important source during all seasons; it produced the longest chain, with three trophic positions. Whatever the season and trophic source, all collected macroinvertebrates contained methyl mercury and the latter was biomagnified in all trophic chains that we identified. The biomagnification of methylmercury through invertebrate trophic chains accurately reflected the existence and length of these chains. Biomagnification was virtually non-existent in the sediment-based chain, low and restricted to the dry season in the macrophyte-based chain. It was significant in the seston-based chain, but limited by the existence of only two trophic levels and restricted to the wet season. Finally, it was very effective in the periphyton-based chain, which offers the highest rate of contamination of the source but, above all, the largest number of trophic levels.

1. Introduction

The high toxicity of mercury (Hg) and its widespread distribution in the ecosystems are among the major environmental problems of the Amazon (Lacerda 1997b; Boudou and Ribeyre, 1997; Fréry et al., 2001). Methylmercury (MeHg), the most abundant organic form of this metal, is efficiently biomagnified along food chains and responsible for very serious damage to human health (Dolbec et al., 2000; Dolbec and Fréry, 2001; Mergler and Lebel, 2001).

The sources of mercury in the Amazonian region are diverse. A few years ago, gold mining activities were considered to be the main mercury source to the aquatic environment (Nriagu et al., 1992; Boischio et al., 1995; Lacerda, 1997a; Meech et al., 1998; Maurice-Bourgoin et al., 1999). Recent studies have revealed that deforestation and soil erosion following human colonization are responsible for the increased transport and deposition of mercury in the aquatic ecosystems (Roulet and Lucotte, 1995; Roulet et al., 2000). Agricultural practices associated with the clearing and burning of the pristine forests lead to significant releases of Hg (Roulet et al., 1998; Farella et al., 2006). The human communities are mainly exposed to MeHg by fish consumption. In Central Amazonia, the deterioration of nerve functions and impaired psychomotor development in children are associated with exposure *in utero* (Dolbec et al., 2000; Dolbec and Fréry, 2001; Boischio and Henshel, 2000; Mergler and Lebel, 2001; Dórea and Barbosa, 2007).

The contamination of fish depends on water uptake and mainly on the functioning of aquatic food webs, which are extremely varied and complex in Amazonia (Meili, 1997; Roulet and Maury-Brachet, 2001). Four major primary producers have been identified: phytoplankton, herbaceous macrophytes, flooded forest and periphytic algae. Macrophytes generally produce the greatest biomass (Junk and Piedade, 1997; Melack and Forsberg, 2001). They are often assumed to be an important food source for herbivorous and detritivorous invertebrates and fish (Junk and Piedade, 1997; Leite et al., 2002) but are scarcely

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grazed by the aquatic macroinvertebrates. Still, the respective contributions of these four primary productions to the aquatic food webs have been insufficiently explored, though they are fundamental not only to understand their relative importance as supports of fish production, but also to understand the bioaccumulation and biomagnification of pollutants such as mercury.

Guimarães et al. (1995, 1998, 1999, 2000) have demonstrated that the periphyton covering the floating macrophyte roots in South American tropical aquatic ecosystems, sustains very high net methylation rates, reduced by addition of sodium molybdate, a specific inhibitor of sulfate-reducing bacteria. Later, Achá et al. (2005) demonstrated that sulfate-reducing bacteria are abundant and active in the periphyton of different macrophyte species from lakes of the Beni River floodplain. Research conducted in the lower Tapajós valley by Roulet et al. (2000) has identified the periphyton communities as the first link of the food chain and the main entry point for methylmercury.

Few studies have been published about mercury levels in macroinvertebrates of the Amazon River system (Lacerda et al., 1990; Callil and Junk, 2001; Leady and Gottgens, 2001; Dominique et al., 2007). Research efforts have focused on the fish communities and the available information is scattered throughout the Amazon region (Roulet and Maury-Brachet, 2001; Bastos et al., 2008). Generally, the MeHg concentrations in predator fish are above the critical values: 500 ng g^{-1} wet weight (Roulet and Maury-Brachet, 2001; Sampaio da Silva et al., 2006; Bastos et al., 2008). However, most of the studies attach little importance to the biomagnification of MeHg in aquatic food chains and the factors governing this process in the Amazonian region remain to be described and understood (Roulet et al., 2000). Given this situation, our main objectives were: (1) to measure the total Hg and MeHg concentrations from the trophic sources to the top predators in the invertebrate trophic chains of an oxbow lake, (2) to determine their seasonality and (3) to characterize MeHg transfers in invertebrate food webs.

The exact biology and ecology of any given invertebrate is difficult to define, due to the scarcity of data on this subject for the Amazon River system. The information obtained by simply measuring the concentration of MeHg in an invertebrate would therefore not be very useful. The zoological diversity of these ecosystems is so high that we can never be sure to capture the same taxon from one site to another or from one season to the next. Furthermore, for a given species, trophic sources or levels are subject to unpredictable seasonal changes, even more if these species have a high dietary plasticity, according to the availability of resources. We have therefore chosen to present and analyze our results according to the sources and trophic levels, rather than by taxon. This characterization was achieved through a previous study of carbon and nitrogen stable isotopes ($\delta^{13}C$, $\delta^{15}N$), described by Molina et al. (submitted for publication).

2. Material and methods

2.1. Study area

Our study was carried out in the oxbow lake La Granja (lat. 14°15′ 52″ S and long. 67°28′ 97″ W), in the Beni floodplain. The Beni River, a tributary of the Madeira River, has its origins in the Cordillera Real. Its waters drain the Andean summits and the Yungas region and enter the floodplain at Rurrenabaque, a town a few kilometers upstream from La Granja. The waters are whitewaters with heavy sediment loads, high nutrient concentrations and moderate pH (Guyot et al., 1999). As a result of the meandering of the main channel, there are numerous oxbow lakes of different age and connectivity levels with the main channel. The surrounding vegetation is a transition between the gallery forest and the floodplain (Fig. 1A, B and C).

The flooding dynamics play an important role in the functioning of Amazonian aquatic ecosystems, although in the Beni River system (headwaters of the Madeira River in Bolivia), the floods are shorter and more irregular than in Central Amazonia. The rapid evolution of the main channel, resulting from the deposit of the coarse sediments at the foot of the Andes, creates numerous and constantly evolving oxbow lakes (Gautier et al., 2007). These lakes are major components of the floodplain; they include open water as well as flooded or floating vegetation. During the dry season, when the water level is the lowest, lakes may be reduced to shallow, turbid pools and occasionally completely dry up. At rising and high water levels, the lakes expand, invading riverine forests or savannas and allowing the seasonal growth of emergent aquatic macrophytes in areas locally known as pantanales (floodplains).

In this region, the flood period coincides with the rainy season. The water level starts to rise in September or October and peaks in late February. During the peak of the wet season, the Beni River may become connected to the La Granja Lake and even inundate the adjacent floodplain and the riverine forest. The depth of the lake reaches an average of 2.5 m and an average area of 756 m^2. 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 to 1.5 m and an average area of 545 m^2. The waters of the lake compared to the Beni River have moderate concentrations of nutrients as well as neutral pH. The lake has high sediment load, which is a consequence of the inputs from the river during the wet season, but a consequence of sediment removal by the movements of water created by the winds during the dry season. The temperature variability in this region is low. High temperatures coincide with high precipitations (Fig. 1 E). An organic layer is restricted to the macrophyte belt along the lake shores, including some closed channels containing large wood fragments. Vegetation consists mainly of floating plants (*Eichhornia crassipes, Polygonum densiflorum* and *Salvinia auriculata*) and some marginal emergent plants (*Paspalum repens* and *Hymenachne donacifolia*).

2.2. Sampling methods

All samples were handled using clean field techniques. They were collected during three periods: wet season (high water), dry season (low water) and one transition season (rising water), in 2004 and 2005 (Fig. 1 D). The sampling was carried out in two areas: the open water ("pelagic") and the vegetation belt ("littoral"). In the open water, two sources were collected: seston and bottom sediment. The seston was chosen due to difficulties in acquiring pure samples of phytoplankton or zooplankton that could be used for the isotopes and mercury analyses, due to the amount of detritus and the very wide size distribution of phytoplankton, ranging from single cells to large filaments. Seston was collected as described by Roulet et al. (2000), with a plankton net made of a 63 µm nitex mesh. The net was washed with ultra-pure water for seston removal between each trawl and these were kept short due to net clogging. The bottom sediment samples were taken using a PVC pipe (diameter: 4 cm, length: 30 cm). The sediments of the upper 2 cm of each tube were immediately transferred to a zip-lock plastic bag.

Regarding macroinvertebrates, we used a set of diverse methods to obtain an inventory of the fauna as complete as possible. Some proved inadequate as the aquatic light-trap. Some were redundant: an extensive sampling carried out using a small trawl confirmed the poverty and often lack of the benthos sensu stricto. Baited traps and land light-traps (U.V. and blacklight) were also used to look for possible gaps. In the pelagic zone, the macroinvertebrates were collected with a Ponar grab sampler, specimens being removed from the central part of the sediments to avoid metal contamination. The most abundant species were rinsed using Teflon forceps and were kept alive in containers for approximately 3 h in order to clear their guts. Then, they were identified to family or genus level and placed in small vials.

In the vegetation belt, two types of sources were collected: macrophytes (free floating and emergent plants) and macrophyte-associated

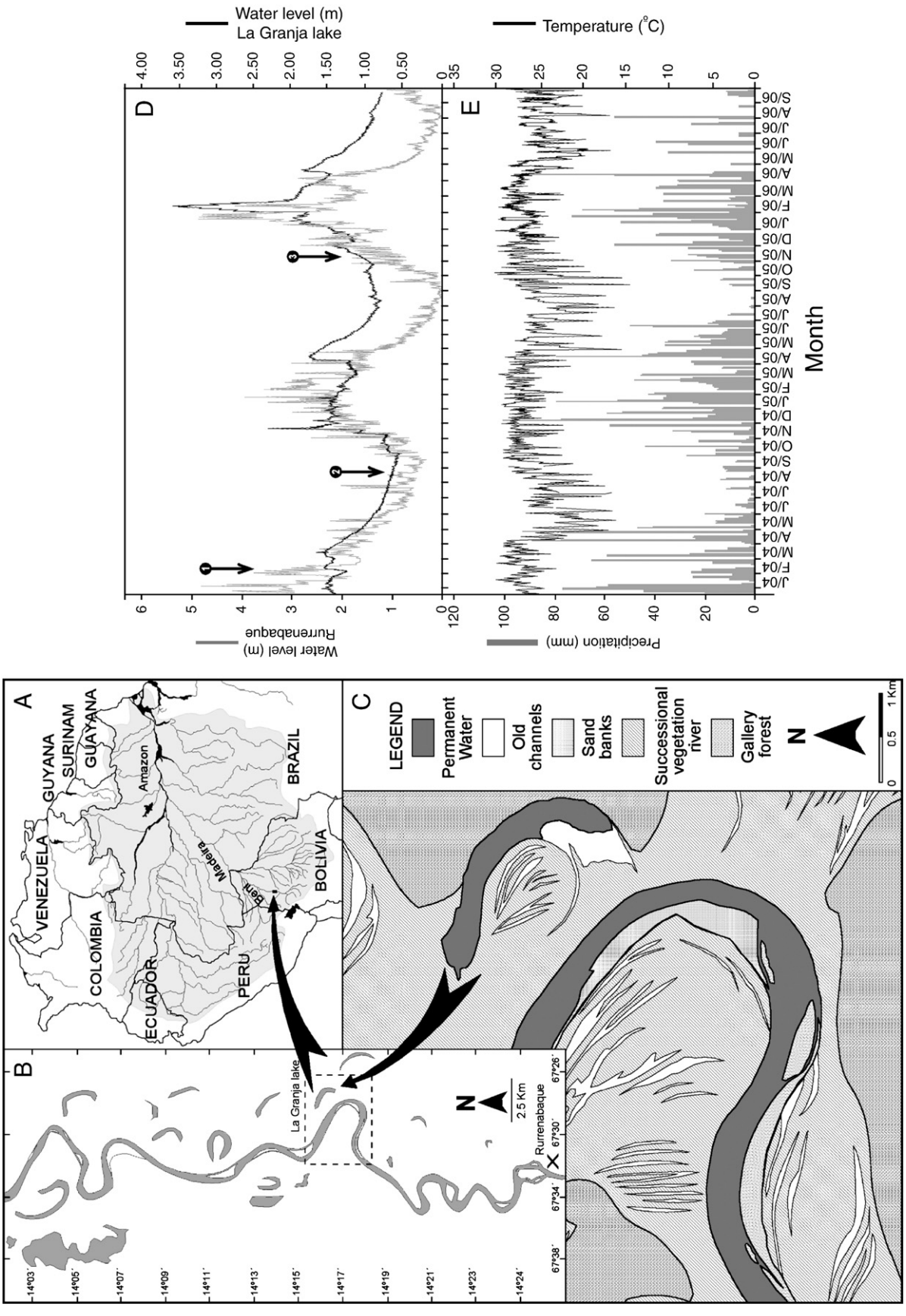

Fig. 1. Geographical location of the study area: (A) the Amazon basin in South America, (B) the Beni River, showing the classic meandering course and (C) geomorphological features of a floodplain, and La Granja Lake. During the inundation period the whole successional vegetation area is flooded. Annual variations for: (D) water levels of Rurrenabaque and the La Granja Lake, (E) mean monthly temperature and precipitation (IRD-SENHAMI). The sampling periods are indicated with a vertical arrow.

periphyton (heterotrophic and autotrophic organisms, as well as adhering particles of detritus). The macrophytes were collected by hand, rinsed several times in-situ to remove detritus and loosely-bound periphyton and placed in plastic bags. Periphyton samples were collected from intact root clusters of the most abundant macrophytes by repeated agitation with local water and centrifugation, as described by Roulet et al. (2000). Small portions of seston and periphyton samples were identified qualitatively under a microscope. The invertebrates were collected with a hand net (isolated with plastic to avoid any contact with metal). The most abundant invertebrates were also rinsed and kept alive in containers, then identified to family or genus level and placed in small vials, immediately frozen in coolers. Later in the laboratory, they were thawed, identified and measured. The samples were then lyophilized for 72 h and later ground into a homogeneous powder. For the isotopic and mercury analyses, we used the whole body of the invertebrates. Small organisms were pooled according to species, up to 1 g (dry weight) in order to perform the analysis.

2.3. Laboratory analyses

2.3.1. Dual stable isotopes

The analyses were carried out by the Stable Isotope Facility (University of California, Davis) using a Europa Hydra 20/20 stable isotope ratio mass spectrometer (IRMS), which determines the $\delta^{13}C$ and $\delta^{15}N$ as well as carbon/nitrogen ratio values. The isotopic compositions were quantified according to international reference material standards (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 differences between the sample and the conventional standard ($\delta^{15}N$ or $\delta^{13}C$ (‰) $= [(R_{sample} - R_{standard})/R_{standard}] \times 10^3$ (Peterson and Fry, 1987; Vander Zander and Rasmussen, 1999). Standards were run in duplicates every twelve measurements (within a run of 100 samples, which included 15 standards). The analytical precision of these measurements was 0.2‰ for $\delta^{13}C$ and 0.3‰ for $d\ \delta^{15}N$.

2.3.2. Total mercury and methylmercury

The total mercury (THg) and methylmercury analyses were determined by cold vapor atomic fluorescence spectrophotometry (CVAFS), following Pichet et al. (1999) and Roulet et al. (2000). For THg, 5 to 10 mg dry weight (DW) of powder samples were transferred to glass tubes and digested in 1 ml of 16 N HNO_3/6 N HCl (10:1) mixture during 6 h at 120 °C (Pichet et al., 1999). The solution was then diluted to 5 ml with ultra-pure water. Hg was reduced to elemental Hg (Hg0) vapor using a $SnCl_2$ solution. For the analysis, 200 µl of the digestion solution was injected in the CVAFS. MeHg was analyzed using the saponification technique (Bloom, 1989; Pichet et al., 1999). The MeHg separation was preceded by the digestion of 2 to 5 mg DW of powder in 0.5 ml of KOH/MeOH (1 g/4 ml) solution during 8 h at 6 °C (Pichet et al., 1999). MeHg was then converted to methylethylmercury (MeEtHg) with sodium tetraethylborate in a buffer solution at pH 4.5 (Bloom, 1989). MeEtHg was trapped in a Tenax® column, separated by gas chromatography and quantified using CVAFS. The detection limit for both THg and MeHg was approximately 10 pg of Hg, which corresponded to 2 ng g^{-1}. The accuracy and reproducibility of the method were calibrated by the analysis of certified reference materials (TORT-2 and DORM-2, National Research Council of Canada). The recovery range was 90.4% to 110% for THg and 88% to 102% for MeHg.

2.4. Data treatment

2.4.1. Dual stable isotope analysis

In order to analyze the trophic structure of the macroinvertebrate communities, we used two main methods of linear relationships. First, we investigated the relationship between the sources, or association of sources with the invertebrates and potential predators. This relationship was 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 of $\delta^{13}C$ and $\delta^{15}N$, based on the concept that a shorter distance between a food item and the isotopic ratios of the consumer implies greater contribution of this food to diet (Ben-David and Schell, 2001). If the isotope values did not show any relationship between sources and consumers, we compared differences in mean $\delta^{13}C$ signatures using the paired Student's *t*-test ($p<0.05$). If the $\delta^{13}C$ signature of a consumer was overlapped between two sources, we examined the relative contributions of these two sources through a linear mixing model (Peterson and Fry, 1987). More details about dual stable isotope analysis can be found in Molina et al. (submitted for publication). Of course, the trophic structure that we propose, although the most likely, remains hypothetical because it is not possible to resolve mathematically four production sources with two isotopes. But, these four sources are those of the entire lake. Most of our taxa are small and their movements are restricted compared with fish which migrate from river to lake or from lake to floodplain. For a large number of specimens, the real choice is between two sources.

2.4.2. THg and MeHg concentrations and biomagnification

Because of the scarcity and heteroscedasticity of the data, we used nonparametric Mann–Whitney *U* tests ($p<0.05$), and evaluated the differences in THg and MeHg concentrations across seasons, trophic chains and trophic levels. As an approximation of the magnification of mercury in the food chains, we assessed biomagnification factors of THg concentrations (BMF), using the following formula:

$$BMF = \textit{THg concentration in the predator} / \textit{THg concentration in the prey}\ \text{(unitless)}.$$

MeHg was expressed as the proportion of MeHg in relation to THg. All statistical analyses were carried out using SPSS Inc. version 11.0.4.

3. Results

3.1. Dual stable isotopes of sources and consumers

3.1.1. Sources

We evaluated 57 samples based on a previous study (Molina et al., submitted for publication). Sources included seston, bottom sediments, periphyton and C_3 macrophytes. The isotopic values are presented in Table 1, and these values were comparable to the ones given 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 and Araujo-Lima 2002; Oliviera et al., 2006). It must be emphasized that terrestrial vegetation (C_3 type) was encountered during the wet and transition seasons, but their values were not statistically different from those of the aquatic macrophytes of type C_3. In contrast, macrophytes of type C_4 (e. g. *P. repens*) had signatures that were well separated from other sources but these were excluded from analyses because they did not show any relationship with their consumers.

3.1.2. Invertebrate consumers and trophic associations

We analyzed 76 invertebrate samples, from a total of 26 species. The major contributors were: *Palaemonetes invonicus* (Crustacea, Decapoda), *Belostoma* sp. (Insecta, Hemiptera), *Tramea* sp. (Insecta, Odonata), *Hydrophilus* spp. (Insecta, Coleoptera), and *Pomacea lineata* (Mollusca, Gasteropoda). The isotopic compositions of the invertebrates showed greater seasonal variations in both $\delta^{13}C$ and $\delta^{15}N$ values than those of their trophic sources, and are presented in Table 2. For each of the three seasons, the invertebrates were grouped

Table 1
Isotope signatures, total mercury and methylmercury in sources. Mercury and methylmercury data show range values in dry weight.

	Molina et al. (submitted for publication)					This study			
Sources	Season	*n*	$\delta^{13}C \pm SD$	$\delta^{15}N \pm SD$	Trophic chains	*n*	THg (ng g^{-1})	*n*	MeHg (ng g^{-1})
Seston	Wet	5	-34.82 ± 2.39	6.33 ± 1.65	Sestonic	5	145–356	5	13.7–49.9
	Dry	4	-34.06 ± 0.76	6.25 ± 1.06		4	53–77	4	4–1.7
	Transition	4	-33.50 ± 1.15	-7.25 ± 0.22		4	89–114	4	3–7.3
Periphyton	Wet	5	-28.83 ± 1.57	3.56 ± 1.38	Periphytic	5	115–182	3	22.6–28.2
	Dry	5	30.53 ± 1.05	2.05 ± 0.52		5	54–86	4	7–12.3
	Transition	4	$-29,27 \pm 1.54$	3.14 ± 0.79		4	64–77	4	12–19
Macrophytes	Wet	11	-28.43 ± 1.79	4.62 ± 0.48	Macrophytic	11	64–102	6	3–10
	Dry	5	-28.92 ± 0.76	4.08 ± 0.43		5	45–67	5	10.2–14.3
	Transition	3	-29.97 ± 0.41	2.69 ± 0.11		3	78–92	3	6–9
Bottom sediments	Wet	5	-28.09 ± 0.57	0.69 ± 0.55	Sediment	5	62–79	4	0.4–1.2
	Dry	3	-29.84 ± 0.49	-0.88 ± 0.43		3	46–65	3	0.7–2.7
	Transition	3	-28.61 ± 0.40	-0.73 ± 0.21		3	64–77	3	0.2–0.5

in trophic chains, and trophic levels (Molina et al., submitted for publication). Six trophic chains were identified, four of which were based on a single source (seston, periphyton, macrophytes and organic matter of the bottom sediment) and two were based on two mixed sources (seston and periphyton in one case, periphyton and macrophytes in the other). The number of trophic levels varied according to the chain and the season. The minimum number of levels was one, which could indicate a trophic deadlock or, more likely, points to the scarcity of the predators. The maximum number of levels was three, with one consumer level and two predator levels (designated as primary and secondary predators).

The trophic chain based on bottom sediments was reduced to *Biomphalaria* sp. and only detected during the wet season. Its role seemed negligible. The chain based on macrophytes contained only one level during the wet season and two levels during the dry season. When the macrophyte chain was present, there was also a mixed chains (macrophytes/periphyton) with the same number of levels. The chains based on seston and periphyton were present throughout the year. They appeared relatively distinct; a one level mixed chain was only noticeable during the wet season. The longest and most diverse was the periphytic chain, which was always composed of three trophic levels. In comparison, the seston-based chain consisted of only two trophic levels during the wet and dry season and was reduced to one level during the transition.

3.1.3. Total mercury (THg) and methylmercury (MeHg) concentrations

THg and MeHg concentrations are given for the sources (Table 1). Such data, particularly MeHg concentrations, are scarce for the Amazon (Table 3). Regarding the macroinvertebrates, some samples were not heavy enough to allow both study of stable isotopes and mercury. Despite this, we analysed 76 samples for THg and 64 for MeHg (Table 2). This information allowed us to describe the biomagnification of methyl mercury for the three hydrological seasons, for the main trophic sources and all the trophic levels (Table 4). The mixed chains, transient and quantitatively unimportant (Molina et al., submitted for publication), were not included in this work.

THg varied from 64 (ng g^{-1} dw^{-1}) in primary consumers of the sediment chain to 555 (ng g^{-1} dw^{-1}) in the secondary predators of the periphytic chain. No significant differences were observed between concentrations in sources and those in primary consumers (Mann–Whitney *U* test, $p>0.05$). Throughout the year and for each chain, the concentrations of THg varied relatively little around 100 ng g^{-1} dw^{-1}, with the exception of the seston which exceeded 200 ng g^{-1} dw^{-1} during the wet season. Quantitatively, the non-MeHg fraction of THg was roughly constant or decreasing (Fig. 2), biomagnification being due to the MeHg fraction.

During the wet season the MeHg concentrations varied from 0.70 ng g^{-1} dw^{-1} in the source of the sediment chain to 489 ng g^{-1} dw^{-1} in the secondary predators of the periphytic chain. In contrast to THg, the MeHg concentrations increased gradually from lower to top trophic positions and significant differences were observed in all trophic levels. The dry season showed lower concentrations than the wet one. MeHg varied from 1.17 ng g^{-1} dw^{-1} in the sediment to 287 ng g^{-1} dw^{-1} in the secondary predators of the periphytic chain. All trophic positions showed statistical differences except the primary predators of the sestonic, periphytic and macrophytic chains. The lowest concentrations were recorded during the transition season, with MeHg values from 0.42 ng g^{-1} dw^{-1} in the source of the sediment chain to 159 ng g^{-1} dw^{-1} in the secondary predators of the periphytic chain. With the exception of the source-consumer step, all trophic positions showed statistical differences.

The biomagnification of MeHg through invertebrate trophic chains reflected the existence and length of these chains quite accurately, as it was virtually non-existent in the sediment-based chain; low and restricted to the dry season in the macrophyte-based chain; significant in the seston-based chain, but limited by the existence of only two trophic levels and during the wet season only; very effective in the periphyton-based chain, which showed the highest contamination at the source but, above all, the largest number of trophic levels. Moreover, it was the only chain that operated during the transition period, although at a lower level (Fig. 3).

4. Discussion

The lowest concentrations, found in sources and primary consumers, are similar to those provided by other studies of disturbed Amazonian regions (Table 3). In the Amazonian basin, data concerning methyl mercury in invertebrates are lacking. The highest concentrations observed in the La Granja Lake (secondary predators) are similar to those found by Dominique et al. (2007) in French Guiana (Table 3). They are also similar to those of some Amazonian predator fish for which data are available (Maurice-Bourgoin et al., 2000; Roulet and Maury-Brachet 2001; Sampaio da Silva et al., 2006; Bastos et al., 2008), confirming the generality of methyl mercury biomagnification whatever the biological model considered.

Cabana and Rasmussen (1994) proposed the use of $\delta^{15}N$ signatures in order to measure the mercury accumulation in aquatic food chains. Our results showed a good relationship between the increase of MeHg and that of trophic positions. In contrast, there was no evidence of biomagnification of the non-methylated fraction of mercury (non-MeHg), which sometimes decreased when the trophic level changed. The balance between organic and inorganic mercury is determined by rates of uptake, defecation, breathing and a combination of retention effects (Roulet and Maury-Brachet, 2001).

In the Bolivian Amazon, a high methylation activity, which is due mainly to sulfate-reducing bacteria, was observed in the periphyton covering the roots of floating macrophytes (Miranda et al., 2004; Achá et al., 2005). Our results are consistent with these studies, in that we found

Table 2
Isotope signatures, total mercury and methylmercury in macroinvertebrates.

Macroinvertebrates	Molina et al. (submitted for publication)						This study			
	Season	*n*	$\delta^{13}C \pm SD$	$\delta^{15}N \pm SD$	Trophic chains	Trophic level	*n*	THg (ng g^{-1})	*n*	MeHg (ng g^{-1})
Bivalvia										
Pisidiidae										
Eupere sp.	Dry	1	−35.79	7.3	Sestonic	1	1	129	1	18
Gastropoda										
Ampullariidae										
Pomacea scalaris	Wet	2	−26.14 ± 0.49	6.48 ± 0.49	Macrophytic	1	2	105–112	2	9–15
	Dry	3	−27.78 ± 1.21	2.65 ± 0.31	Macrophytc	1	3	100–146	3	21–30
	Transition	2	−29.26 ± 0.71	4.38 ± 0.11	Periphytic	1	2	110–147	2	32–51
Planorbidae										
Acrorbis sp.	Transition	1	−29.65	5.91	Periphytic	1	1	120	1	16
Biomphalaria sp.	Wet	1	−29.23	2.13	Sediment	1	1	64	1	1.15
Crustace										
Decapoda										
Palaemonidae										
Palaemonetes invonicuos	Wet	1	−32.36	8.88	Sestonic	2	1	452	1	367
	Dry	3	−31.85 ± 0.30	10.37 ± 0.39	Periphytic	3	3	275–881	3	189–597
	Transition	1	−29.37	9.47	Periphytic	3	1	218	1	159
Trichodactylidae										
Dilocarcinus pagei	Wet	3	−26.57 ± 2.96	6.41 ± 0.55	Penphytic	2	3	86–102	2	52–66
Insecta										
Ephemeroptera										
Baetidae										
Callibaetis sp.	Transition	1	−29.88	5.76	Perlphytec	1	1	134	1	46
Polymitarcydae										
Campsurus violaceus	Wet	2	−34.13 ± 1.30	6.02 ± 0.99	Sestonec	1	2	263–303	2	123–180
	Dry	6	−34.11 ± 1.13	6.80 ± 0.34	Sestonec	1	6	55–167	5	14–54
	Transition	7	−33.37 ± 1.31	6.09 ± 0.59	Sestonic	1	7	65–90	5	3–8
Odonata										
Anisoptera										
Aeshnidae										
Limnetron sp.	Wet	2	−34.11 ± 0.81	9.60 ± 0.59	Sestonec	2	2	459–533	2	319–395
Libellulidae										
Dythemis sp.	Dry	2	−30.85 ± 0.95	5.27 ± 1.29	Penphytic	2	2	137–143	1	47
	Transition	1	−28.70	4.53	Periphytic	1	1	56	1	25
Erythemis sp.	Wet	1	−31.08	7.78	Perlphytic	3	1	555	1	489
Libellula sp.	Dry	4	−33.78 ± 0.52	9.42 ± 0.55	Sestonec	2	4	93–143	3	41–81
Tramea sp.	Dry	2	−32.95 ± 0.86	8.21 ± 0.68	Perphytic	2	2	140–167	1	96
	Transition	1	−29.96	7.38	Periphytic	2	1	137	1	67
Zygoptera										
Coenagrionidae										
Acanthagrion sp.	Wet	2	−34.11 ± 0.81	6.90 ± 0.59	Sestonic	1	2	226–241	2	112–128
	Dry	1	−32.51	6.76	Perlphytic	1	1	67	1	15
Oxyagrion sp.	Dry	1	−32.68	7.08	Periphytic	2	1	137	1	47
Proloneuridae										
Pronuera sp.	Wet	1	−31.23	9.29	Sestonic	2	1	522	1	338
	Dry	1	−32.02	8.09	Sestonec	2	1	83	1	53
Hemiptera										
Belostomatidae	Dry	2	−31.29 ± 2.28	7.23 ± 1.08	Perlphytic	2	2	124–143	1	68
Belostoma spp.	Transition	4	−30.29 ± 0.60	6.96 ± 0.22	Periphytic	2	4	119–187	3	71–89
Naucoridae										
Pelocoris sp.	Wet	2	−30.03 ± 1.40	5.06 ± 0.72	Periphytic	1	2	117–176	2	35–63
	Transition	3	−27.55 1 1.21	6.01 ± 0.21	Perlphytec	1	3	50–123	2	15–17
Nepidae										
Ranatra sp.	Wet	2	−33.46	8.70	Periphytic	2	2	238–443	1	161
	Transition	1	−30.02	6.62	Periphytic	2	1	405	1	342
Coleoptera										
Curculionidae										
Cholus sp.	Dry	1	−28.71	5.13	Macrophytic	2	1	47	1	20
Dryopidae										
Dryops sp.	Wet	1	−27.59	3.70	Periphytic	1	1	122	1	18.3
Dytiscidae										
Celina sp.	Dry	1	−29.33	6.91	Macrophytic	2	1	219	1	116
Gyrinidae										
Gyretes ap.	Dry	1	−32.45	5.96	Sestonic	1	1	55	1	18
Hydrophilidae										
Helocharis sp.	Wet	1	−29.71	3.51	Penphytec	1	1	122	1	28
Hydrophilus spp.	Dry	3	−31.01 ± 0.50	3.94 ± 0.53	Periphytic	1	3	75–97	2	13–18
Noteridae										
Hydrocanthus sp.	Wet	1	−24.86	3.51	Macrophytic	1	1	108	1	9

higher %MeHg in periphyton than in other sources (Table 4 and Fig. 3). Moreover, the periphyton was the source which supported the longest and most stable trophic chains throughout the hydrological cycle.

Seston was the second important food source highlighted for invertebrate communities. The sestonic chain presented only one or two trophic positions and was thus shorter than the periphytic chain,

Table 3
Mercury and methylmercury concentrations in sources and macroinvertebrates from other areas of the Amazon.

Sources	Locality	Hg ng g^{-1} dw	MeHg ng g^{-1} dw	Author
Macrophyte: *Pontederia lanceolata*	Tanque dos Padres drainage Cuiabá (Mato Grosso State, Brazil)	10–130	–	Lacerda et al. (1991)
Macropflyte: *Salvinia auriculata*	Tucuruí reservoir, Pará state, Brazil	25–225	–	Aula et al. (1995)
Macropilyte:	Northern Pantanal Acunzal, Cuiabá, Mato Grosso State, Brazil		–	Leady and Gottgens (2001)
Eichhomia crassipes		23.5–34.0		
Sa1vinia auriculata		24.4–90.7		
Several macrophytes	Northern Pantanal Acurizal, Cuiabá, Mato Grosso State Brazil	46–246	–	Molisani et al. (2006)
Periphyton	Tapajós River basin, Pará State, Brazil	100–254	2.0–8.0	Roulet et al. (2000)
Periphyton	Northern Pantanal Acurizal, Cujabá, Mato Grosso State, Brazil	41.6–46.6	–	Leady and Gottgens (2001)
Periphyton	Petit-Saut, hydroelectric reservoir, Frech Guiana	116–161	32–64	Dominique et al. (2007)
Seston	Tapajós River basin, Pará State, Brazil	191–534	2.0–26	Roulet et al. (2000)
Seston	Petit-Saut, hydroelectric reservoir, Frech Guiana	114–123	10.0–28	Dominique et al. (2007)
Bottom sediment	Tapajós River basin, Pará State, Brazil	195–198	1.3–1.4	Roulet et al. (2000)
Bottom sediment	Northern Pantanal Acunzal, Cuiabá, Mato Grosso State, Brazil	21.1–45.5	–	Leady and Gottgens (2001)
Bottom sediment	Rivers of the Acre State, Brazil	10–184	–	Brabo et al. (2003)
Microinvertibrates				
Pomacea canaliculata	Tanque dos Padres, Cuiabá, Malo Grosso State, Brazil	10–130	–	Lacerda et al. (1991)
Ampullarius sp.	Paconé Pantanal, Mato Grosso State, Brazil	40–930	–	Lacerda et al. (1991)
Pomacea scalaris	Paconé Pantanal, Mato Grosso State, Brazil	70–2040	–	Callil and Junk (2001)
Pomacea lineata		10–1060		
Marisa planogyra		40–100		
Pomace sp.	Northern Pantanal Acurizal, Cuiabã. Mato Grosso State, Brazil	6.20–45.0	–	Leady and Gottgens (2001)
Hydrophilidae		5.50–9.20		
Benthic invertebrates	Petit-Saut, hydroelectric reservoir, French Guyana	283–574	192–503	Dominique et al. (2007)

but revealed the most effective transfer between the source and the consumer. This result was unexpected, because the MeHg production is lower in the water column (Guimarães et al., 2000; Coelho-Souza et al., 2006). However, Roulet et al. (2000) showed that, in lakes of the lower Tapajós River, MeHg can be readily transferred from sediments to the water column.

The low contribution of the macrophytic chain is consistent with the observations of Clarsson and Brönmarck (2006) and Leady and Gottgens (2001). Aquatic plants are incorporated in the aquatic food webs mostly in the form of detritus which floats or lies on the bottom, because direct consumption by aquatic consumers is unusual.

In the bottom sediments, MeHg concentrations were lower than in all other sources we measured, which is consistent with previous observations of lower Hg methylation in sediments than in periphyton (Guimarães et al., 1998, 2000; Miranda et al., 2004; Coelho-Souza et al., 2006). Sediments are an insignificant food source for aquatic macroinvertebrates, possibly because of the anoxic conditions near the sediment, due to the decomposition of plant detritus (Enrich-Prast et al.,

Table 4
Total mercury (THg) and methylmercury (MeHg) concentrations in trophic chains from sources to top predators (median and range values).

Season / Type trophic chains	Sources (S)				Primary consumers (PC)				Primary predators (PP)				Secondary predators			
	THg (ng g^{-1})		MeHg(ng g^{-1})		THg (ng g^{-1})		MeHg (ng g^{-1})		THg (ng g^{-1})		MeHg (ng g^{-1})		THg (ng g^{-1})		MeHg (ng g^{-1})	
	n	Median	*n*	Median	*n*	Median	*n*	Median	*n*	Median	*n*	Median	*n*	Median	*n*	Median
Wet																
Sestonlc	5	213 (154–356)	5	20 (14–50)	4	252 (241–303)	4	125 (112–180)	4	490 (453–522)	4	352 (328–443)	–	– –	–	– –
Periphytic	5	145 (115–182)	3	25 (22–62)	4	122 (117–176)	4	35 (63–18)	5	102 (91–443)	4	66 (52–161)	1	555 –	1	489 –
Macrophytic	11	76 (64–102)	5	6 (3–10)	3	108 (105–112)	3	12 (9–15)	–	– –	–	– –	–	– –	–	– –
Sediment	5	67 (62–76)	4	0.7 (04–12)	1	64 –	1	1.15 –	–	– –	–	– –	–	– –	–	– –
Dry																
Sestonic	4	53 (45–77)	4	4 (1–5)	8	105 (55–167)	7	18 (15–54)	5	97 (83–143)	4	53 (41–81)	–	– –	–	– –
Periphytic	5	72 (54–85)	4	10 (7–12)	4	81 (67–97)	3	15 (13–18)	7	143 (124–167)	4	82 (47–23)	3	435 (227–881)	3	287 (189–597)
Macrophytic	5	50 (45–67)	5	11 (10–14)	3	123 (100.143)	3	25 (21–30)	2	119 (20–219)	2	81 (47–116)	–	– –	–	– –
Sediment	3	55 (46–65)	3	1.17 (0.7–2.7)	–	– –		–		–		–		–		–
Transition																
Sestonic	4	92 (89–114)	4	4 (3–7)	7	79 (72–85)	5	7 (6–9)	–	– –	–	– –	–	– –	–	– –
Periphytic	4	71 (64–77)	4	15 (12–19)	8	110 (50–147)	7	28 (19–51)	6	166 (137–405)	5	79 (67–89)	1	218 –	1	159
Macrophytic	3	86 (78–92)	3	7 (6–9)	–	– –	–	– –	–	– –	–	– –	–	– –	–	– –
Sediment	3	73 (64–77)	4	0.42 (0.2–0.5)	–	– –	–	– –	–	– –	–	– –	–	– –	–	– –

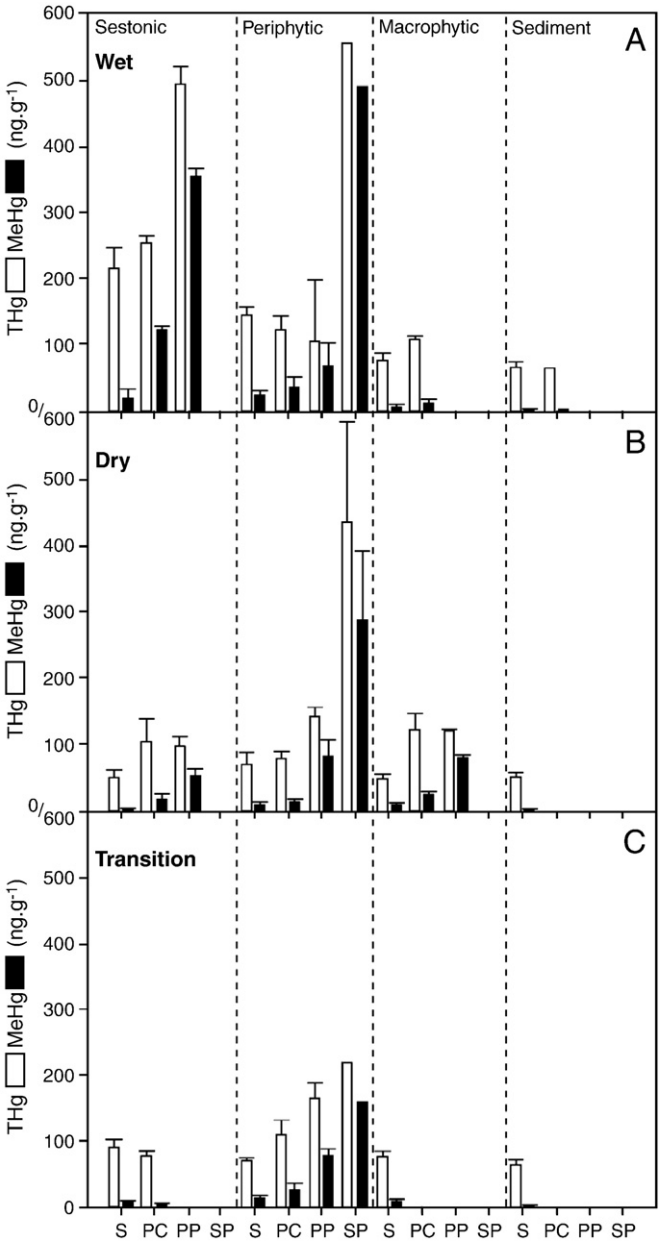

Fig. 2. Seasonal total mercury (THg) and methylmercury (MeHg) concentrations in different trophic chains from sources to top consumers. (A) wet season, (B) dry season and (C) transition season. The bars represent median values and the error bar represents the deviation from the median.

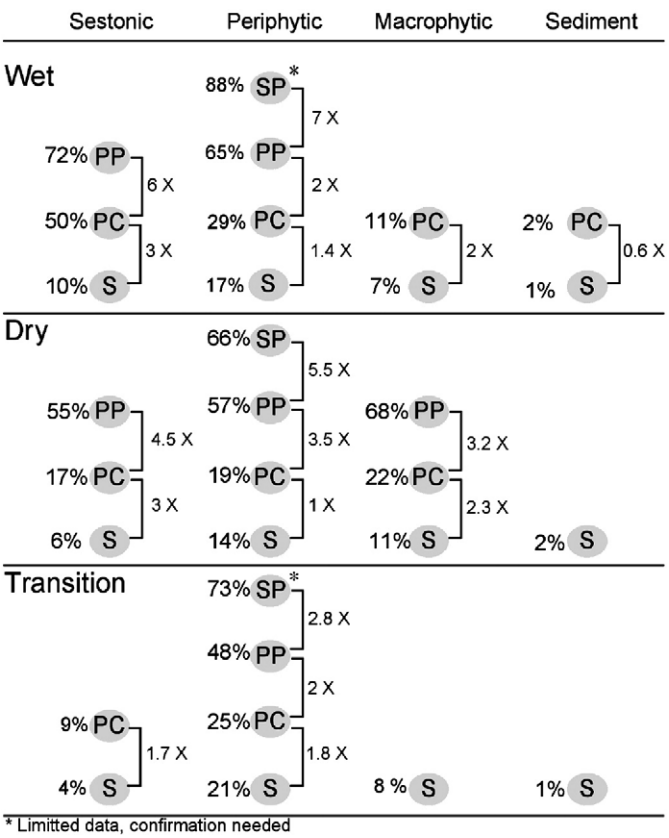

Fig. 3. Biomagnification factors of MeHg and percentages of MeHg (THg/MeHg) for different seasons and trophic chains identified. The letters indicate: S = Sources, PC = Primary consumers, PP = Primary predators and SD = Secondary predators.

2004). This anoxia, and the deposition or movements of sediment during the inundations, do not favor the development of benthic macroinvertebrates, whereas the communities associated with macrophytes, especially the floating ones, are less affected by the fluctuations of the water level.

4.1. Implications of water level changes on mercury transfer

The highest THg and MeHg concentrations were generally found during the wet season, a phenomenon also observed on the lower Tapajós River by Roulet et al. (2000), who suggested that the erosion of deforested soils explains the release of mercury to aquatic systems and its recent enrichment in sediments. In the Beni River, the lakes are connected with the main river channel during the wet season and their waters become loaded with sediments of Andean origin, which contain inorganic mercury associated to Al and Fe oxyhydroxides (Maurice-Bourgoin et al., 2002). Moreover, because of the flooding, the supports (stems and roots) available for the development of the periphyton increase considerably, and the settling of inorganic and organic particles, containing nutrients and labile organic matter, stimulates biological activity and the convertion of inorganic mercury to MeHg (Roulet et al., 2000). We have demonstrated here that the development of aquatic macroinvertebrate communities depends mainly on periphyton and, for this reason, it is much more important in the littoral zone than in the main channel.

The invertebrate contamination may have consequences for human health only in terms of consumption by fish. In the Mamoré River basin, another Bolivian tributary of the Madeira River, studies have reported the dominance of aquatic invertebrates among the food items of the majority of fish from headwaters (Ibañez et al., 2007; Tedesco et al., 2007) to floodplain (Pouilly et al., 2003). This issue requires further study. The Amazon River system has produced the most diverse fish fauna on the planet (Junk et al., 2009). If, as suggested by the flood pulse concept (Junk et al., 1989), the biological productivity of the Bolivian floodplains is due to the annual alternation of flood and recession, the role of flooded areas in fish production must be better documented. These areas, in the Beni, consist of swamps, savannas or pantanales rather than the forests found further north in the Pando or in Brazil (varzea). They are perfect places for periphyton growth and the contribution of the periphyton-invertebrates chain to the overall ecological productivity is probably underestimated. Many fish use the flooded areas for reproduction and large populations remain trapped by the declining water level, which leads to a high predation pressure on the aquatic invertebrates.

5. Conclusion

This work was designed as part of an extensive study of the mercury cycle in the Bolivian Amazon. As the sulfate-reducing bacteria

responsible for the production of methyl mercury are mainly localized in the surface sediments and periphyton, and as the bottom of the aquatic systems and the vicinity of submerged plants are the two richest habitats in macroinvertebrates, we hypothesized that these macroinvertebrates play a key role in the incorporation of methyl mercury in trophic web leading to fish and human populations.

A first ecological study confirmed that invertebrate populations were rich and diverse in vegetation zones but showed that the plankton was part of their food source. In contrast, the bottom was very poor and the organic matter of the superficial sediments did not contribute to the biological production. Such research is new for the Amazon basin and these first results need to be confirmed. Furthermore, we have to distinguish what is due to the local conditions of the Andean foothills from more general phenomena. For example, it is likely that benthic poverty is due to intense sedimentation and accumulation of plant material that creates anoxic conditions, phenomena that diminish downstream.

Regardless of their location or trophic source, all invertebrate food chains showed a biomagnification of methyl mercury without significant differences for a same trophic level. This confirms recent observations on the rapid diffusion of methyl mercury in the aquatic systems. Differences between hydrological seasons are more pronounced, due to the input of mercury during floods. The importance of invertebrates in the methyl mercury cycle is not related to their location in the aquatic systems, but to the importance of periphyton as a food resource.

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