

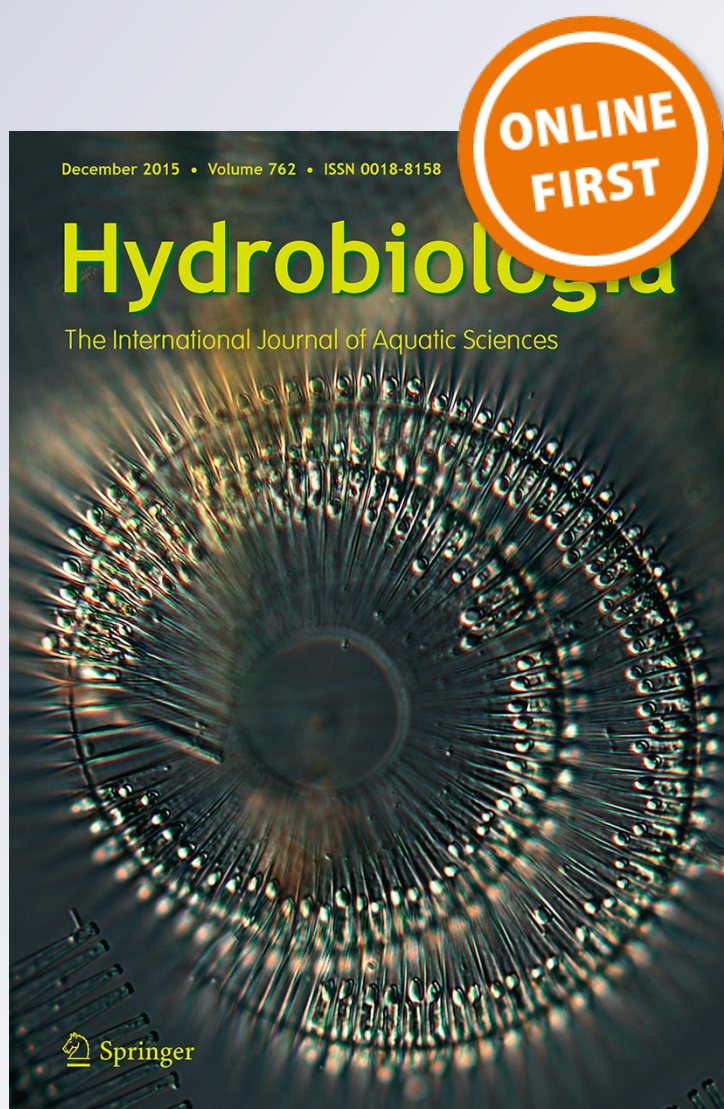
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Sources contribution for benthic invertebrates: an inter-lake comparison in a flood plain system

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Abstract To explore temporal variation in trophic relationships of benthic invertebrates in the Middle Paraná River floodplain, we performed stable isotopes analysis (SIA) in two lakes with contrasting morphologies during both dry and flooding periods. Lake 1 is permanently connected, large and deep with a narrow aquatic–terrestrial transition zone (ATTZ), and Lake 2 is temporarily connected, small and shallow with a wide ATTZ. The source contribution analysis showed that macrophytes and sediment particulate organic matter are important basal resources. We found sharp temporal variations with regard to gatherer–collectors in Lake 2, being sediment particulate organic matter the most important source during dry

period. However, during flooding, macrophytes and epiphyton increased their importance. Our results reveal temporal variations in trophic interactions, suggesting that hydrologic and morphologic characteristics of water bodies can be important factors determining food web structure. Besides, we provide evidence from floodplain lakes of the Middle Paraná River, which contradicts the general idea that algae is the main carbon source in floodplain rivers.

Keywords Benthic invertebrates · Wetlands · Stable isotopes · Trophic relationships · Neotropics

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Introduction

The importance of large rivers for human societies is evident as these ecosystems provide drinking water, navigation networks and fisheries among other ecosystem services. Likewise, these rivers are amongst the most altered and threatened ecosystems on earth. Indeed only 35% of large rivers remain unaffected, by human regulation with the purpose of, for instance, flood control, navigation, hydropower generation and water supply (Nilsson et al., 2005). In this context, it is clear that understanding of the functioning of large rivers and their floodplains is a priority, as it is a first step in order to conserve and restore them (Tockner & Stanford, 2002).

One of the most important aspects of ecosystem function is the relative importance of basal resources

that support food webs. Most of the current knowledge about carbon sources in large floodplain rivers reveals that the relative importance of basal resources can vary among and within ecosystems. For example, benthic and planktonic algae were the most important sources in floodplain lakes of the Macyntrre River (Australia) (Medeiros & Arthington, 2010). However, Reid et al. (2011) concluded that hydrological connectivity of floodplain water bodies can influence the relative importance of basal resources in Australian billabongs. In the Mississippi River, Delong & Thorp (2006) concluded that algal production would support food webs in that system. However, they acknowledged that the detrital pathway could be important for certain consumers and stressed the need for further studies to account for temporal variations in the relative importance of carbon sources. Similar results were reported by Herwig et al. (2007) in the Upper Mississippi River basin. On the other hand, C₃ macrophytes were the most important carbon source in the main channel and oxbow lakes of in the Brazos River (Texas), although in the latter, algae could be important for small fishes (Zeug & Winemiller, 2008). Likewise, in Lower Missouri River basin, C₃ leaf litter from the floodplain forest appeared to support food webs (Delong et al., 2001). Also in Neotropical region several studies have shown that the relative importance of carbon sources varies temporarily and spatially. In the Amazon, the phytoplankton was identified as the main energy source (Araujo-Lima et al., 1986; Forsberg et al., 1993) being C₄ grasses the least important source. More recently, C₃ pathway was confirmed as the main energy pathway for fishes in this system (Oliveira et al., 2006; Mortillaro et al., 2015). Studies in floodplain lakes of the Brazilian Pantanal have indicated a seasonal change between organic matter derived from decomposing macrophytes during the isolation phase, and from fresh C₃ plants and C₄ grasses during early flooding, resulting in significantly different isotope ratios and trophic levels of floodplain fish (Wantzen et al., 2002, 2011). In tributaries of Orinoco River, Jepsen & Winemiller (2007) concluded that algae production would be the most important energy source followed by C₃ macrophytes. Similar results had been reported by Hamilton et al. (1992) and Lewis et al. (2001) from the Orinoco River floodplain. In the Upper Paraná River (Brazil), Hoeninghaus et al. (2007) indicated that in low gradient rivers, C₃ macrophytes are the most important source,

while phytoplankton supports food webs in high gradient rivers and reservoirs. In summary, evidence suggests that algae are the most important source followed by C₃ macrophytes in most of large rivers systems. However, the relative contributions of the C sources (higher C₃ or C₄, plants, or algae) could be composed according to the hydrological-morphological situation of the floodplain and by the connectivity between river mainstem and floodplain water body.

In the Middle Paraná River, the information about carbon sources is limited to one study performed by Marchese et al. (2014) in a highly connected floodplain lake. In that survey, autochthonous production (epiphyton and biofilms) was indicated as the main carbon pathway. Data of carbon and nitrogen isotopes of organic matter sources (primary producers and detritus) and consumers (all taxa) did not reveal significant temporal differences in this lake; however, the basal sources were on average slightly more enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ during low water levels than during high water levels. These results challenge the Flood Pulse Concept (Junk et al., 1989; Junk & Wantzen, 2004) predicting that the relative importance of the autochthonous and allochthonous sources would vary between flood and dry seasons.

The Middle Paraná River is less affected by anthropogenic activities than most of large floodplain rivers, as there are no dams in this reach and the river runs largely through a non-industrialized region of Argentina. This makes the Paraná River a useful control river to compare with other hydrologically more impacted riverine ecosystems. Thus, once morphological and hydrological features of a water body can affect the carbon pathways of their food webs, it is important to extend our knowledge of this system by assessing the importance of basal resources in water bodies with different characteristics such as size, depth and connectivity degree.

In the present study, we aimed to compare the relative importance of carbon sources in two floodplain lakes with different characteristics such as the relative size of the aquatic–terrestrial transition zone (ATTZ sensu Junk et al., 1989), connectivity and size. For that purpose, we selected a large, permanently connected floodplain lake with a narrow ATTZ (Lake 1) and a small, shallow, temporarily connected floodplain lake with a wide ATTZ (Lake 2). We predicted that C₃ macrophytes would be more important in Lake 2 during flood period. This prediction is

based on the great abundance of these macrophytes in the ATTZs.

Methods

Study area

Lake 1 is relatively deep (max depth 8 m) and is permanently connected to the main channel of the Middle Paraná River. The area of this lake ranges from 27.9 ha (during the dry period) to 39.56 ha (during the flood period), which represents an increase of 41%. Lake 2, in turn, is a shallow floodplain lake (max depth 1 m) that is temporarily connected with a secondary channel of the Middle Paraná River when the water level reaches 13.6 m a.s.l (Hydrometric Station Santa Fe Harbour gauge). The area of this lake ranges from 0.7 ha (during the dry period) to 8.34 ha, which represents a drastic area increase of more than 1,000% (Suppl. 1). In order to avoid the mask effect of isotopic turn over time, each lake was sampled at least 1 month after the beginning of each period (flood or dry). Thus, for Lake 1, samples were collected during the flood periods (14.5 m a.s.l.) from November 2009 to March 2010 and during the dry period (water level of 11.5 m a.s.l. at the Santa Fe Harbour Hydrometric Station) from September to December 2010. In Lake 2, samples were also collected during the dry period (12 m a.s.l.) in March 2011 and the flood period (15 m a.s.l.) in October 2012. We sampled three potential organic matter sources for benthic macroinvertebrates: the dominant macrophyte in the Middle Paraná River, *Ludwigia peploides* (Kunth) P. H Raven (Sabbatini & Lallana, 2007; Schneider et al., 2015), sediment particulate organic matter (SOM) and epiphyton. This selection was based on available information of trophic habits of benthic macroinvertebrates in this region (Estebenet, 1995; Saigo et al., 2009; Galizzi et al., 2012).

To sample C₃ macrophytes, we collected leaves of *L. peploides*, and then we rubbed and rinsed them with distilled water to remove any attached materials. Epiphyton, in turn, was collected from the stems and leaves of *L. peploides* and separated from the detritus by density fractionation in colloidal silica Ludox®AM-30 (density 1.210 g/cm³) diluted with deionised water according to Hamilton et al. (2005). The SOM was collected with a Mud Snapper (Rigosha®, 100 cm²) in

non-vegetated areas. We collected the upper 2–3 cm of the sediment layer (including fine and ultrafine organic matter), and the coarse particulate organic matter was removed from the sample.

Benthic macroinvertebrates were collected with a Rigosha® Mud Snapper (100 cm²), except for the apple snails (*Pomacea canaliculata* Lamarck), which were handpicked. After allowing time for gut clearance (12 h approximately), individuals were rinsed with distilled water to remove the attached inorganic and organic materials. Organisms were classified to the species or genus level, except for the Hirudinea, which were identified to class, while the Libellulidae (Odonata) were identified to family.

The foot muscle of *P. canaliculata*, the whole body of the other invertebrates (Oligochaeta, Chironomini, *Hyalella curvispina* Shoemaker, Hirudinea and Libellulidae) and the sampled sources were dried at 50°C to a constant weight. Next, the samples were ground to a fine powder, and known aliquots were stored frozen in tin capsules. To acquire enough invertebrate mass to determine the stable isotopes, we pooled the species of subfamily Chironomini (mainly *Chironomus* sp.) as well as the Oligochaeta species (*Dero* sp. and *Aulodrilus pigueti* Kowalewski). Thus, each isotopic signature represented pooled individuals in the case of Oligochaeta and Chironomini but individuals regarding *P. canaliculata*, Libellulidae and Hirudinea.

Isotopic ratios were determined with an Isolink Thermo Scientific Trace GC mass spectrometer coupled to a Carlo Erba elemental analyser (INGEIS-CONICET-UBA, Argentina).

The ratio of stable isotopes was expressed in delta (δ) notation:

$$\delta = [(R_{\text{sample}} \times R_{\text{standard}}^{-1}) - 1] \times 1000,$$

where δ is the isotopic ratio, and R_{sample} and R_{standard} are the fractions of heavy to light isotopes in the sample and the standard, respectively (Peterson & Fry, 1987). Standard values for $\delta^{13}\text{C}$ was the Pee Dee Belemnite, while standard value for $\delta^{15}\text{N}$ was atmospheric Nitrogen.

As high lipid levels (indicated by a high C:N) may drive $\delta^{13}\text{C}$ values in a negative direction (McConaughy & McRoy, 1979; Matthews & Mazumder, 2005), the consumer $\delta^{13}\text{C}$ data were normalized using the equation $\delta^{13}\text{C} = -3.32 + 0.99 (\text{C:N})$, when C:N ratios were higher than 3.5 according to Post et al. (2007).

Data on isotopic signatures of the sources and consumers of Lake 1 (except for those of Hirudinea and Libellulidae) were obtained from Marchese et al. (2014) (Table 1). Hirudinea and Libellulidae samples in Lake 1 were collected on exactly the same dates as Marchese et al. (2014).

Data analysis

To perform the statistical analysis, we grouped consumers into functional feeding groups (FFG) according to Merritt & Cummins (1996), Cummins et al. (2005) and our own studies (Saigo et al., 2009; Galizzi et al., 2012). Thus, we considered Oligochaeta, Chironomini and *H. curvispina* to be gatherer–collectors. *P. canaliculata* (Gasteropoda) was considered to be a scraper, and Libellulidae nymphs (Anisoptera, Odonata) and leeches (Hirudinea) were grouped as predators.

The changes of the position of isotopic signatures in δ -space could suggest changes in resources use (Schmith et al., 2007). Thus, we assessed the displacement of centroids of each FFG and sources in δ -

space by calculating the direction (angles) and magnitude (length) of shift from the dry period to flooding periods in both lakes.

We determined the contribution of each source to the scrapers and gatherer–collectors by applying a mixing model using the SIAR R package (Parnell et al., 2010), which is based on a Bayesian framework. The trophic enrichment factor (TEF) used for ^{13}C was 0.4‰ (SD = 1.3‰) according to Post (2002). While mixing models are highly sensitive to the ^{15}N TEF, it is very important to apply an objective criterion to decide which ^{15}N TEF to use, and a widely used ^{15}N TEF is 3.4‰ (SD 1‰) as proposed by Post (2002). However, this TEF could be mostly valid for species that feed on protein rich resources (McCutchan et al., 2003). In contrast, Vanderklift & Ponsard (2003) proposed a ^{15}N TEF of 2.5‰ (SD 1‰), and these authors also noted that mollusks and detritivores present significantly lower ^{15}N TEFs (the mean ^{15}N TEFs reported by Vanderklift & Ponsard (2003) are $1.3 \pm 0.3\%$ for molluscs and $0.53 \pm 0.94\%$ for detritivores). Thus, we applied the mixing polygon simulation in R to decide which ^{15}N TEF to use (Smith

Table 1 Isotopic signatures of consumers and sources in Lake 1 and Lake 2 during drought and flooding seasons

	Drought							Flooding						
	$\delta^{13}\text{C}$	S.D. ^{13}C	$\delta^{15}\text{N}$	S.D. $\delta^{15}\text{N}$	C:N	n	n/ pool	$\delta^{13}\text{C}$	S.D. $\delta^{13}\text{C}$	$\delta^{15}\text{N}$	S.D. $\delta^{15}\text{N}$	C:N	n	n/ pool
Lake 1														
Macrophytes	−29.36	1.20	6.48	2.61		6		−28.88	0.80	7.16	1.40		9	
SOM	−26.22	1.20	3.45	0.56		6		−25.05	1.21	3.49	0.12		3	
Epiphyton	−29.90	1.23	9.79	8.13		3		−31.39	8.57	5.67	2.93		3	
Scrapers	−26.62	0.33	6.58	0.42	3.81	3	1	−26.55	1.72	6.45	0.89	3.85	5	1
Gatherer– collectors	−27.95	1.25	7.54	1.00	4.89	7	>10	−26.54	2.18	7.65	1.93	4.99	4	>10
Predators	−25.78	3.26	10.21	0.42	4.30	6	5	−27.25	2.07	9.97	1.34	4.15	4	5
Lake 2														
Macrophytes	−28.20	0.63	6.52	0.24		4		−28.68	0.21	4.75	0.65		4	
SOM	−28.33	0.68	2.76	0.25		4		−28.23	1.16	2.80	0.87		4	
Epiphyton	−18.20	1.99	1.80	0.43		3		−19.88	1.99	4.12	0.43		5	
Scraper	−26.03	1.87	4.27	1.24	4.27	3	1	−25.53	0.49	5.03	0.25	4.53	3	1
Gatherer– collectors	−27.82	1.85	3.35	0.72	5.68	18	>10	−23.98	0.44	5.80	0.72	5.86	4	5
Predators	−29.20	0.81	6.11	2.38	5.01	10	5	−28.73	0.78	8.21	0.71	4.88	8	5

SE Standard error, *n/pool* individuals pooled per sample

*Data obtained from Marchese et al. (2014)

et al., 2013). In our case, while we did not expect to have missed any relevant sources for the studied consumer organisms, we adjusted the model using three alternative ^{15}N TEFs based on values from the literature: Firstly, we applied the $\delta^{15}\text{N}$ TEF of 3.4‰ (SD 1‰) proposed by Post (2002). Alternatively, we used the ^{15}N TEF of 2.5‰ (SD 0.11‰) recommended by Vanderklift & Ponsard (2003). Finally, we used the specific ^{15}N TEFs of 1.3‰ (SD 0.3‰) and 0.53‰ (SD 0.94‰) for molluscs and detritivores, respectively, as reported by Vanderklift & Ponsard (2003).

Results

Isotopic signatures of consumers in Lake 1 (deep) were very similar. However, in Lake 2 (shallow), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of gatherer–collectors showed greater differences. Likewise, $\delta^{15}\text{N}$ of predators in Lake 2 was higher during flood than dry periods (Table 2).

The distances between the centroids of each FFG during dry and flooding periods were larger in Lake 2 than those in Lake 1. On the other hand, sources did not show the same pattern, while the displacement of macrophytes was larger in Lake 2 than that in Lake 1, and SOM and epiphyton showed the opposite pattern. Moreover, unlike Lake 1, in Lake 2, sources and FFG shift in different directions (Fig. 1, Tables 1 and 2).

The mixing polygon analysis showed that only when the specific TEFs for detritivores and molluscs (Vanderklift & Ponsard, 2003) were applied, the simulated mixing region included all the consumers, and thus, the model was consistent (Fig. 2). Therefore, the $\delta^{15}\text{N}$ TEFs applied in the mixing model were 1.3‰ (SD 0.3‰) for scrapers and 0.53‰ (SD 0.94‰) for detritivores.

Generally, source contributions to scrapers and collectors were more equitable in Lake 1 than those in

Lake 2, and the differences between lakes become clearer when temporal variations were considered. In Lake 1, source contributions for scrapers did not vary greatly between dry and flooding periods, and the mean source contributions to gatherer–collectors in the dry and flooding periods were also very similar. Macrophytes were slightly more important for this FFG (Fig. 3). In Lake 2, the source contribution pattern to scrapers was similar to that observed in Lake 1, but the source contribution varied greatly between periods for the gatherer–collectors. During dry, the contribution of SOM ranged from 0.78 to 0.98 (95% confidence interval) being the most important source. The contribution of macrophytes and epiphyton showed confidence intervals of 0–0.13 and 0–0.11, respectively. In contrast, during the flooding period, SOM decreased its contribution (0–0.48, 95% confidence interval), while macrophytes and epiphyton increased in importance, and the contribution of sources was much more homogeneous (Fig. 3).

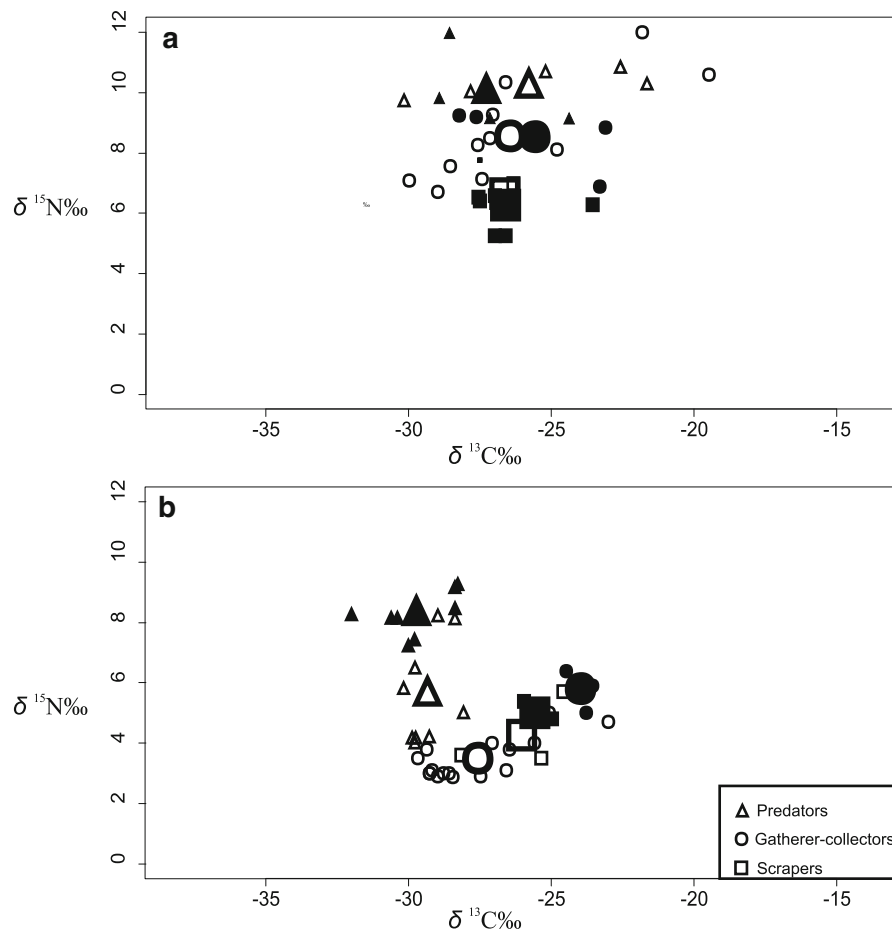
Discussion

Our results uncovered interesting differences between lakes of different morphologies during high and low water levels. In general, most of the evidence from floodplain rivers indicates that algal production is the main carbon source supporting food webs (Araujo-Lima et al., 1986; Hamilton et al., 1992; Delong & Thorp, 2006; Herwig et al., 2007; Jepsen & Wine-miller, 2007; Leigh et al., 2010; Medeiros & Arthington, 2010; Hunt et al., 2011; Reid et al., 2011, Mortillaro et al., 2015). However, C_3 macrophytes can be important sources for some consumers, such as fishes and crabs (Zeug & Winemiller, 2008; Burress et al., 2013; Cogo & Santos, 2013). Moreover, in the Brazilian Pantanal, algae, C_3 macrophytes and C_4

Table 2 Distance and directions of isotopic signatures shift from drought to flooding seasons

	Lake 1		Lake 2	
	Distance	Direction	Distance	Direction
Macrophytes	0.83	055.2°	1.82	257.31°
SOM	1.17	001.84°	0.30	199.29°
Epiphyton	4.38	250.15°	2.86	125.92°
Gatherer–collectors	0.73	002.29°	4.26	046.05°
Scrapers	0.32	271.43°	0.91	057.02°
Predators	1.49	189.20°	2.68	101.48°

Fig. 1 Biplot depicting isotopic signatures of FFGs in dry and flooding period in Lake 1 (a) and Lake 2 (b). Open symbols correspond to dry period and filled symbols correspond to flooding period. Centroids are represented as bigger symbols



grasses supported the food web in floodplain lakes (Wantzen et al., 2002, 2011), and studies in Amazonia have demonstrated the use of aquatic C_4 by floodplain fish (Oliveira et al., 2006).

Isotopic signatures of consumers in the deep Lake 1 did not present important differences between periods. In the shallow Lake 2, however, gatherer–collectors and predators presented substantial differences. Our results about predators do not indicate a change of the relative importance of the carbon sources of the system (as $\delta^{13}C$ did not change). However, the increase $\delta^{15}N$ of this FFG in Lake 2 by 2.8‰ from low to high waters could imply a shift in the trophic position of invertebrate predators. Considering that Vanderklift & Ponsard reported a ^{15}N TEF for invertebrate predators of 1.81‰, this increase could be of more than one trophic level. This result is in coincidence with current ideas about the environmental controllers of food chain length (Sabo et al., 2009).

Trophic position of top predators is considered to depend upon the resources availability at the base of the food web and the ecosystem size (Pimm, 1982; Cohen & Newman, 1992; Post, 2002). While the shallow Lake (Lake 2) increases its size ten times during flood period, an increase of food chain length could be expected as a result of a larger ecosystem size. Besides, the energy inputs of ATTZ organic matter (derived from plants) could also increase of the resource availability in the system. Further efforts (including wide field samplings) should be devoted to determine if the flood pulse can promote the food chain length of floodplain lakes by increasing their resources availability and size.

The differences of isotopic signatures (both $\delta^{13}C$ and $\delta^{15}N$) of gatherer–collectors in Lake 2 between periods could imply a change in sources contribution. This result is confirmed by the sources contribution analysis which indicated that during the dry period,

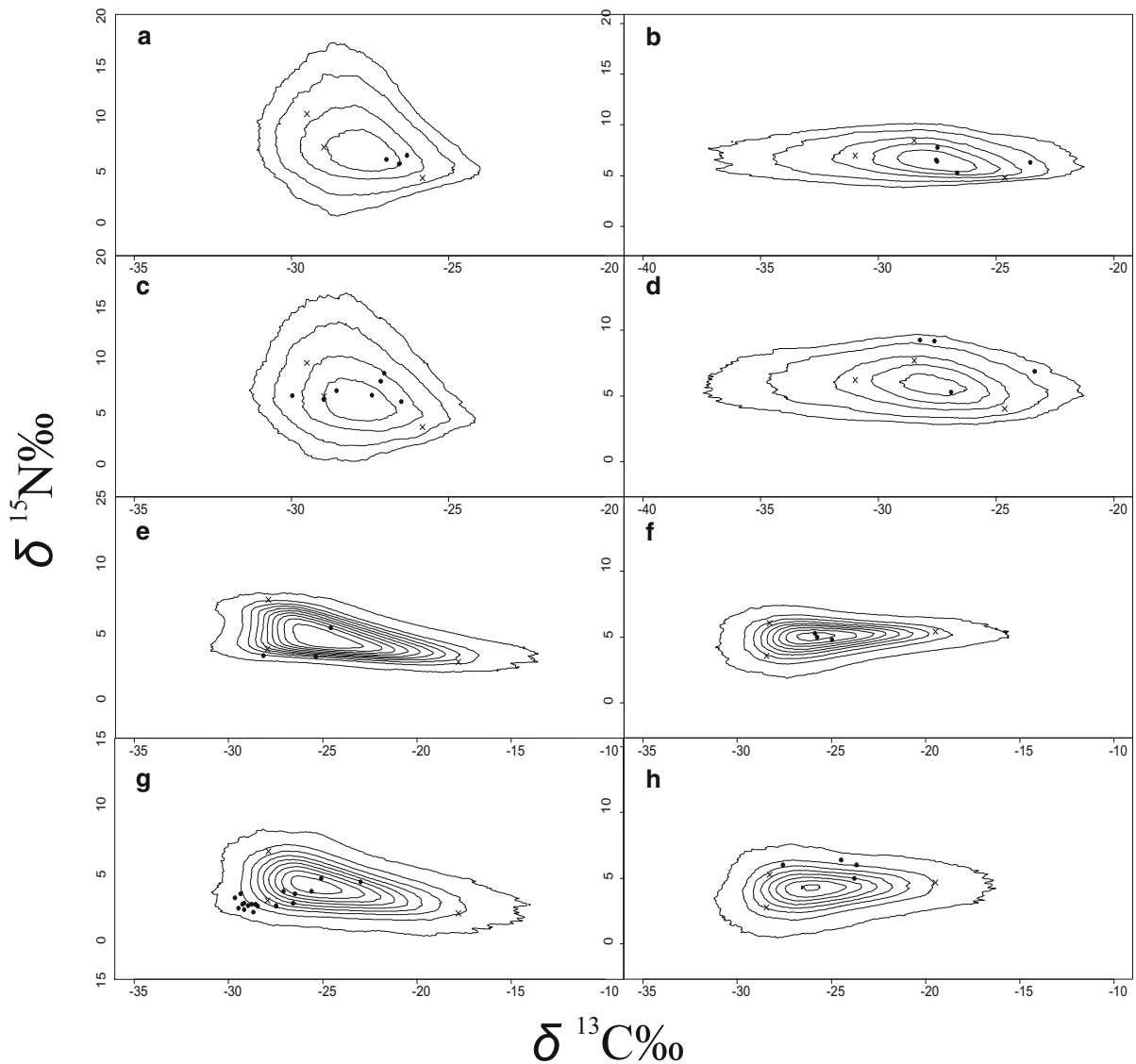


Fig. 2 The simulated mixing region for the mixing models in Lake 1 and 2. *Black crosses* depict the sources and *black dots* the consumers. Probability contours are at the 1% level (all *black dots* have to lay within the outermost contour to validate the mixing model). *a* scrapers in Lake 1 during dry, *b* scrapers in

Lake 1 during flooding, *c* gatherer–collectors in Lake 1 during dry, *d* gatherer–collectors in Lake 1 during flooding, *e* scrapers in Lake 2 during dry, *f* scrapers in Lake 2 during flooding, *g* gatherer–collectors in Lake 2 during dry, *h* gatherer–collectors in Lake 2 during flooding

SOM was the most important source, but during the flood period, epiphyton and macrophytes increased in importance. Our findings of sharp temporal differences in source contributions to gatherer–collectors in Lake 2 could be explained by the relatively large Aquatic Terrestrial Transition Zone or ATTZ that becomes flooded. Unlike Lake 1, in which the flooded ATTZ represents 41% of the lake area, the ATTZ of Lake 2 represents more than 1,000% of the lake area.

Although gatherer–collectors in Lake 2 showed different sources contribution between periods, the sources contribution for scrapers did not change in either of the lakes. This may be explained by their different mouth morphologies and behaviour. Scraper snails may use their radulae to feed on detritus and algae as well as on living (and senescent) plants. It is known that scrapers, such as *P. canaliculata*, are polyphagous and occupy a wide trophic spectrum

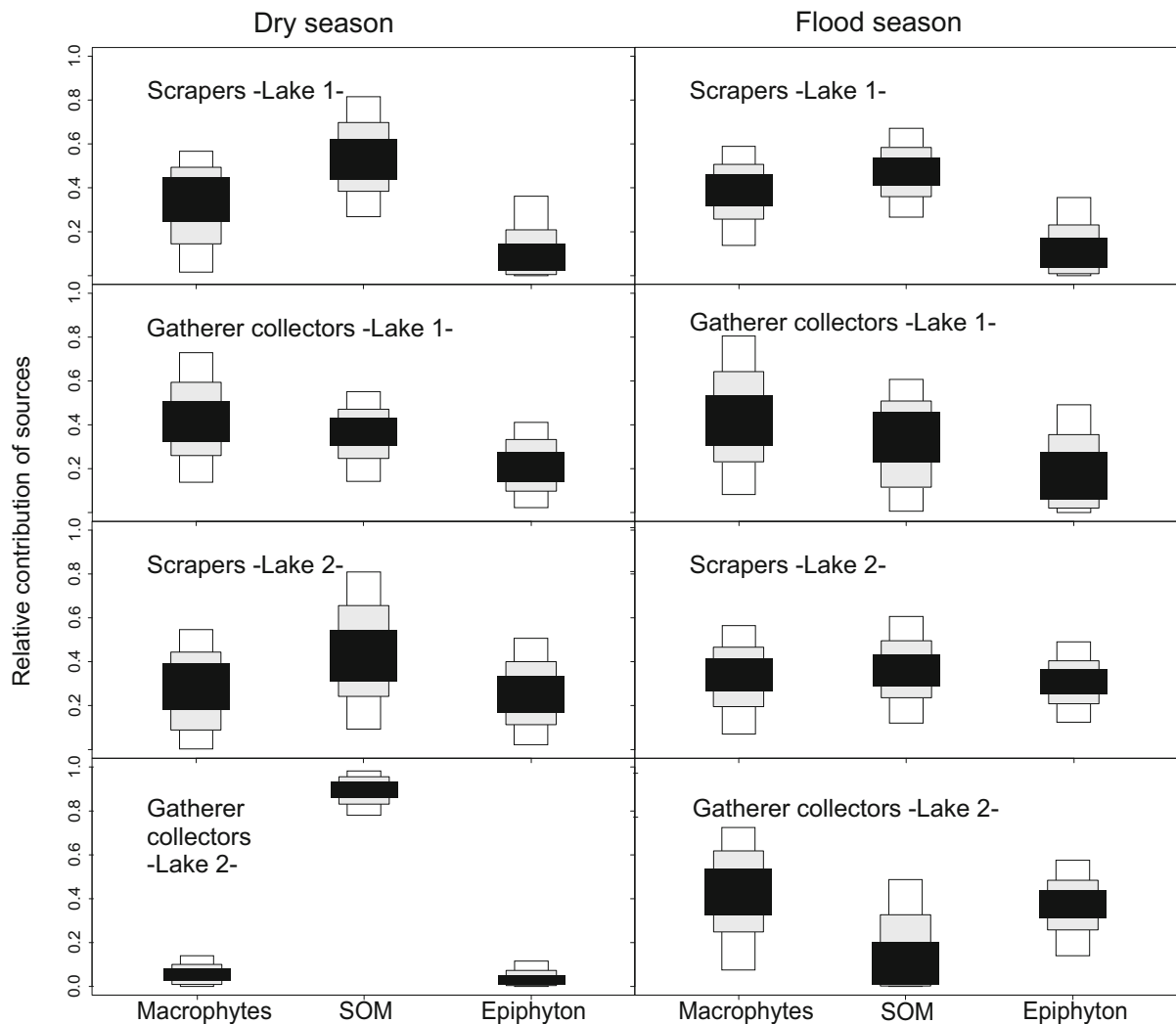


Fig. 3 Relative contribution of sources to each feeding functional group (FFG) during dry and flooding periods in both lakes. Box represent the confidence intervals of 50% (black) 75% (grey) and 95% (White)

(Cazzaniga & Estebenet, 1984). Moreover, Fellerhoff (2002) reported a wide range of isotopic signatures in *Pomacea lineata* Spix in the rainy season of the Brazilian Pantanal (2.8–12.4‰ and –24.2 to –16.4‰ for ^{15}N and ^{13}C , respectively), which suggests a diverse use of food resources by this species. We propose that the scrapers could maintain their generalist feeding habits during different periods, regardless of the relative availability of trophic resources. On the other hand, the mouth morphology and low displacement capacity of gatherer–collectors restrict their feeding habits to the consumption of detritus and algae, so macrophytes are only available as a food

source for this FFG when the plants are decomposing. The large abundance of macrophytes during flooding may result in an increased availability of this source to gatherer–collectors as large amounts of these plants begin decomposition.

In summary, our data show that the relative importance of carbon sources may differ among floodplain lakes and between hydrologic periods. While in the deep lake (Lake 1) we did not find important variations between periods, we report that in the shallow lake (Lake 2), the importance of the sources may present considerable changes between dry and flood period. In that lake, SOM is the most

important source during low waters, but during high waters, macrophytes and epiphyton increase their importance. Disentangling the precise role of morphology and hydrology as drivers of food web changes would require broader studies with replication. Moreover, it would be necessary to know inter-annual variation of isotopic signatures to a better understanding of temporal variations in food webs.

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