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## Trophic level, food chain length and omnivory in the Paraná River: a food web model approach in a floodplain river system

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**Abstract** To determine the mean trophic level and food chain length and to quantify omnivory in a floodplain lake of the Middle Paraná River, we constructed a food web model based on available data. Because proper selection of basal resources is essential, we performed stepwise model selection to decide which sources to include in the model. We estimated mean trophic level, food chain length and omnivory using a binary web (non-weighted trophic links) and a weighted web (trophic links weighted using stable isotopes). Model selection excluded macrophytes as relevant resources for the food web of this floodplain lake. In general, trophic links were relatively even, leading to similar estimations of mean trophic level and omnivory in both binary and weighted webs. Food chain length, however, was higher for the binary web, which was caused by the strong link of top predators with lower-trophic level prey in this ecosystem. Overall, the estimate of food chain length in the Paraná River was not particularly high, despite the high productivity and size of this ecosystem. We suggest that the periodical hydrological fluctuations of large rivers could be a major factor precluding the occurrence of long food chains.

**Keywords** Stable isotopes · Fishes · Macroinvertebrates · Floodplains · IsoWeb

### Introduction

Food web structure reflects important ecosystem properties; thus, this field has garnered great interest since the early years of ecological research (Lindeman 1942).

Interest in food web structure is both theoretical and applied, as food web structure can impart important information for environmental management. In particular, the trophic structure of wetlands has generated much investigation because of the essential functions and ecological services these ecosystems provide (Mitsch et al. 2010). The Paraná River is the second largest river of South America, with a catchment area of 1.51 million km<sup>2</sup> that includes a large number of riverine wetland ecosystems (Iriondo et al. 2007). Although several studies have assessed trophic relationships of different invertebrates and vertebrates in this system, mainly through gut content analysis (Luz-Agostinho et al. 2006; Iriondo et al. 2007; Saigo et al. 2009; Galizzi et al. 2012), understanding of the Paraná River food web structure remains limited.

Most essential questions in food web theory involve the concept of trophic level (TL). The TL of an organism represents the number of feeding links separating it from the producer level (Thompson et al. 2007). While the TL concept has been oft applied, it has also been the focus of much debate. Food webs have traditionally been conceived as systems of simple chains in which a consumer feeds on the TL immediately beneath it, creating a web composed of integer TLs. Omnivory blurs trophic status, however, because that consumer feeds at more than one TL. Increasing awareness of the extensiveness of omnivory in ecosystems has given rise to a long-standing discussion about the applicability and utility of the TL concept (Cousins 1987; Burns 1989; Polis 1991; Vander Zanden et al. 1999; Post et al. 2000; Post 2002a).

The number of TLs in a food web, termed the food chain length (FCL), is a central feature of the vertical structure of food webs as it reflects the ecological processes that sustain top predators (McHugh et al. 2010). Therefore, much effort has been invested in understanding the mechanisms that control FCL in natural environments. For example, while trophic energy transfer is somewhat inefficient and involves some energy loss, FCL has traditionally been considered to be limited by the available energy at basal levels (Pimm 1982). Others suggest, however, that ecosystem size limits FCL rather than primary productivity. This

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hypothesis is based on the assumption that ecosystem size determines species richness and habitat diversity (Post et al. 2000). Currently, evidence indicates that a complex system of multiple interacting constraints including resource availability, predator–prey interactions and disturbances together limit the number of trophic levels in an ecosystem (Post 2002a; Thompson and Townsend 2005). Recently, Sabo et al. (2010) has also suggested that ecosystem size positively affects FCL by negatively affecting environmental variation. Accordingly, studies of tropical rivers have found highly variable FCL, ranging from 2.6 (Jepsen and Winemiller 2002) to 4.35 (Hoeinghaus et al. 2007).

One of the factors that hinders the analysis of food web structure is the difficulty of quantitatively measuring trophic link interactions (Winemiller and Layman 2005). For this reason, food webs that lack information about the strength of trophic links (termed binary webs) are more abundant in the literature and typically include more species than link weighted food webs. The strength of trophic links has traditionally been measured using gut content analysis. Gut analysis alone, however, may be inaccurate for estimations of TLs, omnivory and FCL because ingestion and assimilation rates can differ. For example, higher TL prey items (e.g. fish) may be more easily assimilated than lower TL prey items (e.g. plants). Thus, assuming that ingestion rate accurately measures energy flow can lead to the underestimation of TL. For this reason, diet information (i.e. volumetric or mass estimation and consumption rate) combined with stable isotope analysis (SIA) may be the most suitable technique for determining trophic position, FCL and omnivory (Post 2002b; Williams and Martinez 2004).

Another difficulty in assessing the vertical structure of food webs involves establishing the critical components of the basal level. The accuracy of TL and FCL measurements rely on the suitable selection of the baseline (Post 2002b), and in floodplain rivers, this has been a matter of great debate. Although macrophytes are abundant in floodplain river ecosystems, their importance as a food resource has historically been regarded negligible, particularly for C<sub>4</sub> grasses (Hamilton et al. 1992; Winemiller 2004). This perspective regards algal production as the primary basal resource supporting floodplain river food webs; however, several recent studies have suggested that macrophytes may also play an important role (Leite et al. 2002; Oliveira et al. 2006; Zeug and Winemiller 2008).

In the present study, we determined the TL and FCL and quantified omnivory in the dominant fishes and invertebrates of the Middle Paraná River floodplain and constructed a food web model based on available data for this ecosystem. We used SIA to measure the strength of trophic links and to determine the important basal resources in the food web. Finally, we estimated FCL, TLs and omnivory using the binary food web (non-weighted TLs) and compared them with those estimated from weighted TLs.

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## Methods

### Data

To construct topological food webs, we obtained published diet data based on gut content analyses from organisms in the Middle Paraná River system (Table 1).

We obtained isotope data of adult fishes collected from a permanently connected floodplain lake in the Middle Paraná River (31°41'S, 60°43'W) between November 2009 and December 2010. We dried fish dorsal muscle, prawn (*Macrobrachium borellii* and *Palaemonetes argentinus*) and crab (*Trichodactylus borellianus*) muscle, and entire individuals of Libellulidae and Hirudinea at 50 °C to constant weight. We ground dried tissue to powder with a mortar and pestle and placed approximately 1 mg into tin capsules. We incorporated invertebrate and resource data from a study on the relative importance of basal resources for primary consumers in the Middle Paraná River (Marchese et al. 2014) into our food web. Marchese et al. (2014) collected benthic invertebrates using an Ekman grab (225 cm<sup>2</sup>) in four sampling events (two each during the low and high water seasons). Seston samples were collected from integrated subsurface water samples that were filtered onto precombusted (450 °C) glass fiber filters (Whatman® GF/F Berlin, Germany), which were then frozen until isotope analysis. Benthic organic matter (BOM) was collected from the upper 2–3 cm of deposited sediment using a Tamura grab (312 cm<sup>2</sup>). Epiphytes were collected from the leaves and stems of macrophytes, separated from detritus using silica Ludox®AM-30 (density 1.210 g/cm<sup>3</sup>) and diluted with deionized water following the methods of Hamilton et al. (2005). Macrophyte leaves were collected, rinsed with distilled water and stored frozen until further processing. All samples were dried at 50 °C to constant weight and ground to fine powder. Isotopic determination of carbon and nitrogen were performed using a mass spectrometer (IRMS Finnigan MAT Delta S Massachusetts, USA) coupled with an elemental analyzer (CATNAS, Montevideo, Uruguay). Our samples and those of Marchese et al. (2014) were taken from the same sites on the same dates (Table 2).

### Food web model selection

We performed stepwise model selection using the isotope data to determine which basal resources (C<sub>3</sub> macrophytes, C<sub>4</sub> grasses, epiphyton, BOM and seston) to include in the food web model. We generated reduced models from the complete model that included all resources by eliminating one resource from each new model. Reduced models were then evaluated with the deviance information criterion (DIC) calculated using the IsoWeb R package (Kadoya et al. 2012). This process was repeated using the selected model and contin-

**Table 1** Possible trophic links of analyzed taxa based on previous findings in the literature

Taxa	Trophic resource	References
Oligochaeta-Naididae (aquatic worms)	Benthic organic matter (BOM), epiphyton	(McElhorne 1980; Harper et al. 1981)
Insecta-Diptera-Chironominae larvae (midges)	BOM, epiphyton	(Henriques-Oliveira et al. 2003; Motta and Uieda 2004; Galizzi et al. 2012)
Crustacea-Amphipoda- <i>Hyalella curvispina</i> (amphipods)	Epiphyton, BOM, macrophytes	(Saigo et al. 2009)
Crustacea-Decapoda- <i>Trichodactylus borellianus</i> (crabs)	Epiphyton, macrophytes, Naididae, Chironominae, <i>H. curvispina</i>	(Azevedo-Carvalho et al. 2011)
Crustacea-Decapoda- <i>Macrobrachium borellii</i> (shrimps)	Epiphyton, macrophytes, Naididae, Chironominae	(Collins and Paggi 1998; Collins et al. 2007)
Crustacea-Decapoda- <i>Palaemonetes argentinus</i> (shrimps)	Epiphyton, macrophytes, Naididae, Chironominae	(Collins 1999; Collins et al. 2007)
Mollusca-Gastropoda- <i>Pomacea canaliculata</i> (snails)	BOM, filamentous algae, macrophytes, bryozoans, Naididae, Chironominae	(Cazzaniga and Estebebet 1984; Estebebet 1995)
Bivalvia-Mytilidae- <i>Linnoperna fortunei</i> (golden mussel)	Seston	(Rojas Molina et al. 2010)
Insecta-Odonata- libellulid nymphs (dragonflies)	Oligochaeta, Chironominae, crustaceans	(Corbet 1999)
Hirudinea (leeches)	Naididae, Chironominae, <i>P. canaliculata</i>	(Ringuelet 1972, 1985; Cross 1976; Guimarães et al. 1984; Sawyer 1986; Damboronea and Gullo 1996)
<i>Leporinus obtusidens</i>	Macrophytes, <i>L. fortunei</i>	(Oliveiros and Parma 1985; Montalto et al. 1999; Pen-chaszadeh et al. 2000; Garcia and Montalto 2006)
<i>Pimelodus maculatus</i>	Naididae, Chironominae, <i>H. curvispina</i> , <i>P. argentinus</i> , <i>M. borellii</i> , <i>T. borellianus</i> , Hirudinea, <i>L. fortunei</i>	(Bonetto et al. 1963; Baiz and Cabrera 1968; Alonso 1978; Oliva et al. 1981)
<i>Pseudoplatystoma reticulatum</i>	<i>Prochilodus lineatus</i> , <i>P. maculatus</i> , <i>C. platatanus</i> , <i>Salminus brasiliensis</i>	(Ringuelet et al. 1967)
<i>Pterodoras granulosus</i>	Epiphyton, macrophytes, <i>L. fortunei</i>	(Panatieri and del Barco 1981; Ferriz et al. 2000; Garcia and Montalto 2006; Agostinho et al. 2009)
<i>Salminus brasiliensis</i>	<i>M. borellii</i> , Libellulidae nymphs, <i>P. lineatus</i> , <i>C. platatanus</i> , <i>Ageniosus brevifilis</i> , <i>H. malabaricus</i> , <i>P. maculatus</i> , <i>L. obtusidens</i>	(Fuster de Plaza 1950; Sverfij and Espinach-Ross 1986; Rossi 1989; del Barco 1990)
<i>Schizodon borellii</i>	Macrophytes, <i>L. fortunei</i>	(DosSantos 1981; Resende et al. 1998; Hahn et al. 2004; Casciotta et al. 2005; Esper Amaro de Faria and Benedito 2011)
<i>Prochilodus lineatus</i>	BOM, epiphyton	(Emiliani and Brandi 1972; Bowen et al. 1984)
<i>Ciphocharax platatanus</i>	BOM	(Oliveiros 1980)
<i>Brycon orbignyanus</i>	Macrophytes	(Thormählen De Gil 1949; Panatieri and del Barco 1982)
<i>Hoplias malabaricus</i>	<i>M. borellii</i> , <i>P. lineatus</i> , <i>L. obtusidens</i> , <i>P. maculatus</i> , <i>S. brasiliensis</i>	(Oliveiros and Rossi 1991; Bistoni et al. 1995, 1996; Carvalho et al. 2002)
<i>Ageniosus brevifilis</i>	<i>P. lineatus</i> , <i>P. maculatus</i> , <i>C. platatanus</i>	(Ringuelet et al. 1967; Oliveiros and del Barco 1991)

**Table 2** Isotopic signatures of consumers and resources in the study lake

Taxa or resource	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	N
BOM*	-25.78	1.27	03.46	0.43	8
Seston*	-25.86	1.45	08.06	2.57	20
Epiphyton*	-30.93	8.26	07.46	2.75	4
C <sub>3</sub> *	-28.95	0.98	06.90	1.83	17
C <sub>4</sub> *	-11.92	0.21	06.81	1.23	6
Naididae*	-27.23	1.38	07.14	0.70	6
Chironominae*	-26.99	1.38	07.88	1.63	5
<i>Hyalella curvispina</i> *	-23.16	3.70	10.17	1.43	4
<i>Trichodactylus borellianus</i> *	-25.64	1.78	10.32	0.78	6
<i>Macrobrachium borelli</i> *	-25.32	1.80	11.97	0.19	6
<i>Palaemonetes argentinus</i> *	-25.93	2.23	11.06	0.74	3
<i>Pomacea canaliculata</i> *	-26.58	1.31	06.50	0.71	8
<i>Limnoperna fortunei</i> *	-26.32	0.81	07.15	1.34	3
Libellulid nymphs	-27.49	3.78	10.39	0.85	6
Hirudinea	-26.13	1.62	09.70	0.74	4
<i>Prochilodus lineatus</i> *	-28.20	2.00	08.80	0.80	13
<i>Cyphocharax platanus</i>	-28.54	2.67	08.56	1.27	5
<i>Schizodon borellii</i>	-25.50		09.10		1
<i>Brycon orbignanus</i>	-25.45	0.33	08.54	0.79	3
<i>Leporinus obtusidens</i>	-25.30		08.40		1
<i>Pterodoras granulosus</i>	-25.32		09.50		1
<i>Pimelodus maculatus</i>	-26.20	1.85	10.78	0.99	3
<i>Hoplias malabaricus</i>	-27.11	0.92	11.35	0.35	2
<i>Salminus brasiliensis</i>	-26.94	0.92	10.26	0.07	3
<i>Ageneiosus brevifilis</i>	-26.38	0.08	10.63	0.66	3
<i>Pseudoplatystoma reticulatum</i>	-28.40	0.23	11.00	0.27	2

All  $\delta$  values are expressed per mil (‰)

BOM benthic organic matter

(\*) indicates values published in Marchese et al. (2014)

ued until the elimination of resources did not produce a reduced model with lower DIC.

### Estimating food web parameters

To calculate food web parameters we followed the trophic aggregation procedure proposed by Yodzis and Winemiller (1999). Similarity was calculated using the Jaccard index with a threshold of 0.50. All trophic links of each taxon with its preys and its predators were considered additively (additive topological similarity). The links among tropho-species were defined following the criterion of maximum linkage (Martinez 1991; Yodzis and Winemiller 1999).

We used two kinds of food webs to perform estimations: binary webs in which links among tropho-species are binary, and weighted webs in which TLs among tropho-species are measured quantitatively.

We estimated the TL of consumers as the prey average trophic level (PATL). PATL is defined as one plus the mean trophic level of all the resources of a consumer (basal resources were assigned TL = 1) (Williams and Martinez 2004) and was calculated as:

$$PATL_i = \sum_{j=1}^n PATL_j P_{ji} \quad (1)$$

where  $PATL_i$  is the trophic level of consumer  $i$ ,  $PATL_j$  is the trophic level of the  $j$ th trophic resource of consumer

**Table 3** Stepwise model selection using the deviance information criterion (DIC)

Models	DIC
All sources included	1404.63
<b>C<sub>3</sub> excluded</b>	<b>1233.32</b>
C <sub>4</sub> excluded	1390.03
Seston excluded	1233.61
Epiphyton excluded	1332.75
BOM excluded	1344.25
C <sub>3</sub> and seston excluded	1096.73
C <sub>3</sub> and BOM excluded	1100.87
C <sub>3</sub> and epiphyton excluded	1165.01
<b>C<sub>3</sub> and C<sub>4</sub> excluded</b>	<b>0588.33</b>
C <sub>3</sub> , C <sub>4</sub> and seston excluded	1018.50
C <sub>3</sub> , C <sub>4</sub> and BOM excluded	1095.20
C <sub>3</sub> , C <sub>4</sub> and epiphyton excluded	1096.47

C<sub>3</sub>, C<sub>4</sub> and BOM refer to C<sub>3</sub> macrophytes, C<sub>4</sub> grasses and benthic organic matter, respectively. Lowest DICs are highlighted in bold

$i$  and  $P_{ji}$  is the mean relative contribution of resource  $j$  to consumer  $i$ .

To calculate  $PATL_i$  using a binary web,  $P_{ji}$  was considered as:

$$P_{ji} = n_i^{-1} \quad (2)$$

where  $n_i$  is the number of resources of consumer  $i$ .

For the weighted web,  $P_{ji}$  was calculated using the IsoWeb R package, which uses stable isotope data to estimate the proportion of each component of the diet of every consumer in a food web (Kadoya et al. 2012). We



used a trophic enrichment factor (TEF) of 0.40 for  $\delta^{13}\text{C}$  and 3.4 for  $\delta^{15}\text{N}$  (Post 2002b).

The omnivory of consumer  $j$  was measured as the standard deviation of the TLs of its resources. The mean TL of the whole food web was the average TL of all consumers (basal resources not included). Overall omnivory in the food web was calculated as the average omnivory of all consumers.

We performed three different estimations of FCL. Binary FCL (BFCL) was calculated as the maximum TL in the binary food web, while weighted FCL (WFCL) was the maximum TL in the weighed web. Constructing an entire food web to measure FCL requires huge effort, however. Thus, FCL is more commonly calculated using the trophic enrichment factor of  $\delta^{15}\text{N}$ . To facilitate comparison across studies, we also calculated the simplified FCL (SFCL) following Post (2002b). Thus, we selected as bases the primary consumers *Pomacea canaliculata*, which feeds on littoral resources, and *Limnoperna fortunei*, which consumes pelagic resources.

$$\text{SFCL} = \lambda + \{\delta^{15}\text{N}_{\text{TP}} - [\delta^{15}\text{N}_{\text{BASE1}} * \alpha + \delta^{15}\text{N}_{\text{BASE2}} * (1 - \alpha)]\} / 3.4 \quad (3)$$

where  $\lambda$  is the trophic level of the organisms used as base,  $\delta^{15}\text{N}_{\text{BASE1}}$  is  $\delta^{15}\text{N}$  of *P. canaliculata*,  $\delta^{15}\text{N}_{\text{BASE2}}$  is  $\delta^{15}\text{N}$  of *L. fortunei* and  $\alpha$  is defined as:

$$\alpha = (\delta^{13}\text{C}_{\text{TP}} - \delta^{13}\text{C}_{\text{BASE1}}) / (\delta^{13}\text{C}_{\text{BASE1}} - \delta^{13}\text{C}_{\text{BASE2}}) \quad (4)$$

where  $\delta^{13}\text{C}_{\text{TP}}$  is  $\delta^{13}\text{C}$  of the top predator,  $\delta^{13}\text{C}_{\text{base1}}$  is the  $\delta^{13}\text{C}$  of *P. canaliculata* and  $\delta^{13}\text{C}_{\text{base2}}$  is the  $\delta^{13}\text{C}$  of *L. fortunei*.

## Results

### Food web model selection

Stepwise model selection indicated that BOM, seston and epiphyton were the important basal resources, while macrophytes (neither  $\text{C}_3$  nor  $\text{C}_4$ ) were not (Table 3).

### Trophic aggregation

Trophic aggregation yielded 11 groups. Naididae, Chironomina and *Hyalella curvispina* comprised a tropho-species group termed the collectors. *Palaemonetes argentinus*, *Macrobrachium borellii* and Libellulidae nymphs formed a tropho-species group of predatory invertebrates. *Prochilodus lineatus*, *Ciphocharax platanus* and *Brycon orbignanus* formed the group of detritivorous fishes. The generalist fishes group was composed of *Schizodon borellii*, *Pterodoras granulosus* and *Leporinus obtusidens*. *Hoplias malabaricus* and *Salminus brasiliensis* made up the predatory fish group. *Ageneiosus brevifilis* and *Pseudoplatystoma reticulatum* were grouped together as

large siluriformes. *Limnoperna fortunei*, *Pomacea canaliculata*, Hirudinea, *Trichodactylus borellianus* and *Pimelodus maculatus* formed, each one, their own group (Fig. 1).

### Link strength

In general, the links connecting a consumer and its resources had similar strengths. For some top predators, however, resources had uneven contributions. For example, detritivorous fishes were the main prey for both large siluriformes and predatory fishes, particularly for the former (Fig. 2).

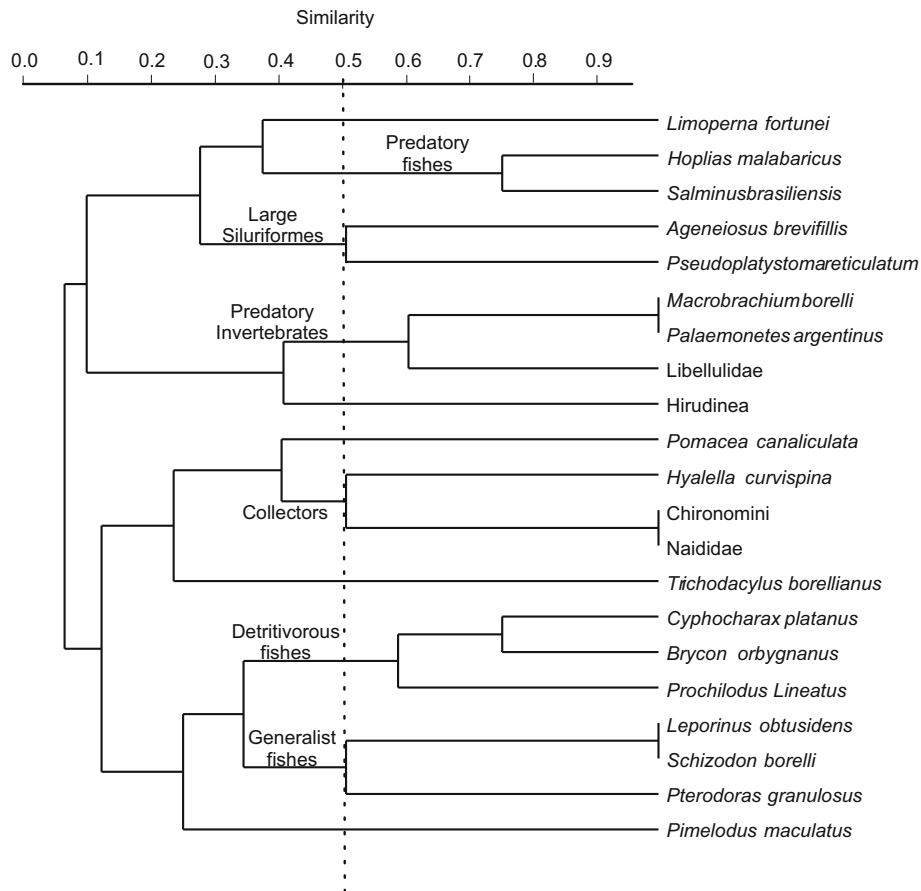
### Estimations of TL, FCL and omnivory based on topological and isotopic data

Mean TL estimations were similar whether calculated from the binary or weighted web (2.67 and 2.63, respectively). Estimates of omnivory were also very similar, at 0.36 and 0.35 for the binary and weighted web, respectively. In contrast, BFCL was higher than WFCL (4.0 and 3.66, respectively), and SFCL was lower than WFCL (3.41 and 3.66) (Table 4).

## Discussion

### Food web model selection

Model selection led to the exclusion of macrophytes from the food web, indicating that epiphyton, seston and BOM were the important basal resources. Our results support previous findings in Neotropical floodplain rivers (Araujo-Lima et al. 1986; Hamilton et al. 1992) that macrophytes, though abundant in biomass, have negligible importance as a basal resource in these river systems. In contrast, several recent studies have concluded that macrophytes may be an important food resource in floodplain rivers (Leite et al. 2002; Oliveira et al. 2006; Zeug and Winemiller 2008). Moreover, a study in the Upper Paraná River (Hoeinghaus et al. 2007) showed that hydrological features such as river slope, floodplain width and impoundments may affect the relative importance of food resources. The lake studied here is directly and permanently connected to the main stem of the Paraná River. In highly connected lakes, it has been suggested that detritus inputs may be important trophic resources for invertebrates (Poi de Neiff et al. 1994). A high degree of connection allows large amounts of suspended material (seston) to enter the lake from the river and settle (BOM). Although detritus can be a low-quality trophic resource in terms of nutrient content and palatability, it may become a good food resource with the colonization of bacteria and fungi (Edwards and Meyer 1986; Edwards 1987; Carlough and Meyer 1989). The restriction of vegetation to the littoral



**Fig. 1** Cluster analysis showing the trophic similarity among taxa calculated using the Jaccard index. The vertical dotted line depicts the 0.50 threshold similarity level

zone and the resulting large pelagic area in the study lake may be the reason for the negligible importance of macrophytes as a basal resource. Even in similar floodplain systems, the relative importance of resources may vary in lakes with different characteristics (e.g. lower connectivity, narrower pelagic area or wide seasonal variation). Thus, spatially and temporally comprehensive studies are needed to fully understand the patterns of resource contribution in the Middle Paraná River.

#### Mean TL, omnivory and FCL

Binary web and weighted web-based measurements of mean TL and omnivory were similar because binary webs assume equivalent strengths of all trophic links between consumers and resources. Although SIA revealed differences in strength among TLs for several consumers, the assumption of TL equivalency was generally met. Similarly, comparison of flow-based and binary link-based webs yielded similar estimates of mean TL and omnivory (Williams and Martinez 2004).

Our results suggest that the prevalence of even trophic interactions in the Middle Paraná River may be explained by periodic fluctuations in resources availability driven by flood pulses in floodplain rivers (Junk et al. 1989; Wantzen et al. 2002, 2008, 2010; Junk and Wantzen 2004). Thus, the existence of generally weak interactions in the Paraná floodplain may promote the stability and persistence of communities and meta-communities as has been shown in other systems (McCann et al. 1998; Maser et al. 2007).

Our estimates of mean TL and omnivory in the Middle Paraná River floodplain were similar to those reported for nine food webs from marine, estuarine, grassland and desert ecosystems (Williams and Martinez 2004). Mean TL in these nine webs ranged 2.03–2.89, except the Coachella Valley desert food web, which was 4.11. Williams and Martinez (2004) also reported low degrees of omnivory in all food webs except that of the Coachella Valley. Our results provide further evidence that mean TL and omnivory may be similar in food webs across different environments and regions.

Despite similarity in mean TL and omnivory estimated using the binary or the weighted web, the FCL

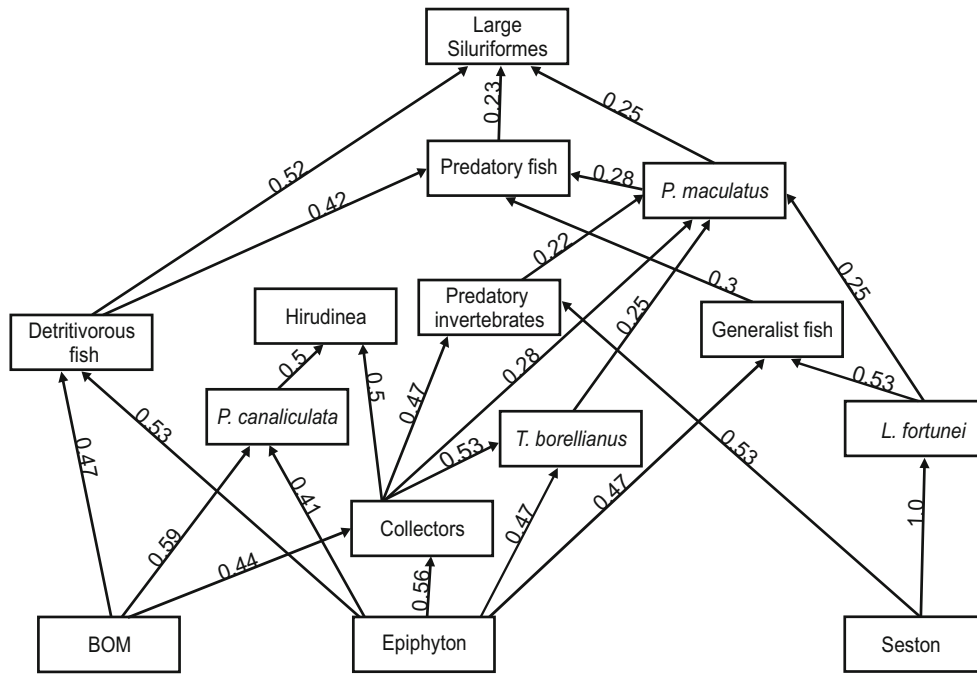


Fig. 2 Selected food web model where the relative strengths of trophic links are depicted by arrow width. BOM benthic organic matter

Table 4 Food web parameter estimates

	Mean TL	Omnivory	FCL		
			BFCL	WFCL	SFCL
Binary web	2.67	0.36	4		
Weighted web	2.63	0.35		3.66	3.41

FCL food chain length, BFCL binary food chain length, SFCL simplified food chain length, WFCL weighted food chain length

estimate from the binary web was slightly higher than that of the weighted web. FCL is a measure that involves only top predators; thus, the assumption of general link equivalency was not met as particularities of these species become important in the weighted web. For example, interactions between large siluriformes (the top predators of the food web) were stronger with detritivorous fishes (prey with lower TL) than with *P. maculatus* or predatory fishes. This is not surprising because inefficient trophic energy transfer should result in primary consumers comprising the greatest proportion of secondary production in any system. Indeed, in the middle Paraná River, the detritivorous fish *P. lineatus* is the most abundant species (Rossi et al. 2007). As a result, the assumption of link equivalence would lead to overestimation of the trophic position of large siluriformes. Thus, while binary-based estimates of mean TL and omnivory may be reliable, estimation of FCL requires consideration of link strength.

Similarly, SFCL was lower than WFCL. SFCL, which is calculated using isotopic data without prior information on species feeding habits, is highly sensitive to  $\delta^{15}\text{N}$  TEF. Although 3.4 ‰ is commonly used as

an approximation of  $\delta^{15}\text{N}$  TEF, this value is based on consumers that feed on protein-rich material (e.g. fishes) (McCutchan et al. 2003).  $\delta^{15}\text{N}$  TEF is likely to be lower in lower trophic levels (e.g. benthic invertebrates) and has been shown to be roughly 1.5–1.8 ‰ for the benthos (Cremona et al. 2010, 2014). Overestimation of  $\delta^{15}\text{N}$  TEF would lead to a direct underestimation of FCL.

Despite the difference in estimates of SFCL and WFCL, both suggested that top predators in the Middle Paraná River floodplain occupy a trophic position of only about 3.5. Whereas previous riverine studies have reported values of FCL ranging 2.6–5.0 (Jepsen and Winemiller 2002; Thompson and Townsend 2005; Hoeninghaus et al. 2007; Doi et al. 2009; McHugh et al. 2010; Sabo et al. 2010), the FCL in the Middle Paraná River was relatively short. We suggest that neither productivity nor ecosystem size limit FCL in the Middle Paraná River floodplain. Instead, flood pulses drive profound variation in food availability, habitat diversity and inter-specific interactions (inter alia); thus, the fluctuating nature of these factors may prevent the development of long food chains. Further investigation is needed to disentangle the complex system of constraints on FCL in floodplain rivers.

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