

Quantitative food webs and invertebrate assemblages of a large River: a spatiotemporal approach in floodplain shallow lakes

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Abstract. To test the hypothesis that the hydrological regime of large Rivers affects the structure of invertebrate communities and food webs in floodplain lakes, we studied invertebrate assemblages and stomach contents of fish and decapods in two shallow lakes in the Paraná River floodplain, Argentina, with different connectivity (indirect and permanent, IPC; direct and temporal, DTC) to the fluvial system over three hydroperiods (flooding, transition, drought). Invertebrate assemblages exhibited temporal variation, with higher dissimilarity during the drought phase. However, zooplanktonic and pleustonic attributes varied spatiotemporally, and were better explained by other environmental variables. The food webs in the two lakes differed, with higher connectance and fewer predators in the DTC Lake. In general, the use of trophic resources by fish and decapods reflected the local and abundant resources in the system. The persistence of communities in floodplain lakes with temporary connectivity to the river may relate to the foraging decisions of consumers to buffer environmental fluctuations. The consumption of abundant resources highlighted the importance of autochthonous inputs into floodplain lakes. However, the variation in food supply as a key factor governing food-web structure and stability should be further investigated.

Additional keywords: bipartite networks, communities, hydrological regime, Paraná River, web metrics.

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Introduction

Ecological patterns and processes undergo temporal and spatial variation, changing the structure and dynamics of communities (Winemiller 1996). The floodplains of lowland rivers are systems of high spatiotemporal variability in constant disequilibrium (Neff 1990). In South America, the Paraná River is a fluvial macrosystem characterised by a seasonal hydrological regime of flood and drought pulses, which are considered to be the most important factor driving the ecological function and biodiversity patterns of floodplain systems (Junk *et al.* 1989; Neff 1990; Bunn and Arthington 2002). This pulsed regime drives periods of connection and isolation, which gives heterogeneity, forming a mosaic of aquatic bodies. Thomaz *et al.* (2007) supported the hypothesis that floods increase similarity among aquatic habitats (e.g. ecological process and

biological communities) due to a homogenisation during high water levels. In contrast, differences are more evident during low water levels. Superimposed on this are seasonal fluctuations in species composition, algal biomass, detritus supply, food availability and competitive interactions. In this sense, the spatiotemporal scale is a fundamental factor that must be considered in food-web studies (Thompson and Townsend 1999).

Empirical food webs are distorted representations of trophic relationships among species in nature (Pimm 1982). The reality is more complex than the food webs reported in the literature (Polis 1991). The primary reason is the excessive difficulty of acquiring accurate data, combined with the fact that trophic-link estimates are consistently imperfect (Winemiller 2007). Many attributes are used to describe and identify important characteristics of trophic interactions in an ecological community. These

attributes can be obtained from presence or absence or quantitative data. Many methods have been developed to describe and analyse food webs quantitatively (Bersier *et al.* 2002; Almeida-Neto and Ulrich 2011), allowing a more robust description of general community feeding relationships. Stomach contents and stable-isotope methods are among the most used to quantify trophic interactions. Regardless of the method implemented, the magnitude of predator–prey interactions is highly variable in time and space (Paine 1980).

In the middle Paraná River floodplain, crustaceans of the Palaemonidae (prawn) and Trichodactylidae (crab) families have a wide trophic spectrum comprising a variety of algae, invertebrates and plant material from the littoral–benthic community (Collins and Paggi 1997; Collins *et al.* 2007b; Williner and Collins 2013). Many fish species and macrocrustaceans feed on similar resources (Bonetto *et al.* 1963; Oliveros and Rossi 1991; Mantel *et al.* 2004) and can be potential intraguild predators (Polis *et al.* 1989). Omnivores are frequent in freshwater systems (Warren 1989; Rawcliffe *et al.* 2010; González-Bergonzoni *et al.* 2012), often including both plant and animal material in their diet. Crustaceans such as prawns and crabs, which are larger than most aquatic invertebrates, develop abundant populations (Collins *et al.* 2007b; Carvalho *et al.* 2013), and are mobile and long-lived. Diehl (1993) predicted that this type of invertebrate predator should have a strong and direct trophic influence on community structure, as demonstrated in previous studies (Pringle *et al.* 1993; Lodge *et al.* 1994; Pringle and Hamazaki 1998).

Considering the spatial scale, in the middle reach of the Paraná River, there is a gradient running from the main channel to the alluvial plain that is characterised by progressive complexity of community organisation (Marchese and Ezcurra de Drago 1992; Ezcurra de Drago *et al.* 2007). Increased spatial heterogeneity promotes the presence of more invertebrate species (Thompson and Townsend 2005; Thomaz and Cunha 2010). However, community structure and trophic connections are strongly influenced by the energy available in the system (Thompson and Townsend 2005, Frauentorf *et al.* 2013). Macrophytes are an important basal energy source in the Paraná floodplain (Ezcurra de Drago *et al.* 2007). Previous studies have indicated that C3 carbon sources, derived mainly from macrophytes, largely support secondary production in floodplain food webs via herbivorous and omnivorous fish and invertebrates (Winemiller and Jepsen 1998, Hoinghaus *et al.* 2007; Marchese *et al.* 2014). However, other authors have suggested that macrophytes are underexploited in the La Plata basin, which contains the Paraná River, owing to the low abundance of shredders (Neiff and Poi de Neiff 1990; Poi de Neiff 2003; Ezcurra de Drago *et al.* 2007). Among macrocrustaceans, decapods exhibit feeding habits as shredders and predators (Collins *et al.* 2007a) and are considered ‘true’ omnivores in the sense that they eat both animal and plant material (Thompson *et al.* 2012).

Nevertheless, the hydrological regime can strongly influence trophic interactions by seasonal changes in environmental factors and resource availability in water bodies of floodplains. Furthermore, lakes with different characteristics (e.g. connectivity degree, time of water residence, deepness) may respond differently to these seasonal changes. In this study, we test the

hypothesis that the structure of invertebrate communities and food webs varies according to the hydroperiod (flooding, transition and drought). We considered two lakes with different connectivity to the fluvial system (indirect and permanent, direct and temporal). We expected that during the flooding pulse, communities and food webs are more similar between lakes than other parts of the hydroperiods. To answer the hypothesis, we estimated the trophic interactions of fish and decapods using weighted and unweighted food-web metrics.

Material and methods

Study sites

The Paraná River is the second largest river in South America, with a catchment area of 1.5×10^6 km² from 15 to 35°S. The middle Paraná River extends 700 km from the confluence with the Paraguay River to Diamante, with a wide floodplain characterised by a series of islands, swamps, paleochannels and oxbow lakes (Drago 2007; Iriando and Paira 2007). We chose the following two lakes of the Middle Paraná alluvial valley, between the cities of Santa Fe (Santa Fe Province, Argentina) and Paraná (Entre Rios Province, Argentina): Lake Irupé (31°40′17.2″S, 60°34′07.4″W) and Lake Larga (31°40′44.31″S, 60°37′55.9″W). These lakes are located between the main channel of the Paraná River and a secondary channel, the Colastiné River (Fig. 1). The selection of these study sites was based on the water-residence time and the degree of connection to the fluvial system. The Lake Irupé has an indirect but permanent connection (IPC, indirectly and permanently connected) to the fluvial system via the Mini stream, thus reducing water residence time. The maximum depth recorded during the sampling period was 2.15 m in the littoral zone and 3.75 m in the centre of the lake. The lake surface has an oval morphology, ranging from ~60 000 m² in the drought period to 190 000 m² during the flood pulse. Lake Larga, in contrast, has a temporary direct overbank connection (DTC, directly and temporarily connected) with the Colastiné River and the inflow of river water occurs only during the inundation phase (Drago 2007). This increases the time of water residence during the intermediate phase; during ordinary drought periods, the lake is isolated and usually dry. It is a shallower lake with a maximum recorded depth of 0.8 m in the littoral zone and 1.4 m in the centre. The length of this lake is ~10 times more than its width, with a surface area ranging from ~19 000 m² (before complete drying) in an ordinary drought period, to 160 000 m² in the flooding phase. Both lakes are surrounded by native forest composed of trees and shrubs and have large coverage of floating and rooted macrophytes. The Paraná River is subject to an annual hydrological regime characterised by flood pulses during the summer–autumn (December–April) and drought in the spring, with an intermediate phase that generally coincides with the winter. The samples were taken for the present study in the following three distinct phases of the hydrological regime during 2010 after extraordinary flood and drought events: flooding (March and April), transition (June and July) and drought (October and December). Samples were collected from both lakes on the same day, totaling two replicates from the same hydric level and from each lake. Lake Larga was not sampled during the low-water phase because it was completely dry.

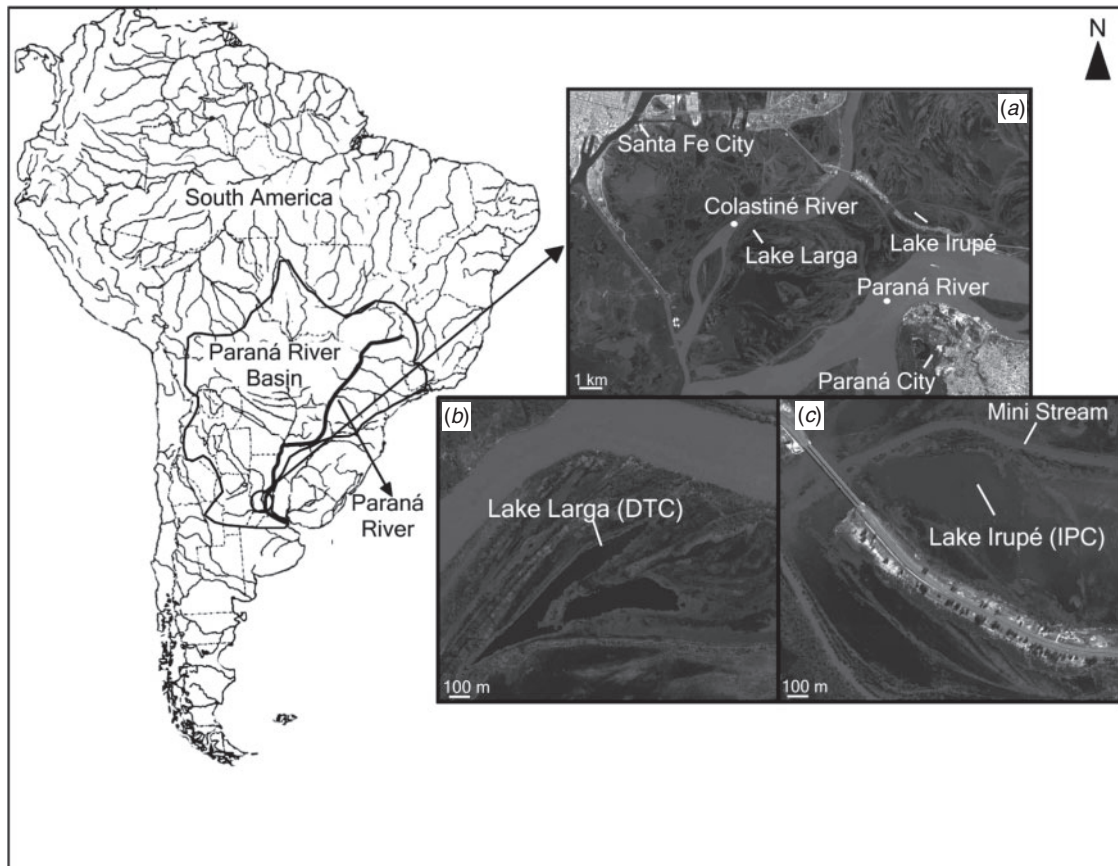


Fig. 1. Drainage basin and tributaries of the Paraná River and study-area location. (a) Sampling-site locations and (b) detail of the lake with indirect and permanent connection (Irupé) and (c) the lake with direct and temporary connection (Larga), showing the degree of connectivity with the Colastiné River.

Environmental parameters

At each sample site (Lake Irupé and Lake Larga) and at each hydroperiod (flooding, transition and drought), we measured vegetation cover and chlorophyll-*a* levels (Lorenzen 1967). Temperature, pH, conductivity, dissolved oxygen and transparency (Secchi disc depth) were measured in the field with the aid of digital sensors when necessary (Hanna HI 98129, Mauritius). Hydrometric level was recorded at the Santa Fe River Harbor Station. The proportions of floating and rooted macrophytes were estimated visually and converted to the Domin–Krajina scale of importance (Thomaz *et al.* 2004). So as to verify differences between the lakes and hydrometric levels in biotic and abiotic parameters, we applied the Wilcoxon test for dependent data using PAST (ver. 2.17; Hammer *et al.* 2001).

Invertebrates

The composition and abundance of aquatic invertebrates were determined through the characterisation of benthic, pleustonic and zooplanktonic samples at each lake and date. All samples were collected randomly from the littoral zone. According to methods described by Marchese *et al.* (2005), we collected three samples of benthos with an Ekman grab (225 cm²). In the laboratory, samples were sieved (250- μ m mesh size). One sample of pleuston was collected with a 500- μ m-mesh hand

net (1260-cm² opening area and 47-L volume). This sample was divided in three subsamples of 400 cm². To obtain zooplankton samples, 20 L of water lake was filtered with a Schindler–Patalas trap (36- μ m mesh size), counting at least 100 individuals of the dominant taxa in three subsamples of 1 and 5 mL for micro- (Rotifers, nauplii and veliger) and macrozooplankton (Cladocera and Copepoda) respectively. Further methodological details can be found in Marchese *et al.* (2005) for benthic fauna, Poi de Neiff (2003) for pleustonic organisms and José de Paggi and Paggi (2008) for zooplankton. Animal composition and density were obtained by counting the organisms present in each sample according to standard techniques (Edmonson and Winberg 1971; José de Paggi 1995; Paggi 1995; Bicudo and Bicudo 2004). Taxonomic identification followed the descriptions detailed in Lopretto and Tell (1995), Merritt and Cummins (1996), Dominguez and Fernández (2009).

Fish

We collected fish using a 50 \times 1-m net with 5-cm mesh in areas with little aquatic vegetation during 1 h. We adopted the same catch per unit effort (CPUE) in both lakes. In laboratory, we identified fish at a specific level, following the descriptions of Lopretto and Tell (1995) and Almirón *et al.* (2008). We decided to include in analyses only fish species with more than three

individuals with full stomachs. The total number of stomachs analysed was 128 in Lake Irupé (IPC) and 34 in Lake Larga (DTC). Stomach contents were quantitatively analysed under a stereomicroscope using the keys mentioned above. To verify whether the number of stomachs used depicted the trophic spectra of fish species, we performed rarefaction curves with the software EstimateS (Colwell 2013), using the non-parametric estimator Chao 2 for consumer species with more stomachs analysed (*Salminus brasiliensis*, *Pimelodus maculatus*, *Prochilodus lineatus*, *Brycon orbignyanus*, *Leporinus obtusidens*, *Pygocentrus nattereri*; Fig. 2). Observed species may reflect prey richness, but they are susceptible to total abundance, the number of specimens in the sample and sample size (Gotelli and Colwell 2001). In this case, richness estimators such as Chao2 are recommended (Gotelli and Colwell 2001; Colwell and Coddington 1994). We computed 100 randomisations without replacement and used the bias-corrected formula of Chao2. For detritivorous (*Cyphocharax platanus*), herbivorous (*Schizodon borellii*, *Schizodon platatae*), insectivorous (*Charax stenopterus*), zooplanktivorous (*Parapimelodus valenciennis*) and fish-eating species (*Acestrorhynchus pantaneiro*, *Crenicichla lepidota*, *Hoplias malabaricus*, *Serrasalmus maculatus*, *Sorubim lima*), this analysis was not accomplished. In these cases, prey items were identified in general taxonomic groups because of an advanced degree of digestion that did not allow better identification or because of stomach contents that had different prey types to perform a rarefaction curve. We did not carry out this approach in species whose abundance was low (three specimens or less, i.e. *Gymnotus inaequilabiatus*, *Tetragonopterus argenteus*, *Triporthes nematurus*, *Crenicichla vittata*, *Bryconamericus* sp., *Eigenmania trilineata*). However, we still decided to include these species in food webs because we consider that the number of stomachs collected is appropriate considering the abundances and population dynamics of the species (P. A. Scarabotti, pers. comm.) and the results of observations of

digestive contents were consistent with those recorded in previous studies (Rossi *et al.* 2007).

Decapods

We collected two species of decapod, the crab *Trichodactylus borellianus* and the prawn *Macrobrachium borellii*, both commonly found in the littoral–benthic areas of the studied lakes. We manually removed decapods from the stems and roots of aquatic vegetation, by using a hand net of 500- μ m mesh size. We analysed stomachs of 144 crabs and 109 prawns and estimated the minimum number of stomachs needed to reach a representative sample of trophic diversity by the Chao 2 estimation index, as previously described for fish samples (Colwell 2013; Fig. 2). Further details of sampling techniques and analysis of stomach contents are found in Collins *et al.* (2007b). Prey were identified to the lowest resolution possible by using the keys above.

Structure and composition of communities

We assessed spatiotemporal variation in invertebrate assemblages using a two-way PERMANOVA (Anderson 2001) for the effects of sample sites (shallow lakes) and hydrometric levels (flooding, transition and drought). We described the community structure specific to each shallow lake and hydrometric level by using community attributes such as density, richness and diversity (Simpson index) (Magurran 1988). These attributes were calculated separately for each community (benthos, pleuston and zooplankton) and together as a single group. Using these data, we compared the structure and composition within a community for each sampling event using a Wilcoxon test for dependent data using PAST (ver. 2.17; Hammer *et al.* 2001). We compared the attributes of both lakes over the three hydrometric levels by using a cluster analysis.

Food-web construction and web-metric calculations

We compiled food webs by using the taxa identified in fish, crab and prawn gut contents, considering only two trophic levels (predator–prey). Predator species were ordered in columns and prey species in rows, indicating trophic interactions as quantitative data in the matrix. Quantification of vegetal remains and detritus abundance was based on categorical values according to the volume that these items occupied in the stomach of each. Because of the variable number of individuals of each fish species captured, we decided to quantify the diet on the basis of the sum of each item in all stomachs multiplied by the frequency of occurrence (number of stomachs with the prey item \div total number of stomachs). These values were obtained for each fish and decapod species and are considered as quantitative trophic links between predators and prey. The taxonomic resolution of predators was at a specific level, whereas prey resolution was variable because of the different resolution possibilities among fish and decapods species.

Samples from the same hydrometric level were pooled for each lake in quantitative matrices to describe the magnitude of fish and decapod interactions. Using the Bipartite 2.04 package (Dormann *et al.* 2014) for R, ver. 2.15.1 (R Foundation for Statistical Computing, Vienna, Austria), we calculated weighted (connectance, nestedness (NODF), linkage density,

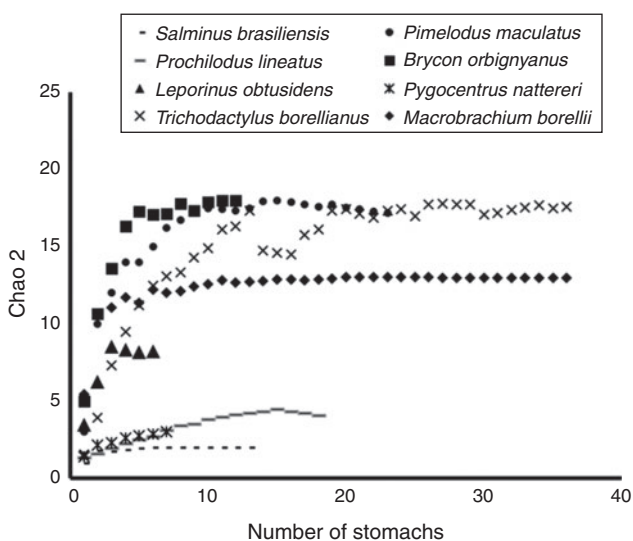


Fig. 2. Chao 2 estimation of taxa richness to verify the number of stomachs used to depict the trophic spectra of consumer species with higher amount of stomachs analysed.

generality, vulnerability) and unweighted (connectance, links per species and nestedness) web metrics. Qualitative descriptors (weighted web metrics) give the same weight to all trophic interactions, decreasing the sensitivity to sampling effort. To briefly define these terms, connectance is the realised proportion of possible links between species (Dormann *et al.* 2009), nestedness is the species composition of small assemblages that is a nested subset of larger assemblages (Ulrich *et al.* 2009), linkage density is the average number of links per species, generality is the mean number of prey per predator, and vulnerability is the mean number of predators per prey (Dormann *et al.* 2009). We also calculated the number of predators and prey for each food web. For additional details, see Bersier *et al.* (2002), Dormann *et al.* (2009), Almeida-Neto and Ulrich (2011) and Dormann *et al.* (2014). The statistical significance of network indices was tested against null models that generate 1000 random matrices in Bipartite 2.04 (Dormann *et al.* 2014) with the same marginal totals (fixes both row and column sums) of the observed matrix (Connor and Simberloff 1979). The relevance of the results of this algorithm is based on the assumption that neither fish nor decapod abundance are effected by network structure. We compared web metrics of both lakes over the three hydrometric levels by using a cluster analysis.

Statistical analyses

We assessed the spatiotemporal variation of food-web attributes using a two-way PERMANOVA (Anderson 2001) for the effects of sample sites (shallow lakes) and hydrometric level (flooding, transition and drought). So as to evaluate the effects of site and hydroperiods on individual attributes, we used a paired Student's *t*-test for dependent samples after previous analysis of normality and homoscedasticity. We performed these test with the software PAST (ver. 2.17; Hammer *et al.* 2001).

The relationships between the environmental parameters and all food-web metrics (weighted and unweighted) and community attributes (density, richness and diversity) were

tested using generalised linear models (GLM set as Gaussian distribution) in R (R Foundation for Statistical Computing). We considered a Spearman's *r*-value of 0.6 to account for multicollinearity and eliminate highly correlated explanatory variables. Two variables with an *r*-value of 0.6 or more are considered highly correlated and one of them was removed. After running the models for each attribute, we evaluated the variance inflation factor (VIF) considering values above four to remove correlated explanatory variables. The environmental variables with low correlation were used to run a GLM. Then, we chose the best-fit models according to the Akaike information criterion (AIC) for each dependent variable. Finally, we fit the GLM for the best-fit models and applied 5000 random permutations (Manly 2007; Benitez-Vieyra *et al.* 2012).

Results

Environmental parameters

The period preceding the study was characterised by hydrometric levels below 4 m for more than 2 years as a result of La Niña (Fig. 3). During this prolonged drought, macroinvertebrate fauna decreased considerably in macrophytes (D. A. Carvalho, pers. obs.). Then, during the summer of 2010, a flood pulsed the system, with water levels exceeding 6 m. Sampling began in this hydric context. Most environmental variables recorded during sampling did not vary significantly between the lakes and hydrometric levels (W: $P > 0.05$). As expected, only temperature (W: $P = 0.02$) and water level (W: $P = 0.03$) varied from high during summer and early autumn and low in late autumn and winter. In the spring, temperature increased, whereas water level decreased. However, a trend could be seen in chlorophyll-*a*, which generally decreased during the low-temperature months (Table 1).

Structure and composition of communities

In total, 116 taxa were identified in all communities during the study. Benthic and pleustonic fauna were dominated by



Fig. 3. Hydrometric level from 2007 to 2011 recorded at the Santa Fe River Harbor Station. Grey points indicate sampling dates.

Table 1. Environmental parameters from lake with indirect and permanent connection (IPC, Lake Irupé) and from lake with direct and temporary connection (DTC, Lake Larga) at specific hydrometric levels

Asterisks indicate variables with a significant difference (5% level) between hydrometric levels. ppm, parts per million

Parameter	Lake IPC				Lake DTC					
	Flooding		Transition		Drought		Flooding		Transition	
	Mar.	Apr.	June	July	Oct.	Dec.	Mar.	Apr.	June	July
Chlorophyll- <i>a</i> ($\mu\text{g m}^{-3}$)	0.55	0.24	0.16	0.11	0.53	1.11	0.33	0.12	0.09	0.28
Floating macrophytes (%)	80	60	90	100	90	90	80	40	80	0
Rooted macrophytes (%)	20	40	0	0	10	0	20	60	20	0
Hydrometric level (m)*	4.86	4.64	3.53	2.97	2.3	2.15	4.86	4.64	3.53	2.97
Transparency (m)	0.46	0.41	0.24	0.3	0.14	0.2	0.13	0.29	0.34	0.08
pH	6.43	6.54	6.31	6.95	6.15	7.5	6.43	6.42	6.67	7.26
Conductivity ($\mu\text{S cm}^{-2}$)	64	64	79	80	89	101	81	55	104	100
Dissolved oxygen (ppm)	2.7	3.5	1.8	4.7	3.8	5.4	4.3	6.5	3.0	10.1
Temperature ($^{\circ}\text{C}$)*	26	22.7	11.9	11.6	18	26.3	28.1	23.7	10.3	11.3

oligochaetes and chironomids at all hydrometric levels, whereas copepods and rotifers (Brachionidae and Synchaetidae families) dominated the zooplanktonic community. Others invertebrates reached high abundance for brief periods, such as mayflies (Caenidae family), the non-native golden mussel (*Limnoperna fortunei*) and palaemonid prawns during the drought phase in Irupé (IPC; see Table S1, available as Supplementary material for this paper).

The effects of hydroperiod and lake type on the community structure were significant for zooplankton (between lakes: $F = 61.35$, $P = 0.007$; hydroperiod: $F = 55.18$, $P = 0.011$) and pleuston (between lakes: $F = 33.38$, $P = 0.049$; hydroperiod: $F = 50.66$, $P = 0.032$) according to two-way PERMANOVA with Morisita distance. The interaction between hydroperiod and lake type was statistically significant only for zooplankton ($F = 66.29$, $P = 0.003$).

Within lakes, we found a significant influence of hydroperiod on community structure only in the IPC lake. The transition and flooding periods were statistically different for all communities (zooplankton: $P = 0.005$; benthos: $P = 0.026$; pleuston: $P = 0.001$), whereas the flooding phase was different from transition for zooplankton ($P = 0.0006$) and from drought phase for pleuston ($P = 0.005$; Table 2).

Between the lakes, the structure of zooplanktonic and benthic communities differed during the flooding phase (zooplankton: $P = 0.001$; benthos: $P = 0.028$) and between the flooding and transition periods (zooplankton: $P = 0.047$; benthos: $P = 0.009$). Moreover, the drought phase of Lake Irupé (IPC) differed in the flooding ($P = 0.0003$) and transition ($P = 0.008$) periods of Lake Larga (DTC) for the pleustonic community (Table 2).

These results are also supported by descriptive analyses of community attributes. During the transition phase in Lake Irupé (IPC), the zooplanktonic community had lower richness and abundance values than at other times, whereas diversity was otherwise quite similar between the lakes and hydroperiods (Table 3; see Table S1). In the benthic community, abundance was higher in the IPC lake, whereas richness varied between flooding and transition phases in both lakes. In the pleustonic community, there was higher abundance and lower diversity of invertebrates in the drought phase than at other sampling dates (Table 3).

Table 2. Comparison within and between lakes of the communities throughout the hydric cycle using the Wilcoxon test

Only significant differences in invertebrate assemblages are shown. IPC, indirectly and permanently connected lake; DTC, directly and temporarily connected lake

Lake	Hydric moment	Community	<i>P</i> -value	
Within lake				
IPC (Lake Irupé)	Flooding v. transition	Zooplankton	0.0006	
	Flooding v. drought	Pleuston	0.0031	
	Transition v. drought	Zooplankton	0.0052	
DTC (Lake Larga)	–	Benthos	0.0263	
		Pleuston	0.0015	
Between lakes				
DTC (Lake Larga)	Flooding v. flooding	Zooplankton	0.0015	
		Benthos	0.0287	
IPC (Lake Irupé)		Flooding v. transition	Zooplankton	0.0471
		Transition v. flooding	Benthos	0.0098
		Drought v. flooding	Pleuston	0.0003
		Drought v. transition	Pleuston	0.0088

Using the attribute values from a summary encompassing all the communities studied (pleuston, benthos and zooplankton) at specific lake and hydroperiods, we identified the following three different groups clearly separated in temporal scale: lakes Larga (DTC) and Irupé (IPC) during the flood pulse, lakes Irupé (IPC) and Larga (DTC) during the transition phase and Lake Irupé (IPC) during drought. The first two groups were more compositionally similar to each other than to the last group (Fig. 4a). This result corroborates our prediction that invertebrate assemblages are more similar during the flooding phase.

Spatiotemporal variation of food-web attributes

Food-web attributes were significantly different between the lakes ($F = 2.61$, $P = 0.04$) but not between hydrometric levels ($F = 0.17$, $P = 0.92$) or the interaction ($F = 0.54$, $P = 0.71$) according to two-way PERMANOVA with Euclidean distance. We made these comparisons between flooding and transition

Table 3. Community attributes of zooplankton, benthos and pleuston taxa identified in lakes with indirect and permanent connection (IPC, Lake Irupé) and with direct and temporary connection (DTC, Lake Larga) at specific hydrometric levels

Community	Attribute	IPC lake			DTC lake	
		Flooding	Transition	Drought	Flooding	Transition
Zooplankton	Richness	37	27	32	34	24
	Abundance	12 462	4929	21 376	6239	6217
	Diversity	0.778	0.735	0.758	0.737	0.734
Benthos	Richness	13	20	15	12	26
	Abundance	333	273	166	116	83
	Diversity	0.416	0.549	0.543	0.518	0.802
Pleuston	Richness	39	41	43	30	37
	Abundance	745	903	31252	634	1158
	Diversity	0.729	0.629	0.167	0.787	0.867
Total	Richness	74	73	76	69	77
	Abundance	5009	3822	36 398	5302	3468
	Diversity	0.925	0.903	0.619	0.882	0.887

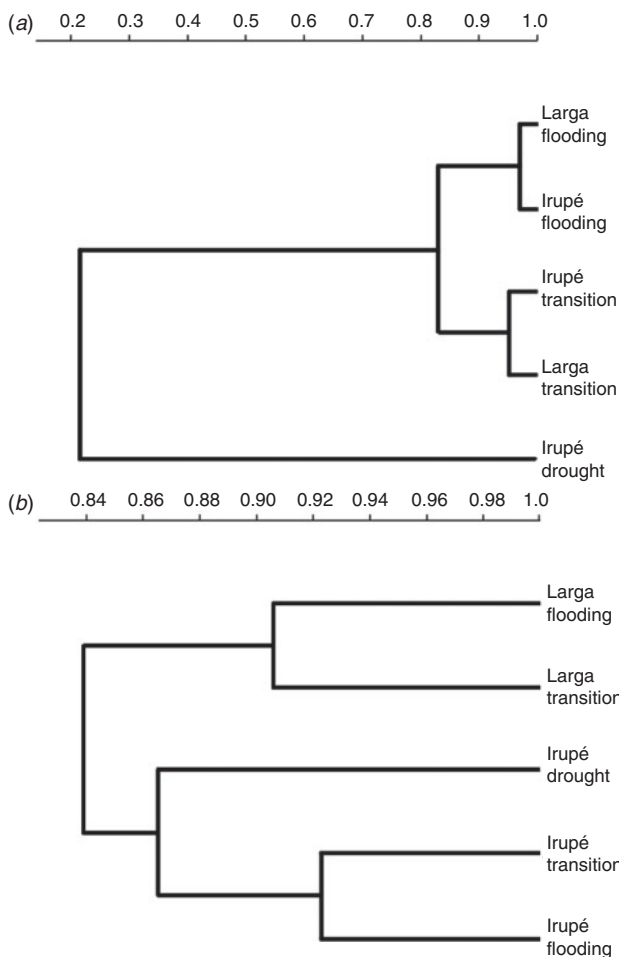


Fig. 4. Cluster analysis using the Bray–Curtis similarity index of attributes with a summary (a) of all communities and (b) of food-web attributes specific to each hydrometric level and lake. Irupé, a lake with indirect and permanent connection; Larga, a lake with direct and temporary connection.

Table 4. Student’s *t*-values and *P*-values (in parentheses) for the differences in bipartite food-web attributes between lakes and hydrometric levels

NODF, connectance, nestedness; UW, unweighted; W, weighted. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The sample size for all web metrics is four

Parameter	Lake	Hydrometric level
UW		
Predators	9 (0.002)***	1.56 (0.21)
Prey	1.29 (0.28)	0.51 (0.64)
Connectance	−10.33 (0.002)***	0.47 (0.67)
Links per species	−0.526 (0.63)	2.44 (0.09)
Nestedness	−2.036 (0.13)	0.20 (0.85)
W		
Connectance	−3.43 (0.04)*	−0.15 (0.89)
Generality	−2.33 (0.10)	−0.17 (0.87)
Vulnerability	0.43 (0.89)	1.29 (0.28)
NODF	0.91 (0.43)	−2.04 (0.13)
Linkage density	−1.5 (0.21)	0.48 (0.66)

phases for occasions when data were available for both lakes. Notwithstanding, the analysis was performed separately for each attribute, and also highlighted differences between the lakes (Table 4). Bipartite webs of the DTC lake had a significantly lower number of predators and higher connectance (both weighted and unweighted) than did the IPC lake (Tables 4, 5). All web metrics were significantly different from the random networks generated by null models.

Using attribute values for lake and hydroperiods, the following three different groups were clearly separated in a spatial scale: one group comprised the DTC lake during flooding and transition phases, other the IPC lake, also during flooding and transition phases, and the IPC lake during the drought period. The two last groups were closely related (Fig. 4b). This result contradicts our prediction that food webs are more similar during the flooding phase.

Table 5. Weighted (W) and unweighted (UW) food-web attributes for lakes with indirect and permanent connection (IPC, Lake Irupé) and with direct and temporary connection (DTC, Lake Larga) at specific hydrometric levels

Parameter	Meaning of web metrics	Lake IPC			Lake DTC	
		Flooding	Transition	Drought	Flooding	Transition
UW						
Predators	Number of predators	12	11	10	7	7
Prey	Number of prey	38	31	26	31	25
Connectance	Percentage of possible links among species	0.15	0.15	0.14	0.24	0.24
Links per species	Mean number of links per species	1.34	1.19	1.22	1.39	1.31
Nestedness	Species composition of small assemblages that is a nested subset of larger assemblages	13.4	10.69	17.89	32.14	24.15
W						
Connectance	Weighted percentage of possible links among species	0.04	0.06	0.04	0.08	0.08
Generality	Mean number of prey per predator	2.49	3.62	2.05	4.63	3.71
Vulnerability	Mean number of predator per prey	1.62	1.43	1.51	1.86	1.48
NODF	Weighted nestedness	16.24	16.15	20.75	17.46	16.49
Linkage density	Average number of links per species	2.06	2.53	1.78	3.25	2.59

Food webs

We observed that the characin fish *Brycon orbgnyanus* and the prawn *M. borellii* were involved in a high proportion of the trophic interactions during the flooding phase of the IPC lake. Algae was the primary resource for prawn, whereas macrophytes were more important to *B. orbgnyanus*, the crab *T. borellianus* and the characin *Schizodon borellii*. Of all macroinvertebrates found in stomach contents, mayflies of the family Polymitarcidae were the most important prey, primarily because of high consumption by the characin *B. orbgnyanus* (Fig. 5a). A high proportion of trophic interactions involving fish, mainly *B. orbgnyanus* and the catfish *Pimelodus maculatus*, characterised the DTC lake during the high-water period. Although the proportion of trophic interactions involving crustaceans was smaller, the number of trophic links was equal or higher than that involving fish. Macrophytes were an important basal resource for many species, whereas chironomids, mayflies (Caenidae) and coleopterans (Curculionidae) were important as trophic connectors (Fig. 6a).

During the transition phase in both lakes, the prawn *M. borellii*, catfish *P. maculatus* and sábalo species of the genus *Prochilodus* were involved in the highest proportion of trophic interactions. A high intake of algae by *M. borellii* increased the proportion of interactions involving this species in the IPC lake. During this phase, the importance of detritus as a primary resource increased because of consumption by sábalo species, which resulted in a lower relative importance of macrophytes (Figs 5b, 6b). Again, mayflies and chironomids appeared to be important trophic connectors in the DTC lake, although microcrustaceans (Fig. 6b) and dragonflies (Fig. 5b) were also significant invertebrate prey. The crab *T. borellianus* was also a trophic resource for the catfish *P. maculatus*. Moreover, during this phase, an increase in piscivory was registered in both shallow lakes.

The drought period in the IPC lake was characterised by a more even distribution of interactions among prey species. The diets of prawns and crabs were the richest, with these species consuming 12 and 13 taxa respectively, followed by eight prey types ingested by boga specimens (*L. obtusidens*). The three

types of basal resources (algae, macrophytes and detritus) identified in stomach contents were equally important. The most important trophic connectors were molluscs, such as the exotic golden mussel (*L. fortunei*) and mud snail species of the family Hydrobiidae, prawns, and, to a lesser extent, cladocerans and copepods (Fig. 5c).

Environmental variables v. communities and food-web attributes

The environmental variables without collinearity used to explain community and food-web attributes were chlorophyll-*a* ($\mu\text{g m}^{-3}$), hydrometric level (m), transparency (m), pH, free-floating macrophytes (%) and rooted macrophytes (%). From these variables, the AIC choose the best-fit models to each attribute, explaining the variability of one food-web attribute (link per species) and three community attributes (pleuston richness, benthos abundance and zooplankton abundance). For these attributes, we ran GLM models with randomisation and showed only those models with one or more significant variables. Four environmental parameters (hydrometric level, chlorophyll-*a*, transparency and pH; $D^2 = 88.68$) provided the best model explaining variation in links per species variability, and the relationship was statistically significant for hydrometric level ($P = 0.004$), chlorophyll-*a* ($P = 0.009$) and transparency ($P = 0.019$). Hydrometric level and chlorophyll-*a* had a positive relationship with links per species, whereas pH was negatively related. Considering community attributes, the best model explaining the variability of pleuston richness used five variables (hydrometric level, free-floating macrophytes, rooted macrophytes, transparency and pH; $D^2 = 92.99$); however, the direct correlation was statistically significant only for free-floating macrophytes ($P = 0.021$) and rooted macrophytes ($P = 0.046$). The best-fitted model explaining the variability of benthos abundance comprised six variables (hydrometric level, chlorophyll-*a*, free-floating macrophytes, rooted macrophytes, transparency and pH; $D^2 = 92.97$), with pH ($P = 0.033$) and rooted macrophytes ($P = 0.020$) having a significant and negative relation with the benthos abundance. Finally, the model that best explained the variability of zooplankton abundance

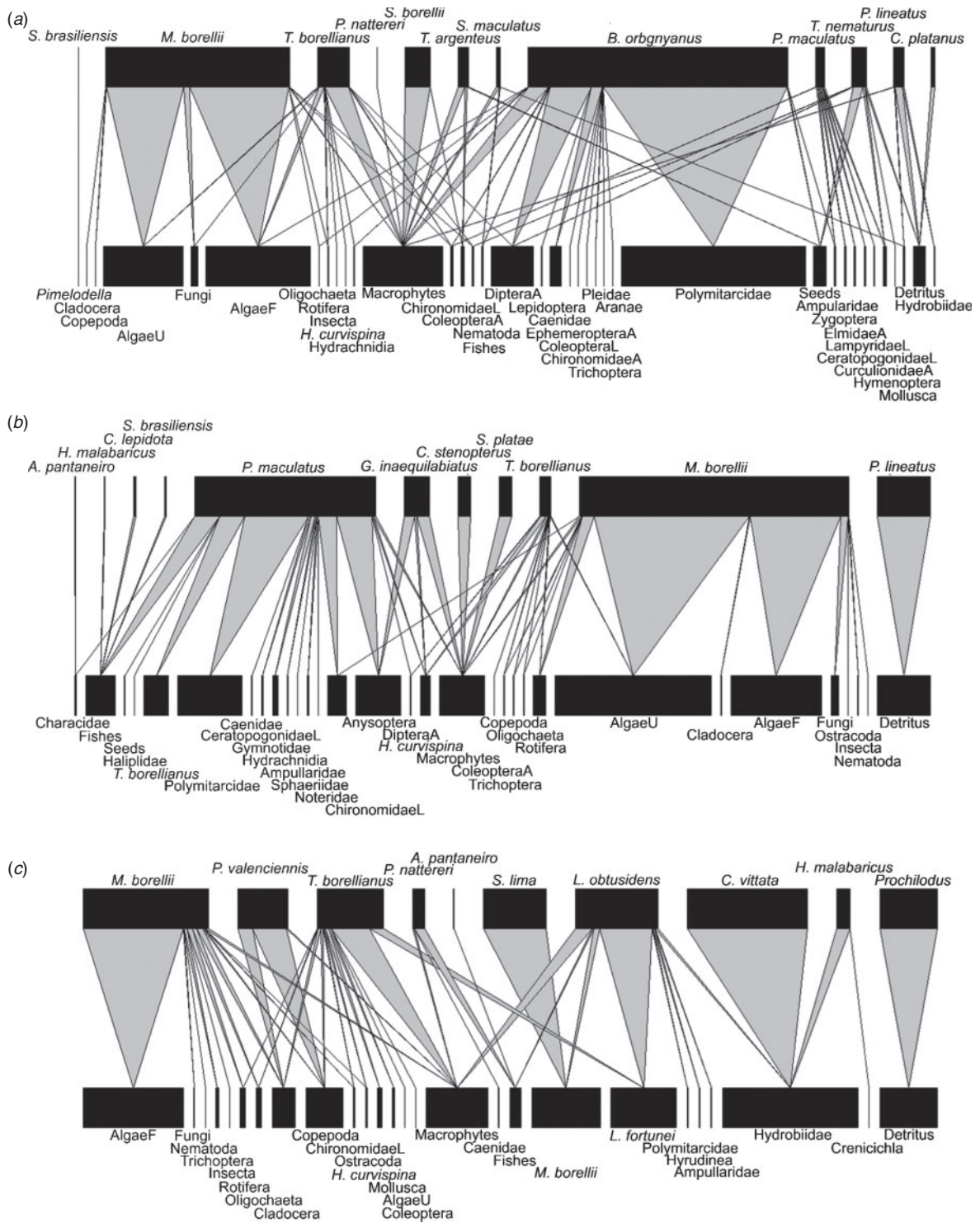


Fig. 5. Weighted bipartite graphics of predator–prey interactions during the (a) flooding, (b) transition and (c) drought hydroic phases in the lake with indirect and permanent connection (Irupé). Rectangles represent predator (superior) and prey (inferior), and the width is proportional to the sum of the interactions involving this species. Connecting line width is proportional to the number of interactions involving species. We used the method ‘cca’, which leads to as few crossings of interactions as possible. Abbreviations preceding taxa names: A, adults; L, larvae; N, nymph; T, terrestrial; U, unicellular; F, filamentous.

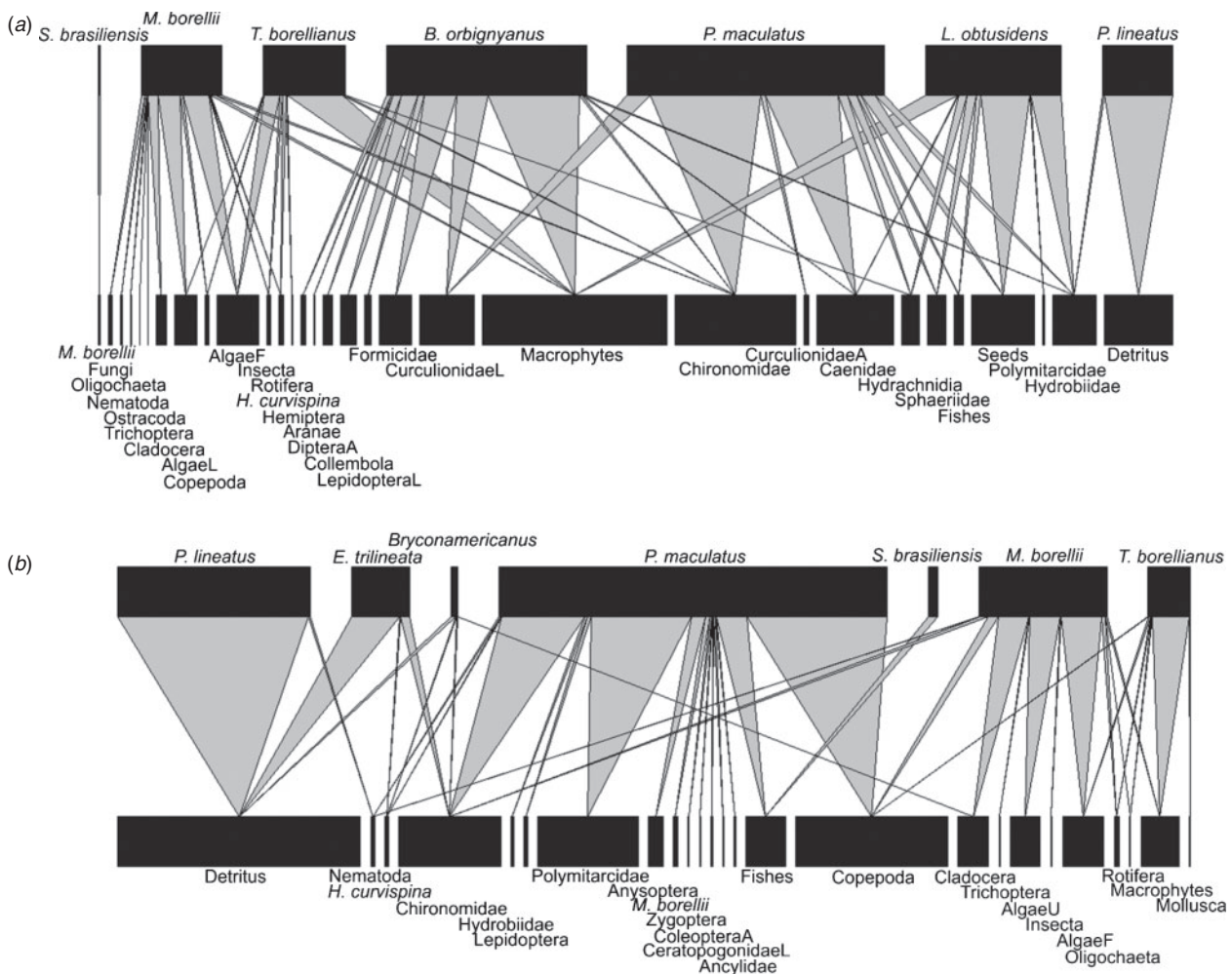


Fig. 6. Weighted bipartite graphics of predator–prey interactions during the (a) flooding and (b) transition hydric phases in the lake with direct and temporary connection (Larga). Rectangles represent predator (superior) and prey (inferior), and the width is proportional to the sum of the interactions involving this species. Connecting line width is proportional to the number of interactions involving species. We used the method ‘cca’ which leads to as few crossings of interactions as possible. IPC, indirect and permanent connection; DTC, direct and temporary connection. Abbreviations preceding taxon names: A, adults; L, larvae; N, nymph; T, terrestrial; U, unicellular; F, filamentous.

included three environmental variables (chlorophyll-*a*, transparency and pH; $D^2 = 81.5$) and was statistically significant for chlorophyll-*a* ($P = 0.003$) and pH ($P = 0.012$). Chlorophyll-*a* had a positive relationship with zooplankton abundance, whereas pH was negatively related.

Discussion

Spatiotemporal variation of food web and communities

We hypothesised that the structure of invertebrate communities and food webs varied according to the hydroperiod. On the basis of our results, we can partially accept this hypothesis. In the food webs studied, spatial differences in web metrics were more important than was temporal variability, corroborating the spatial groupings observed in the cluster analysis that had clearly assembled samples from the same lake as did similar groups. This finding contradicts our prediction that food webs are more similar during the flooding phase. In contrast, the

attributes of the communities analysed as a group were more similar by season than by lake. This result showed that communities are more similar during the flooding phase, corroborating our prediction, but also indicated a high similarity during the transition period. However, when analysing communities separately, we noticed that the structure of zooplankton and pleuston communities are significantly affected by spatial and temporal factors.

Food webs

In accordance with present results, Winemiller (1990) found that seasonal variation had less influence on aquatic food webs than did site. However, seasonally determined changes in food-web attributes may be masked by the absence of data for Lake Larga (DTC) in the drought phase. The desiccation process during this period precluded data collection and compromised the comparison among the three hydrometric levels.

Regarding spatial variation, we found that weighted and unweighted connectance were significantly higher in the DTC lake. This lake had lower species richness, which increases connectance. This is the most widely discussed pattern in food-web structure and is associated with the instability of highly connected networks (Cohen and Newman 1988, Pimm *et al.* 1991; Montoya and Sole 2003). However, Beckerman *et al.* (2006) demonstrated that high connectance is related to highly constrained diet breadth. This suggests that the foraging decisions (switches in food choice in response to qualitative and quantitative resource changes) made by consumers could be important in stabilising the food-web structure, buffering environmental fluctuations (Kondoh 2003; Beckerman *et al.* 2006). Many web descriptors are scale-dependent and results are heavily influenced by the sampling effort and the number of observations (Blüthgen 2010). Therefore, the weight assigned to network metrics may produce a more realistic picture of food-web structure (Kenny and Loehle 1991), with increased robustness against variation in sampling effort (Bersier *et al.* 2002; Banašek-Richter *et al.* 2004). The weighted attributes in the present study, with the exception of connectance, did not show significant spatiotemporal differences. However, food webs are much simpler when considered quantitatively (Banašek-Richter *et al.* 2009) and may reveal less variable patterns. The application of null models is a valuable tool in such cases to evaluate whether the empirically observed patterns are real or an artefact of web dimensions.

Invertebrate assemblages

We verified that temporal factors have more influence when considering all communities as a unique assemblage, whereas the composition of each community can exhibit spatial and temporal variations that are related to the ecological context specific to each lake and hydroperiod. Our results showed that the main variation in the composition and abundance of zooplankton were both within and between lakes. The total abundance of zooplankton may be the main driver of these differences because abundance was lowest during the transition period in both lakes. GLM indicated that chlorophyll-*a* and pH could explain the variation in the zooplankton abundance. In the present study, the total abundance of zooplanktonic organisms was lower during cold months (transition phase) and higher in warm months (mainly during drought phase). In warm months with low water level, the density of phytoplankton increases because of high temperatures and lower velocity of water (Zalocar de Domitrovic *et al.* 2007), increasing the food availability for zooplankton. With respect to pH, this parameter is considered one of the most important abiotic variables in aquatic ecosystems, but also the most difficult to be interpreted because of the many factors that can influence it (Esteves and Marinho 2011). However, pH may be related to the balance of primary production and respiration, and, hence, a reflection of chlorophyll-*a*. Previous studies have indicated that the highest zooplankton abundance observed in lakes in the middle Paraná River occurred during the isolation or drought phases (Bonetto and Martinez de Ferrato 1966; José de Paggi 1993). This suggests a higher availability of zooplankton as food resource for vertebrate and invertebrate predators during this water phase.

Benthic community highlighted differences in the transition and drought phases in the permanent connected lake and in flooding and transition periods between lakes. Present results also showed a marked decrease in abundance with a decreasing hydrometric level. Benthic structure and composition are primarily controlled by hydrological regime, the degree of connectivity, the vegetation coverage and the water quality (Ezcurra de Drago *et al.* 2007). Here, GLM results indicated the indirect relation of rooted macrophytes and pH with the abundance of benthos. Again, pH may be related to the balance of primary production and respiration and might not be considered a driver factor. The increase in vegetation coverage during inundation increases the amount of organic matter that accumulates at the bottom of the lake in the subsequent stages of the hydrological regime. This deposition produces hypoxic or anoxic conditions and negatively affect less tolerant organisms (Ezcurra de Drago *et al.* 2007) and is likely responsible for the reduced abundance of benthic organisms as hydrometric levels decrease. In this way, benthic organisms may be more available during high water level, and in indirect and permanent connected lakes.

In contrast, the increase in the vegetation coverage may have a positive effect on pleustonic invertebrates. *Eicchornia crassipes* is a free-floating macrophyte frequently found in large South American rivers (Thomaz *et al.* 2004; Neiff *et al.* 2008), and formed dense meadows in the shallow lakes studied. This water hyacinth can support abundant and diverse invertebrates, and increasing diversity is positively correlated with plant biomass (Poi de Neiff and Neiff 2006). GLM indicated that the percentage of floating, mainly represented by water hyacinth, and rooted macrophytes were the environmental variables that most significantly explained pleuston richness. *Eicchornia crassipes* roots provide habitat, refuge and food for a variety of organisms (Poi de Neiff and Carignan 1997). In the present study, pleuston structure and composition were different between the drought phase and all the others sampling events in the IPC lake. This distinct sample was characterised by low diversity and high abundance of invertebrates, contrasting with the results found by Poi de Neiff and Carignan (1997), who pointed out that macroinvertebrate abundance increased with water height because of increased flow through the roots. The drought phase coincided with warmer months (October and December), which probably promoted an increase in invertebrate populations, particularly of the golden mussel (*L. fortunei*). The dominance and abundance of Chironomidae, Caenidae, Hyallellidae and Hydrobiidae, in addition to oligochaetes and golden mussels, was associated with low diversity and drives the differences observed.

Use of trophic resource in floodplain food webs

In the present study, the relative importance of basal resources varied seasonally. During the flooding pulse, the consumption of macrophytes comprised the largest proportion of the interactions between basal resources and predators. In isotopic studies, M. Saigo, M. R. Marchese and F. L. Zilli (unpubl. data) observed that the use of macrophytes by benthic invertebrates was higher during the flooding pulse in lakes of the Paraná floodplain. Algae were also involved in a high proportion of the interactions, largely owing to consumption by *M. borellii*. However, the quantification of trophic interactions was

estimated through the total abundance multiplied by the frequency of occurrence of a specific item in the stomach content of predators. This may have skewed the interaction magnitude towards prey abundance in stomachs, as opposed to volume or biomass, which would increase the relative importance of small and abundant items such as algae.

When water levels descended to intermediate levels, detritus emerged as an important resource, primarily owing to the presence of *Prochilodus* species. The senescence of macrophytes with falling water levels increases the input of detritus at the base of aquatic floodplains (Winemiller 1996; Marchese *et al.* 2014). According to Winemiller (1996), the intake of detritus by prochilodontids enhanced the efficiency of fish production because of the rapid transference of matter and energy to the upper trophic levels (piscivorous fish) through short food chains.

During the drought phase, the relative importance of basal resources use was more equable, but macrophytes, as in all hydrometric stages, were consumed by a great variety of fish and crustaceans. Previous studies have shown that macrophytes are the major carbon source supporting the aquatic primary consumers of floodplains (Winemiller and Jepsen 1998, Marchese *et al.* 2014). Present data suggested that this basal resource is also important for omnivorous consumers, emphasising the importance of autochthonous inputs into the food webs of large rivers (Thorp and DeLong 2002; Bunn *et al.* 2003).

In the Paraná River, littoral–benthic organisms are the most consumed trophic resources for omnivorous fish (Almeida *et al.* 1997; Rossi *et al.* 2007) and macrocrustaceans (Collins *et al.* 2007b). Indeed, *P. maculatus*, *L. obtusidens*, *B. orbignyanus* and decapods were the predator species with the greatest number of littoral–benthic organisms in their stomach contents. Feeding on more than one trophic level is an important feature of predators from freshwater systems (Warren 1989; Vadas 1990; Rawcliffe *et al.* 2010, González-Bergonzoni *et al.* 2012). However, the consumption of plant and animal resources can have a dual function in the Paraná floodplains, because shredders, which process a widely available basal resource, structure invertebrate communities (Pringle and Hamazaki 1998). In addition, predators can indirectly affect leaf breakdown rates by consuming shredder taxa (Ruetz *et al.* 2002) such as mayflies and chironomids (Dominguez *et al.* 2006; Zilli *et al.* 2008). These invertebrates were involved in a large proportion of the trophic interactions in both lakes, standing out as primary connectors between basal resources and secondary consumers, as also previously documented (Mantel *et al.* 2004).

In the transition phase, mayflies and chironomids, dragonflies, microcrustaceans and crabs become relevant connectors between fish and macrocrustaceans. A reduction in hydrometric levels and the subsequent concentration effect may have increased the probability of encounters between predators and prey (Titelman 2001) and reduced the swimming activity of zooplanktonic organisms (Dodson *et al.* 1997; Carvajal-Salamanca *et al.* 2008). This would have facilitated the capture of small organisms with a fast escape response, such as calanoid copepods (Ohman 1988). This process may be more intense in the DTC lake, where cladocerans and copepods comprised a large proportion of the trophic interactions. However, the concentration effect may not favour slow macroinvertebrates,

such as the crab *T. borellianus*. This decapod occupied a large proportion, by volume, of *P. maculatus* gut content, representing a trophic interaction of greater magnitude than actually estimated. In addition, an increase in piscivory was observed in both shallow lakes.

In the IPC lake, molluscs, prawns and microcrustaceans comprised the greater proportion of trophic interactions during the drought season, although the proportion of trophic interactions among predators was more equable. As previously mentioned, increased temperatures and organism abundance characterised this hydroperiod. Molluscs were primarily represented by the exotic golden mussel (*L. fortunei*) and mud snails (Hydrobiidae). Maximum densities were $\sim 456\,000$ mussels m^{-2} and 2900 snails m^{-2} . The epifaunal habit of these organisms facilitates their availability for predation by fish (Montalto *et al.* 1999) and decapods (Torres *et al.* 2012). Prawns and microcrustaceans also reached maximum densities in this season, with 644 prawns m^{-2} and 26 microcrustaceans L^{-1} . Prawn consumption was dominated by the siluriform *Sorubim lima*, which was previously mentioned as a ‘shrimp-eating’ fish in Amazon rivers (Goulding and Ferreira 1984), whereas microcrustaceans were preyed on by decapods and the planktivorous siluriform, *Parapimelodus valenciennis*. These results suggest that the consumption of these predators reflect the abundance and availability of organisms in the environment. Indeed, the most abundant and dominant organisms of the littoral and benthic communities of the Paraná River (e.g. mayflies, chironomids, oligochaets; Marchese *et al.* 2005; Ezcurra de Drago *et al.* 2007; Montalto 2008) were those with the highest number of predators.

The present study has exemplified a quantitative approach to floodplain food-web analysis, which can be a valuable tool for the analysis of spatiotemporal variation in trophic interactions. Despite the fact that all communities had a similar structure throughout the flooding and transition phases, habitats within the floodplain may host different local food webs. Lakes with direct and temporal connection had higher values of connectance, suggesting that most unstable habitats may present a higher degree of trophic generalisation. In general, predator species exhibited trophic plasticity by consuming abundant prey. Future studies are necessary to determine whether species buffer environmental fluctuations, such as those changes related to the hydrological regime.

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